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CHANGEMENTS GLOBAUX ET DISTRIBUTION SPATIALE DES ESPECES DE POISSONS D'EAU DOUCE : OBERVATIONS RECENTES ET PREDICTIONS FUTURES

A Gisèle Saltet d'Alzon

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Tout au long de ce manuscrit, il est fait référence à sept articles soumis ou publiés dans des revues à comité de lecture. La synthèse des travaux de recherches s'articule autour de cinq articles ($\boldsymbol{P_I}$ – $\boldsymbol{P_V}$) qui composent le cœur de la thèse. Les deux articles figurant en annexe ($\boldsymbol{A_I}$ – $\boldsymbol{A_{II}}$) sont des articles collaboratifs développés en marge du travail de thèse qui sont utilisés afin de développer les perspectives de recherche. Les versions intégrales de ces articles sont présentées à la fin du manuscrit.

$\boldsymbol{P_I}$: Comte L, Buisson L, Daufresne M & Grenouillet G (2013) Climate-induced changes in the distribution of freshwater fish: observed and predicted trends. ***Freshwater Biology*** 58: 625–639.

$\boldsymbol{P_{II}}$: Comte L & Grenouillet G (2013) Species distribution modelling and imperfect detection: comparing occupancy versus consensus methods. ***Diversity and Distributions*** 19: 996–1007.

$\boldsymbol{P_{III}}$: Comte L & Grenouillet G (2013) Do stream fish track climate change? Assessing distribution shifts in recent decades. ***Ecography*** 36: 1236–1246.

$\boldsymbol{P_{IV}}$: Grenouillet G & Comte L (Under Review) Illuminating geographical patterns in species' range shifts. Submitted to ***Global Change Biology***.

$\boldsymbol{P_V}$: Comte L & Grenouillet G (Under Review) Species' traits and phylogenetic conservatism of climate-induced range shifts. Submitted to ***Nature Communications***.

$\boldsymbol{A_I}$: Paz-Vinas I, Comte L, Chevalier M, Dubut V, Veyssière C, Grenouillet G, Loot G & Blanchet S (2013) Combining genetic and demographic data for prioritizing conservation actions: insights from a threatened fish species. ***Ecology and Evolution*** 3: 2696–2710.

$\boldsymbol{A_{II}}$: Conti L, Comte L, Hugueny B & Grenouillet G (Under Review) Drivers of freshwater fish colonisations and extirpations under climate change. Submitted to ***Ecography***.

INTRODUCTION GENERALE

Changements climatiques et distribution spatiale des espèces

“Nature n'endure mutations soudaines sans grande violence."

François Rabelais (1534)

L’augmentation de la concentration des gaz à effet de serre (GES) a changé le climat global de la Terre, avec un réchauffement constaté des températures moyennes de surface récemment ré-évalué à 0.85 °C durant la période 1880–2012 (IPCC, 2013). Malgré les politiques mises en place, ces changements continuent de s’accroitre, suggérant que les températures vont vraisemblablement continuer d’augmenter, et ce à un rythme accéléré (Figure 1). Durant le siècle prochain, la température globale pourrait augmenter de l’ordre de 4°C ou plus, avec une augmentation concomitante de la fréquence des événements extrêmes (tempêtes, cyclones), et l’apparition de climats non-analogues (Easterling *et al.*, 2000; Ackerly *et al.;* IPCC, 2013). Bien que la Terre ait connu de profondes modifications climatiques par le passé, la magnitude et la vitesse des changements climatiques actuels pourraient être dix fois supérieures au réchauffement constaté depuis le dernier maximum glaciaire (IPCC, 2013), bien que cette vision soit aujourd’hui remise en cause par la mise en évidence de changements climatiques abrupts s’étant produits durant le Quaternaire (Steffensen *et al.*, 2008).

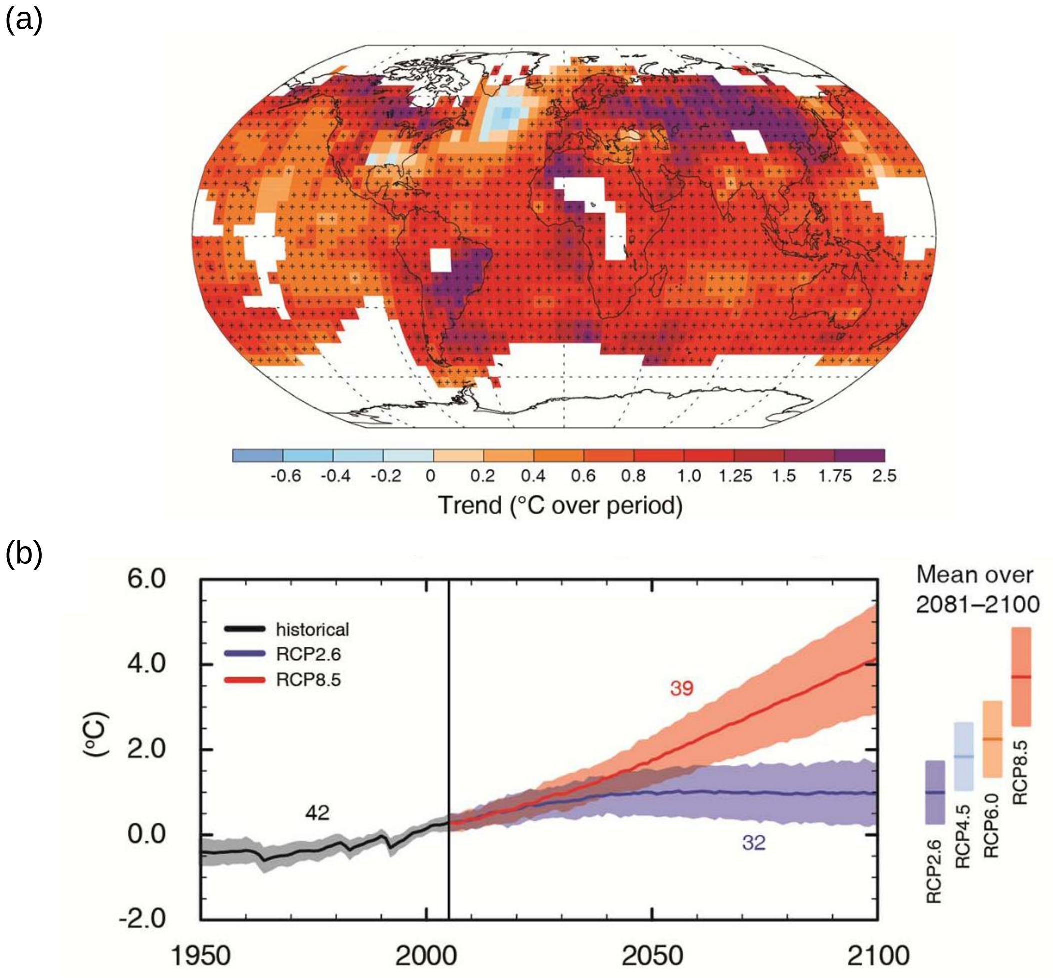


Figure 1 : (a) Carte représentant les changements de température en surface observés pour la période 1901-2012 et (b) projections moyennes et fourchettes probables pour la période 2005-2100 selon différents sénarios RCP. Les courbes bleues ne tiennent compte que des forçages naturels (variabilité solaire et volcans) tandis que les courbes en orange tiennent compte des forçages naturels et des forçages anthropiques (gaz à effet de serre et aérosols). La courbe noire représente l’évolution historique modélisée. Le nombre de modèles utilisés pour calculer les moyennes est indiqué sur le graphique. Les écarts de température sont donnés par rapport à la période 1986–2005 © IPCC, 2013

Alors que les changements climatiques reçoivent depuis plusieurs années une attention grandissante, leurs impacts biologiques potentiels restent mal appréhendés. La très grande majorité des études abordant l'impact des changements climatiques sur les communautés végétales ou animales se base aujourd'hui sur des approches prédictives consistant à comparer les distributions actuelles des espèces avec les distributions futures projetées sous différents scénarios climatiques (Guisan & Zimmermann, 2000). Ainsi, les prédictions issues de ces études font état de déclins dramatiques de la biodiversité (Thomas *et al.*, 2004; Thuiller *et al.*, 2005b; Xenopoulos *et al.*, 2005), conduisant à des réorganisations rapides des communautés et des interactions biotiques qui les composent, ainsi qu'à des altérations profondes du fonctionnement des écosystèmes et des services écosystémiques (Lovejoy & Hannah, 2005; Pereira *et al.*, 2010; Walther, 2010). Cependant, les espèces ont été continuellement exposées à des changements climatiques durant leur histoire évolutive, et les patrons de biodiversité géographiques observés aujourd'hui reflètent largement l'empreinte des épisodes glaciaires et interglaciaires du Pléistocène (Davis & Shaw, 2001; Roy *et al.*, 2001). Bien que les changements climatiques passés aient conduit à l'extinction spécifique de certaines lignées du vivant (McKinney, 1997; Roy *et al.*, 2009; Lyons *et al.*, 2011), les fluctuations du Quaternaire ne semblent pourtant pas coïncider avec des épisodes d'extinctions massives. Cela suggère que de nombreuses espèces auraient la capacité de mettre en place des stratégies leur permettant de survivre à des épisodes de changements climatiques rapides, bien que ces mécanismes restent encore à clarifier (Parmesan, 2006; Hof *et al.*, 2011). Il semble donc primordial d'aborder la contradiction apparente entre les conséquences catastrophiques qui sont prédites pour les distributions futures, et l'apparente résilience des espèces observée par le passé (Moritz & Agudo, 2013). Ainsi, un des enjeux majeurs pour la conservation de la biodiversité mondiale consiste à comprendre comment les espèces, et plus généralement les systèmes biologiques, sont d'ores et déjà en train de répondre aux changements climatiques actuels. Ces données constitueront des éléments de réflexion primordiaux quant à notre capacité à anticiper les changements à venir et à initier des politiques de gestion adaptées, dont les missions futures ne peuvent désormais plus être conçues sans tenir compte de l'évolution du climat (Hannah *et al.*, 2007; Williams *et al.*, 2008; Dawson *et al.*, 2011; Foden *et al.*, 2013).

1- Climat et distribution spatiale des espèces

De manière générale, la réponse des espèces face aux changements climatiques peut être synthétisée par 3 grands processus : l'adaptation, la dispersion ou l'extinction, auxquelles viennent s'ajouter des modifications comportementales, physiologiques et morphologiques (Hughes, 2000; Walther *et al.*, 2002; Parmesan, 2006). En effet, des impacts sont déjà largement décelables à travers de nombreux groupes taxonomiques et régions du globe, incluant principalement (1) des changements phénologiques avec une avancée des phénomènes printaniers (Root *et al.*, 2003; Menzel *et al.*, 2006), (2) des changements de distribution en altitude et vers les pôles (Parmesan & Yohe, 2003; Chen *et al.*, 2011), et (3) une réduction de la taille des individus (Daufresne *et al.*, 2009; Gardner *et al.*, 2011; Sheridan

& Bickford, 2011). Comprendre les mécanismes sous-jacents nécessite alors de s'intéresser au rôle du climat dans la détermination de la distribution spatiale des espèces.

1.1- Le concept de niche écologique

La majorité des espèces présentent des distributions spatiales fortement localisées, indiquant ainsi l'existence de limites prévenant leur expansion (Soberón, 2007; Gaston, 2009). Les aires de distribution peuvent ainsi être définies comme des patrons de densité ou d'occurrence qui sont généralement fortement contraints par des gradients environnementaux (MacArthur, 1968), et pour lesquels les niveaux d'occurrence décroissent vers les limites et présentent généralement des fragmentations marquées de la structure des populations (Gaston, 2009; Holt, 2009). Joseph Grinell a défini la niche écologique (niche *Grinellienne*) comme un jeu de conditions environnementales limitant une espèce dans un espace géographique permettant sa survie (Grinnell, 1917). A l'inverse, Charles Elton a développé le concept de niche fonctionnelle (niche *Eltonienne*) basée sur des variables reliées aux interactions écologiques et à l'impact de l'espèce sur son environnement (Elton, 1929). Au-delà de cette distinction, la définition de la niche écologique des espèces peut être étendue à l'ensemble des conditions biotiques et abiotiques, généralement représenté par un hyper-volume dans l'espace multidimensionnel des variables écologiques, au sein duquel une espèce peut maintenir une population viable (Hutchinson, 1957; Chase & Leibold, 2003). Il devient ainsi possible de représenter schématiquement la distribution spatiale des espèces par le diagramme BAM (Biotique, Abiotique, et Mouvement ; Figure 2).

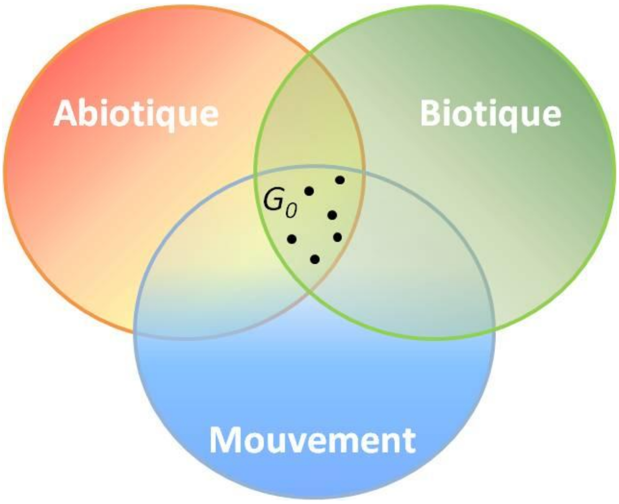


Figure 2 : Diagramme BAM

Il s'agit d'une représentation abstraite de l'espace géographique. La zone A (Abiotique) représente les régions géographiques favorables à l'espèce d'un point de vue environnemental. La zone B (Biotique) représente les régions où les conditions biotiques sont favorables à l'espèce. La zone M (Mouvement) est la région à laquelle l'espèce a accès en fonction de ses capacités de mouvement et de colonisation durant une période de temps définie. G_0 représente l'aire actuellement occupée par l'espèce comme la résultante de l'interaction de ces trois facteurs. (Modifiée d'après Soberón, 2007)

La zone A correspond à la niche Grinellienne, où les conditions abiotiques (e.g. températures, précipitations) permettent la survie de l'espèce dans une région et à un temps donné, définissant ainsi la niche potentielle de l'espèce. La zone B est la région où les conditions biotiques, déterminées principalement par les facteurs Eltoniens (e.g. compétition, prédation, parasitisme), permettent l'existence de populations viables. Finalement, la zone C délimite la région accessible à l'espèce par dispersion et colonisation (e.g. barrière géologique) durant un intervalle de temps donné. L'intersection de ces trois zones représente la niche réalisée de l'espèce, correspondant à l'aire géographique actuellement occupée dont les limites sont la résultante de l'interaction entre les taux de natalité, de mortalité et les processus de dispersion dans l'espace (Parmesan *et al.*, 2005; Gaston, 2009).

1.2- Conservation vs. Evolution de la niche écologique

Malgré le fait que ce postulat soit encore sujet à débat (Beale *et al.*, 2008), les facteurs climatiques sont considérés par de nombreux biogéographes comme les facteurs principaux limitant la distribution des espèces, tout du moins à large échelle spatiale (Pearson & Dawson, 2003). Ainsi, si les distributions spatiales des espèces sont conditionnées par des limitations physiologiques qui restent fixes dans le temps (i.e. conservation de la niche ; Wiens *et al.*, 2010), lors d'un changement climatique rapide, ces espèces devraient se déplacer dans l'espace géographique de manière à rester dans l'espace qui leur est climatiquement favorable, un processus appelé ' *niche-tracking* ' (Tingley *et al.*, 2009 ; Figure 3a; La Sorte & Jetz, 2012). Cependant, comme nous l'avons vu précédemment, la distribution des espèces est également limitée par des interactions biotiques, elles même potentiellement soumises à des contrôles climatiques, particulièrement à la limite inférieure de leur distribution (Brown *et al.*, 1996; Normand *et al.*, 2009). Ainsi, les changements climatiques pourraient affecter les espèces de manière directe, par des modifications des taux de mortalité et de natalité, mais également de manière indirecte par des modifications des interactions biotiques, conduisant potentiellement à des changements directionnels similaires (Parmesan *et al.*, 2005; Thomas, 2010). Au contraire, des adaptations évolutives (génétiques) pourraient permettre aux espèces de modifier leurs exigences écologiques vis-à-vis des facteurs climatiques (i.e. évolution de la niche), modifiant ainsi leur niche climatique afin de rester dans leur espace géographique (Jezkova *et al.*, 2011 ; Figure 3b).

Malgré la confusion possible entre les réponses génotypiques et la plasticité phénotypique, un nombre croissant d'études ont reporté des effets des changements climatiques sur la réponse micro-évolutive des populations (Gienapp *et al.*, 2008). Ces exemples de réponses évolutives rapides suggèrent que des adaptations génotypiques pourraient potentiellement aider les espèces à s'adapter aux changements climatiques actuels, bien que l'efficacité de ce type de réponse soit généralement considérée comme limitée compte tenu de la rapidité des changements observés (Bradshaw & Holzapfel, 2006). Cette vison est corroborée par l'analyse de fossiles démontrant que de nombreuses espèces se sont déplacées en réponse aux fluctuations climatiques du Pléistocène (mammifères : Graham *et al.*, 1996; arbres : Davis & Shaw, 2001; bivalves : Roy *et al.*, 2001; poissons : Kettle *et al.*, 2008), suggérant que les espèces seraient plus enclines à modifier leur distribution spatiale pour suivre leur niche climatique plutôt que de s'adapter *in situ* (Parmesan, 2006). Cependant, bien que le rôle des processus évolutifs dans la détermination des limites de la distribution des espèces reste encore mal compris (Holt & Keitt, 2005; Pauls *et al.*, 2013), ces derniers pourraient jouer un rôle important lors des processus d’expansion des gammes de distribution durant des épisodes de changements climatiques rapides (Davis & Shaw, 2001; Lavergne *et al.*, 2010; Hill *et al.*, 2012).

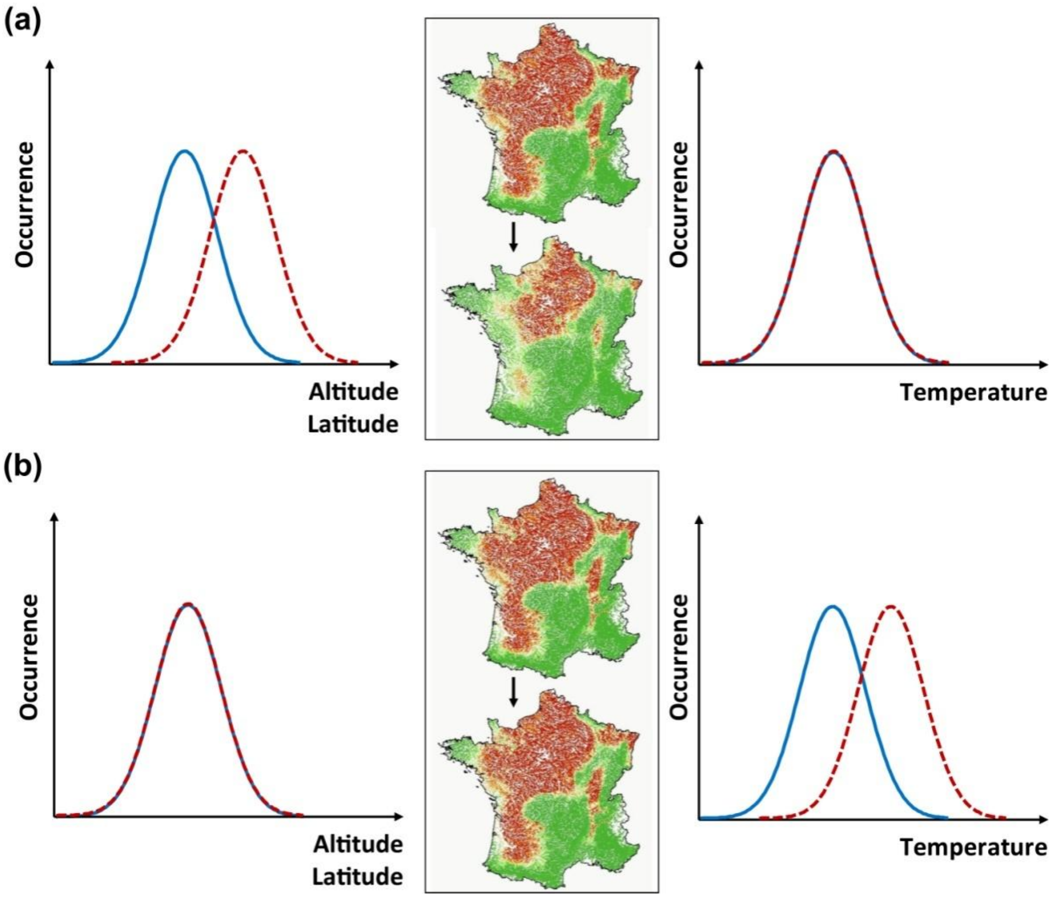


Figure 3 : Représentation de la distribution d’une espèce le long d’un gradient spatial (altitude ou latitude), dans l’espace géographique et le long d’un gradient climatique (température) avant (bleu) et après (rouge) un réchauffement climatique rapide, en supposant que l’occurrence de l’espèce est plus forte au centre de sa distribution : (a) l’espèce conserve sa niche climatique en se déplaçant dans l’espace géographique et (b) l’espèce modifie sa niche climatique pour rester dans son espace géographique.

1.3- Les changements de distribution attendus

Comprendre la réponse des espèces face aux changements climatiques actuels requiert une compréhension plus détaillée de la dynamique de la distribution des espèces, et en particulier des processus se produisant aux limites de leur distribution (Holt & Keitt, 2005; Parmesan *et al.*, 2005). En effet, les modifications de la distribution spatiale sont plus à même de se produire aux limites où les facteurs climatiques affectent les performances de l’espèce, plutôt qu’au sein de la distribution spatiale, et ce particulièrement pour les organismes ectothermes (Deutsch *et al.*, 2008). Ces changements peuvent se traduire par une expansion de la distribution, pendant laquelle les populations vivant à la limite froide de la distribution (à des altitudes ou latitudes élevées) colonisent des sites nouvellement favorables (Thomas, 2010; La Sorte & Jetz, 2012), ainsi que par une contraction de la distribution pendant laquelle les populations vivant à la limite chaude de la distribution (à des altitudes ou latitudes basses), soumises à un fort stress climatique, sont progressivement extirpées (Hampe & Petit, 2005; Chen *et al.*, 2010; Cahill *et al.*, 2013), conduisant de ce fait à une remontée moyenne de la distribution (Figure 4, A). Cependant, si les mécanismes sous-tendant les changements de distribution aux deux extrêmes de la distribution diffèrent, des patrons intermédiaires pourraient également apparaître (Figure 4, C ; E), particulièrement si ces phénomènes sont étudiés sur un court laps de temps (Maggini *et al.*, 2011). En effet, des réponses asymétriques pourraient survenir suite à l'existence d'une topographie hétérogène procurant des micro-refuges temporaires aux populations vivant aux limites inférieures (Thomas *et al.*, 2006) ou au contraire bloquant la colonisation des populations vivant aux limites supérieures (Hill *et al.*, 2002; Moritz *et al.*, 2008), ou encore suite à des différences de réponses démographiques et de capacité de persistance des populations situées aux deux extrêmes de la distribution (Davis & Shaw, 2001; Doak & Morris, 2010). L'importance des interactions biotiques dans la définition des limites de distribution pourrait également être un facteur non négligeable, et de ce fait conduire à des réponses contrastées suite à la relaxation des interactions proie-prédateur ou à l'arrivée de nouveaux compétiteurs (Lenoir *et al.*, 2010 ; Figure 4, D, F; Maggini *et al.*, 2011). Enfin, le stress physiologique du aux changements climatiques pourrait impacter non seulement les populations vivant aux bornes de la distribution, mais également les populations exposées aux plus fortes magnitudes, produisant ainsi des modifications plus fortes au sein de la distribution qu'aux limites (Figure 4, G).

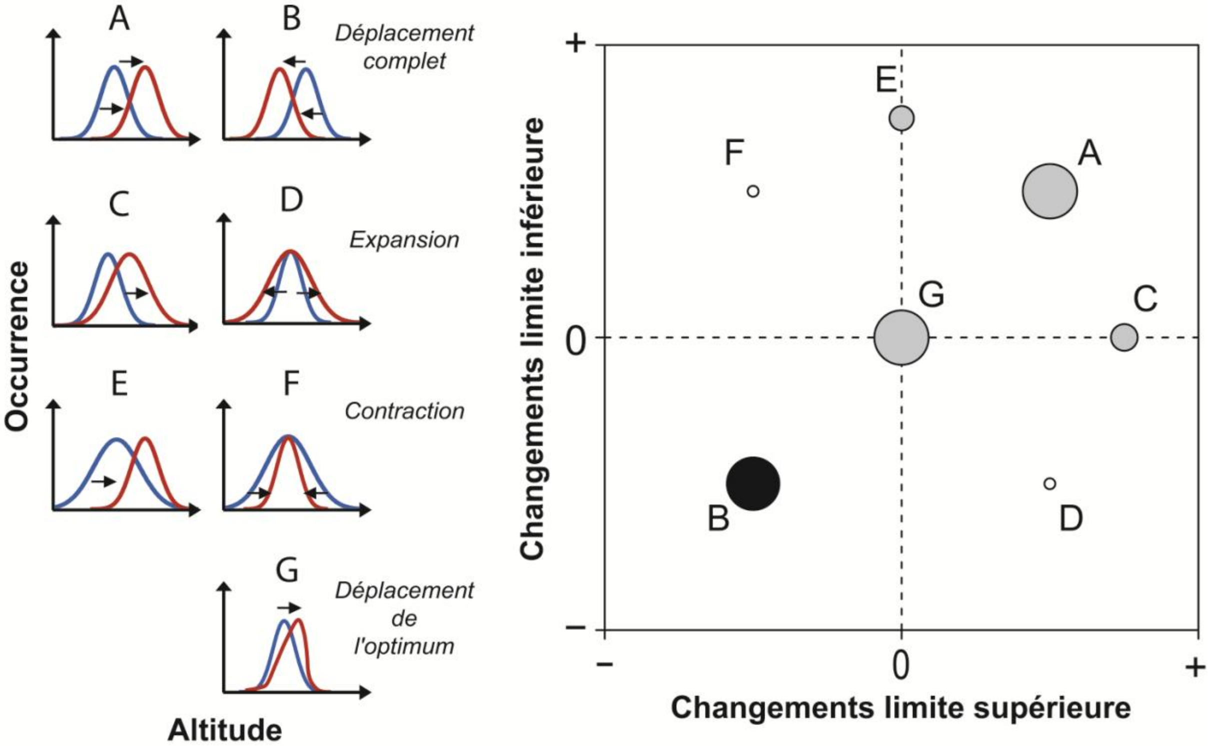


Figure 4 : Figure théorique et courbes de réponses associées décrivant les changements de distribution potentiels se produisant au centre et aux limites supérieure et inférieure de la distribution d'une espèce le long d'un gradient spatial (altitude ou latitude) soumise à un réchauffement climatique rapide (bleu : période 'froide' ; rouge : période 'chaude'). La taille des cercles représente la valeur absolue des changements du centre de la distribution le long de ce gradient et la couleur les changements significatifs ($p < 0.05$) : gris pour une remontée et noir pour une redescente. Les flèches indiquent la direction du déplacement. (Modifiée d'après $\boldsymbol{P_{III}}$, Figure 2)

1.4- Les changements de distribution observés

De manière remarquable, plusieurs méta-analyses indépendantes ont démontré une réponse sans équivoque de nombreuses espèces appartenant à des groupes taxonomiques divers aux changements climatiques récents, et ce malgré une multitude de facteurs confondants potentiels (Parmesan & Yohe, 2003; Hickling *et al.*, 2006; Thomas, 2010; Chen *et al.*, 2011; Poloczanska *et al.*, 2013). Ainsi Parmesan & Yohe (2003) ont évalué que parmi 99 espèces terrestres étudiées, 81% d'entre elles présentaient des modifications de leur distribution spatiale en accord avec la direction attendue due aux changements climatiques, se traduisant par un déplacement moyen de leur limite altitudinale supérieure de 6.1 m.décennie^{-1}. Cette vitesse a été récemment révisée par Chen *et al.* (2011) en incluant 1367 réponses d'espèces terrestres et aquatiques, estimant ainsi un déplacement global à 11.0 m.décennie^{-1}. Poloczanska *et al.* (2013), en analysant 1735 réponses d'espèces exclusivement marines, ont également trouvé que 83% d'entre elles présentaient déjà des déplacements (généralement vers les poles) concordants avec les augmentations de températures. Néanmoins, de fortes variabilités dans la réponse entre espèces ont également été décrites, et ce qu'il s'agisse d'espèces appartenant à des groupes taxonomiques similaires ou différents, et vivant ou non dans les mêmes zones géographiques (Lenoir *et al.*, 2008; Moritz *et al.*, 2008; Woodall *et al.*, 2010; Chen *et al.*, 2011; Crimmins *et al.*, 2011). Par ailleurs, le patron le plus communément décrit à ce jour concerne des expansions plutôt que des contractions de la distribution (Parmesan *et al.*, 1999; Thomas & Lennon, 1999; Warren *et al.*, 2001; Hill *et al.*, 2002; Bergamini *et al.*, 2009; Chen *et al.*, 2010; Moritz & Agudo, 2013), bien que plusieurs études aient reporté des déclins de populations vivant en limite chaude (i.e. à basse altitude ou latitude) de leur distribution (Wilson *et al.*, 2005; Franco *et al.*, 2006; Zuckerberg *et al.*, 2009; Chen *et al.*, 2010; Jiguet *et al.*, 2010; Woodall *et al.*, 2010; Zhu *et al.*, 2012; Felde *et al.*, 2013). Ainsi, alors que ces études ont fourni de précieuses indications sur l'ampleur et la direction des changements de distribution observés, notre connaissance est encore limitée de nombreuses façons.

En particulier, l'étendue spatiale de la majorité des études abordant les impacts des changements climatiques sur la distribution des espèces est généralement restreinte à un gradient spatial (e.g. altitudinal ou latitudinal, Chen *et al.*, 2010), et ne considère qu'un descripteur de la distribution (e.g. optimum altitudinal, Lenoir *et al.*, 2008). Malgré leurs rôles évidents pour la persistance à long terme des espèces soumises à des changements climatiques, les changements des limites inférieures restent encore peu abordés (Hampe & Petit, 2005). Par ailleurs, peu d'études ont jusqu'alors considéré les changements se produisant au sein des aires de répartition prises dans leur entier (La Sorte & Thompson, 2007; Lehikoinen *et al.*, 2013), limitant ainsi notre capacité à appréhender la complexité des mécanismes qui sous-tendent la dynamique de la distribution des espèces (Parmesan *et al.*, 2005; Beever *et al.*, 2011).

2- La vulnérabilité des espèces face aux changements climatiques

Alors qu'un grand nombre d'études se sont précédemment attachées à décrire les changements de distribution pour une grande variété de groupes taxonomiques, la question des mécanismes sous-jacents, qu'il s'agisse de facteurs intrinsèques (caractéristiques des espèces) ou extrinsèques (spatialisation des changements climatiques, interactions avec d'autres facteurs anthropiques), demeure un des enjeux majeurs pour le développement de stratégies de conservation et de gestion efficaces (Williams *et al.*, 2008; Angert *et al.*, 2011; Foden *et al.*, 2013).

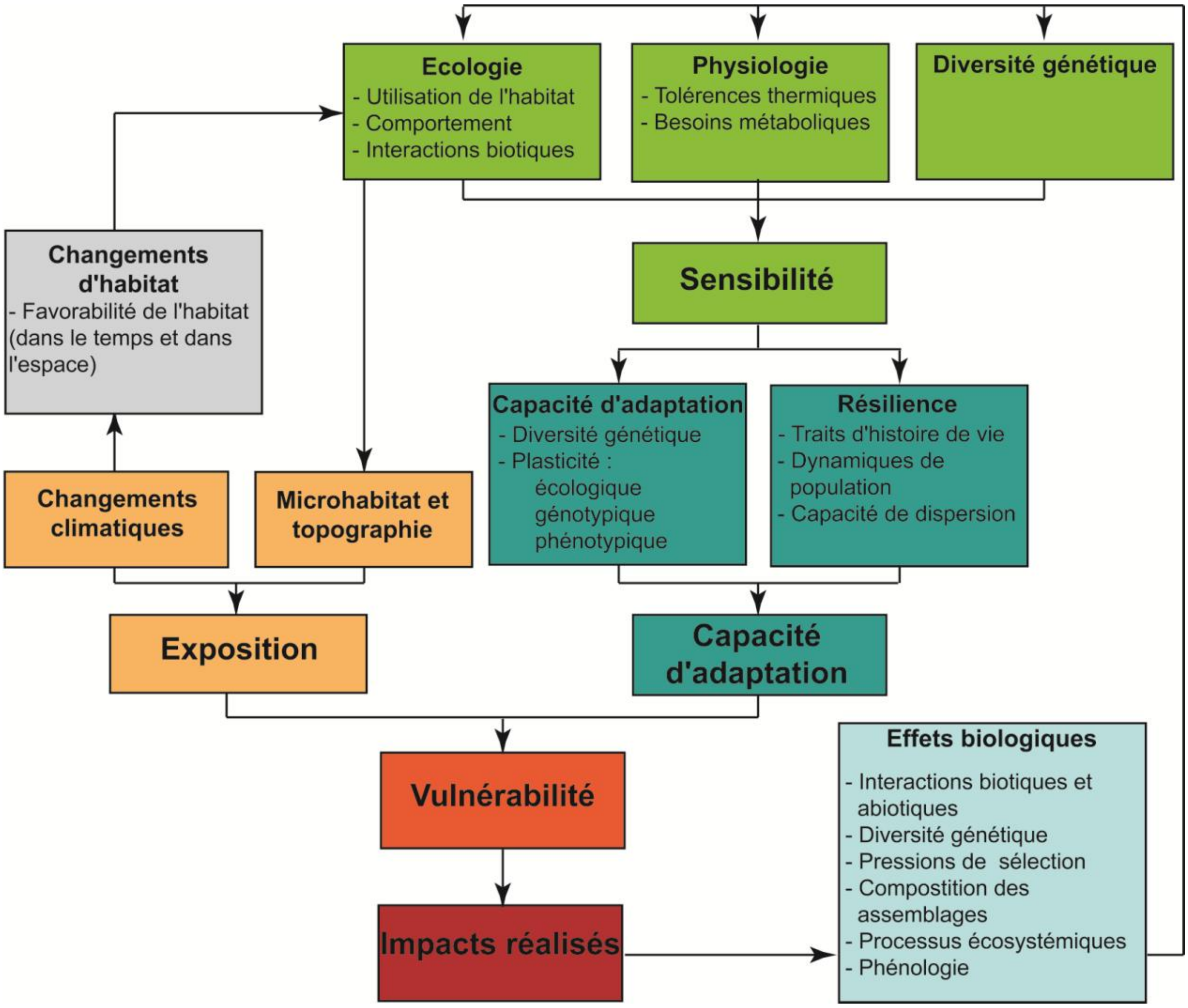


Figure 5 : Diagramme représentant les différents facteurs sous-tendant la vulnérabilité des espèces face aux changements climatiques actuels. La vulnérabilité est fonction de la sensibilité des espèces ainsi que des patrons d'exposition aux changements climatiques, qui sont modérés par la capacité d'adaptation et de résilience de l'espèce. Les effets réalisés sont également à même de causer des effets rétroactifs en cascades à travers tout l'écosystème. (Modifiée d'après Williams *et al.*, 2008)

Plusieurs facteurs sont susceptibles d'influencer la magnitude et la direction des réponses des espèces, et de ce fait d'expliquer les changements de distribution idiosyncratiques observés (Figure 5). En effet, la vulnérabilité d'une espèce peut être considérée comme la résultante (1) de son exposition aux changements climatiques, (2) de sa sensibilité intrinsèque, due par exemple à des limites physiologiques, et (3) de sa capacité d'adaptation ou de résilience aux altérations climatiques, *in situ* via des réponses plastiques (incluant des réponses comportementales) et génétiques, ou via sa capacité à se déplacer afin de suivre les conditions optimales à sa survie (Williams *et al.*, 2008; Foden *et al.*, 2013; Moritz & Agudo, 2013). Ainsi, de nombreux mécanismes et processus physiologiques peuvent agir de concert, et de ce fait conduire à des changements de distribution complexes et multi-facettes (Parmesan *et al.*, 2005; Rabasa *et al.*, 2013).

2.1- Les déterminants extrinsèques de la vulnérabilité

La réponse des espèces dépend en premier lieu de patrons complexes d'exposition aux changements climatiques qui sont généralement hautement dynamiques et spatialement hétérogènes (Burrows *et al.*, 2011; Tingley *et al.*, 2012; Dobrowski *et al.*, 2013). En effet, la topographie ainsi que la variabilité des changements vont déterminer la directionnalité des routes de dispersion offertes aux espèces, en créant à la fois des micro-refuges leur permettant de persister localement, mais également des barrières limitant leur expansion (Early & Sax, 2011; Bennie *et al.*, 2013). Par exemple, une espèce vivant en plaine aura à parcourir une plus grande distance qu'une espèce de montagne pour suivre les déplacements du climat (Loarie *et al.*, 2009). Ainsi, une approche pour caractériser la vulnérabilité des espèces est de comparer la vitesse de leurs déplacements géographiques avec la vitesse nécessaire pour suivre le déplacement des isothermes le long de gradients spatiaux (i.e. la vélocité des changements climatiques ; Loarie *et al.*, 2009; Isaak & Rieman, 2013). Cependant, alors que de nombreuses études se sont précédemment attachées à décrire la vélocité des changements climatiques passés et prédits pour le futur (Loarie *et al.*, 2009; Burrows *et al.*, 2011; Dobrowski *et al.*, 2013), la capacité des espèces à suivre les mouvements actuels du climat reste encore largement inconnue. Néanmoins, le peu d'études qui se sont intéressées à ces questions ont obtenu des résultats mitigés. Par exemple, Devictor *et al.*, (2012), en analysant des données d'observations de 9490 communautés d'oiseaux et 2130 communautés de papillons à l'échelle de l'Europe depuis 1990 ont quantifié un retard moyen dans leurs déplacements vers le nord de près de 135 km pour les papillons et de 212 km pour les oiseaux, alors que deux méta-analyses récentes suggèrent que les déplacements des espèces ne seraient pas toujours en retard par rapport aux changements climatiques observés (Chen *et al.*, 2011; Poloczanska *et al.*, 2013).

Etant donné que les déplacements observés pourraient ne pas être représentatifs de la vitesse maximale que les espèces pourraient atteindre en colonisant de nouveaux habitats, les patrons d'invasions peuvent fournir un cadre de référence dans l'estimation de la vulnérabilité potentielle des espèces (Sorte *et al.*, 2010; Hiddink *et al.*, 2012). Par exemple, Hiddink *et al.* (2012), en comparant les vitesses d'expansion d'espèces marines invasives appartenant à plusieurs groupes taxonomiques aux vitesses des changements climatiques prédits sous différents scénarios climatiques, ont estimé que 20% d'entre elles ne seraient pas en mesure de se déplacer suffisamment vite pour suivre les modifications climatiques. De manière similaire, les relevés paléontologiques, et en particulier ceux des dernières déglaciations, sont particulièrement intéressants pour étudier les réponses écologiques sur des échelles temporelles étendues (Roy *et al.*, 2001; Lyons *et al.*, 2011; Sandel *et al.*, 2011; Turrero *et al.*, 2012; Ordonez & Williams, 2013). Dans une étude récente, Ordonez & Williams (2013), en analysant des pollens fossiles, ont mis en évidence des vitesses de déplacement d'espèces ligneuses en accord avec les changements climatiques observés durant les derniers 16000 ans en Amérique du Nord, suggérant au contraire que ces dernières auraient la capacité de suivre les conditions climatiques qui leur sont favorables dans le temps et l'espace. La contradiction apparente entre les vitesses d'expansion observées par le passé et les capacités de dispersion estimées pour certaines espèces pourraient illustrer l'importance des événements de dispersion longue distance dans les processus de colonisation, de manière concomitante à l'évolution des génotypes disperseurs dans les populations soumises à de fortes pressions de sélection induites par les variations du climat (Davis & Shaw, 2001; Shine *et al.*, 2011; Hill *et al.*, 2012). Néanmoins, d'autres études pointent également le rôle potentiel fondamental des micro-refuges climatiques pour expliquer la persistance de nombreuses espèces soumises à des variations de température rapides lors du Quaternaire (Hof *et al.*, 2011; Sandel *et al.*, 2011). Cependant, la capacité des espèces à faire face aux changements climatiques actuels pourrait être complètement différente de nos jours, compte tenu des modifications sévères ayant affecté les écosystèmes à l'échelle globale (Opdam & Wascher, 2004; Hof *et al.*, 2011; Lawler *et al.*, 2013). Ainsi, la fragmentation et la destruction des habitats pourraient interagir de manière synergique avec les altérations climatiques (Franco *et al.*, 2006; Brook *et al.*, 2008; D'Amen & Bombi, 2009; Hockey *et al.*, 2011), conduisant à une répartition inégale dans l'espace du potentiel des espèces à suivre leur niche climatique ou à persister dans des micro-habitats (Figure 6). Outre l'effet direct de la fragmentation sur le déplacement des espèces, cette dernière pourrait également limiter le potentiel de réponse des espèces en limitant le flux de gènes entre populations, réduisant de ce fait leur variabilité phénotypique et génotypique (Hof *et al.*, 2011).

Ainsi, la comparaison de descripteurs de distribution simples tels ceux couramment employés (e.g. optimum altitudinal) pourrait ne pas être suffisante pour attribuer sans ambiguïté les modifications observées aux changements climatiques seuls (La Sorte & Thompson, 2007). En effet, alors que pour l'heure l'uni-directionnalité des changements a été considérée comme indicatrice d'une réponse cohérente de la majorité des espèces (Parmesan, 2006), d'autres études ont au contraire démontré que les altérations du paysage pouvaient agir de manière synergique (D'Amen & Bombi, 2009; Hockey *et al.*, 2011) ou encore antagoniste (Rowe *et al.*, 2010; Morelli *et al.*, 2012) avec les altérations climatiques récentes, diminuant de ce fait notre capacité à quantifier leur impact sur la distribution spatiale des espèces.

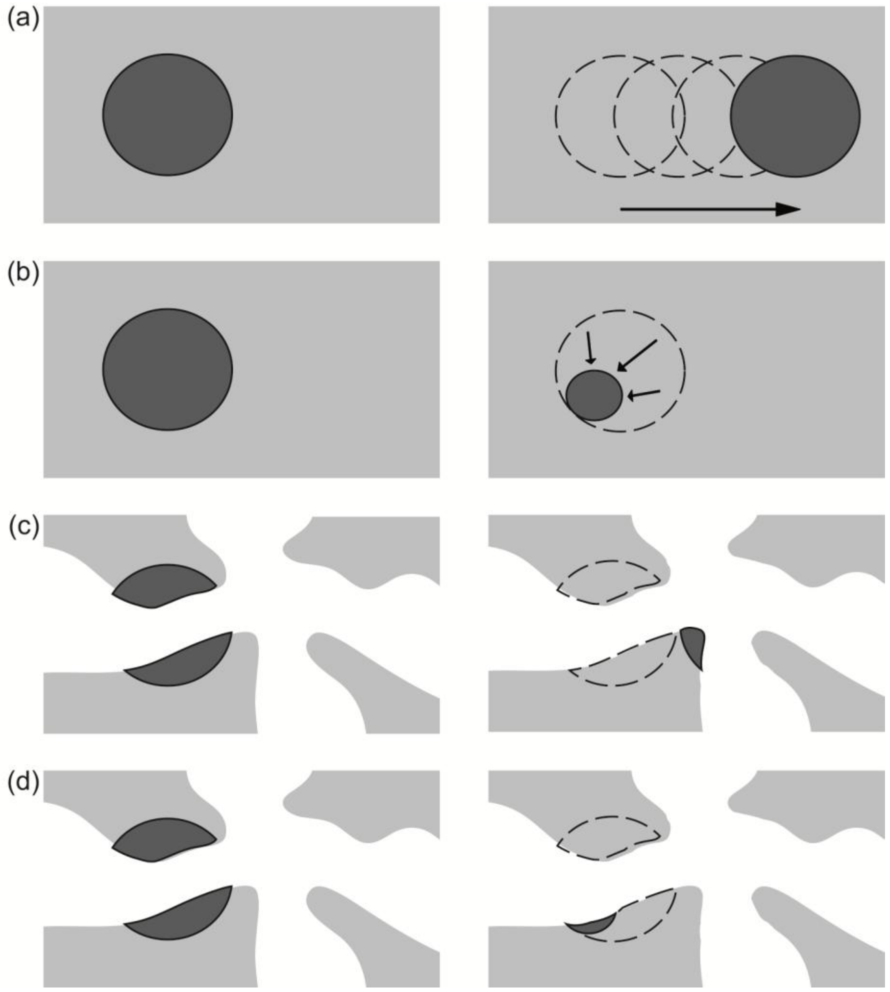


Figure 6 : Illustration schématique de changements potentiels de la distribution spatiale d’une espèce soumise à des changements climatiques dans un milieu (a-b) non fragmenté et (c-d) fragmenté. Les cas (a) et (c) illustrent des réponses où l’espèce suit sa niche climatique et les cas (b) et (d) où l’espèce persiste dans des micro-habitats climatiques. La fragmentation réduit la probabilité de déplacement (c), ainsi que la persistance (d). (Modifiée d’après Hof *et al.*, 2011)

2.2- Les déterminants intrinsèques de la vulnérabilité

La réponse des espèces dépend également de l’interaction des facteurs extrinsèques avec plusieurs traits biologiques, physiologiques et écologiques sous-tendant leur sensibilité et leur capacité d’adaptation (Figure 7). A l’heure actuelle, la conséquence la plus notable des changements climatiques se traduit, à l’échelle du globe, par une augmentation des températures. Or, 99.5% des espèces recensées sur Terre sont des organismes ectothermes, dont la température corporelle et le métabolisme dépendent du milieu extérieur. Les tolérances thermiques devraient ainsi être le facteur principal conditionnant leur vulnérabilité (Pörtner & Knust, 2007; Sinervo *et al.*, 2010; Chessman, 2012), celles-ci déterminant la capacité d’une espèce à endurer les changements induits par les températures (Deutsch *et al.*, 2008; Huey *et al.*, 2012). Les interactions entre les espèces doivent également être mentionnées. En effet, les différences de sensibilité thermiques et de taux de dispersion peuvent avoir des conséquences importantes sur les associations temporelle ou spatiale entre les espèces, et de ce fait venir potentiellement amplifier les effets des changements climatiques le long des réseaux trophiques (Walther *et al.*, 2002; Berg *et al.*, 2010). Par exemple, Luczak *et al.* (2011) ont montré que les changements de distribution d'une espèce d'oiseau prédatrice, le Puffin des Baléares, étaient concordants avec le déplacement de ses proies, démontrant ainsi l'existence d'effets biotiques indirects des changements climatiques.

D'autres caractéristiques pourraient également venir retarder l'extinction en promouvant la persistance locale des populations ou encore en favorisant le potentiel des espèces à compenser les conséquences défavorables, directes ou indirectes, induites par les changements climatiques (Williams *et al.*, 2008; Foden *et al.*, 2013). Cependant, alors que la capacité de dispersion et la disponibilité de l'habitat (e.g. tolérance environnementale, taille de la distribution) sont reconnues comme étant les facteurs clés promouvant l'expansion (Lenoir *et al.*, 2008; Moritz *et al.*, 2008; Pöyry *et al.*, 2009; Tingley *et al.*, 2012), la sensibilité des populations vivant en limite chaude de leur distribution reste encore mal comprise (Hampe & Petit, 2005). Bien que le potentiel d'ajustement des tolérances thermiques elles-mêmes semble limité, et ce qu'il s'agisse de plasticité phénotypique ou de modifications génétiques (Hoffmann *et al.*, 2013), des adaptations des patrons d'activité spatiaux (e.g. utilisation de micro-habitats) et temporels (e.g. dates de migration, floraison) pourraient être des mécanismes cruciaux de survie. Par exemple, des relations entre le risque d'extinction et des traits phénologiques ont été établies chez des plantes, les espèces dont les dates de floraison ne répondaient pas aux températures montrant des déclins d'abondance (Willis *et al.*, 2008). Par ailleurs, la dynamique des populations pourrait également conditionner la capacité à compenser temporairement les extinctions locales en promouvant la recolonisation des habitats soumis à des conditions climatiques défavorables (Trakhtenbrot *et al.*, 2005; Kuussaari *et al.*, 2009). Ainsi, plusieurs traits pourraient être impliqués pour expliquer les changements de distribution observés ces dernières décennies chez de nombreux organismes, bien que ces traits puissent agir de manière antagoniste sur les processus d'expansion et de contraction des gammes de distribution.

Cependant, bien qu'un nombre croissant d'études ait documenté des réponses dépendantes de caractéristiques géographiques et biologiques clés des espèces (Perry *et al.*, 2005; Chessman, 2012; La Sorte & Jetz, 2012), l'utilité des approches basées sur les traits reste controversée (Angert *et al.*, 2011). En effet, ces approches ont eu pour l'heure un succès limité pour élucider les mécanismes sous-tendant la réponse des espèces, et ce à cause de leur faible pouvoir explicatif et de l'existence de nombreuses corrélations entre les traits considérés (Angert *et al.*, 2011; Tingley *et al.*, 2012). Au contraire, comprendre comment l'histoire évolutive des espèces (i.e. la phylogénie) contraint leur vulnérabilité face aux changements climatiques actuels a été pour l'heure un sujet de recherche sous-exploité, et ce malgré son potentiel pour anticiper la manière dont les espèces et les communautés pourraient être exposées aux changements climatiques à venir (Pau *et al.*, 2011). En effet, si les espèces proches d'un point de vue évolutif possèdent des caractéristiques communes les rendant plus vulnérables aux changements climatiques, les extinctions pourraient être hautement sélectives vis-à-vis de certaines lignées du vivant (McKinney, 1997; Thuiller *et al.*, 2011). Identifier les patrons de corrélation phylogénétique dans la réponse des espèces pourrait ainsi être un moyen de clarifier quels sont les mécanismes responsables des changements de distribution observés, mais également d'améliorer notre capacité à prédire les conséquences des changements climatiques sur le monde du vivant (Willis *et al.*, 2008; Roy *et al.*, 2009). Des recherches sont donc encore nécessaires pour élucider les mécanismes qui sous-tendent la capacité d'adaptation des espèces face aux changements climatiques et établir le lien entre leur vulnérabilité et leurs traits biologiques et écologiques. Par ailleurs, la question de la généralisation des caractéristiques prédisposant une espèce à des risques d'extinction reste à établir dans un contexte de menaces multiples s'exercant à l'échelle globale (Brook *et al.*, 2008).

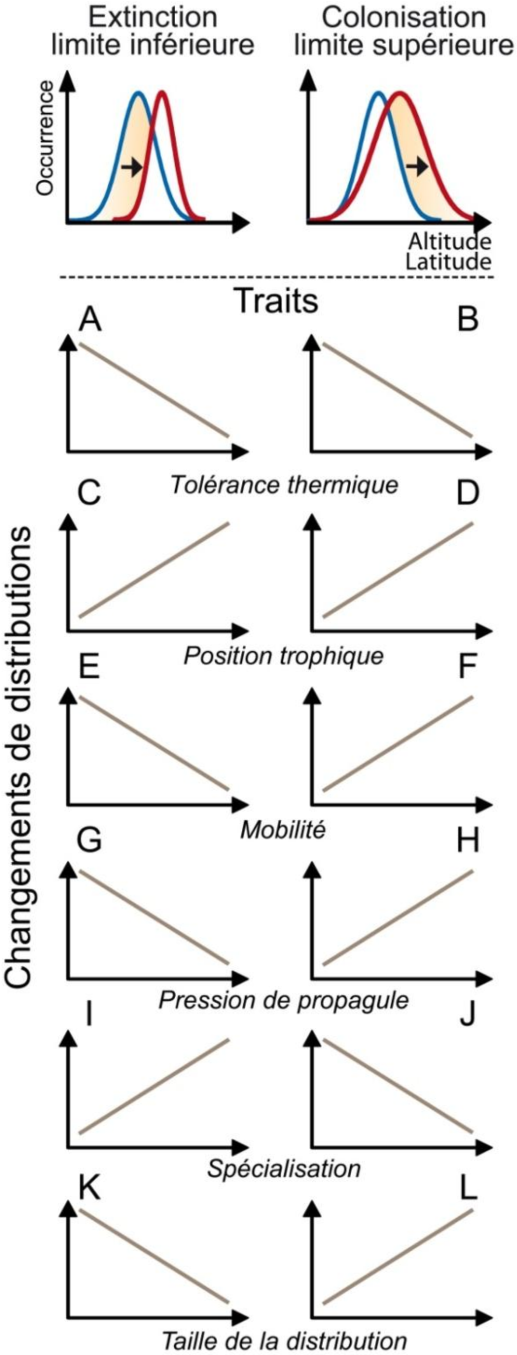


Figure 7 : Illustration des relations potentielles entre les caractéristiques des espèces et la magnitude des changements des limites inférieure et supérieure de leurs distributions le long d'un gradient spatial (altitude, latitude) suivant un changement climatique rapide. (Modifiée d'après $\boldsymbol{P_V}$, Figure 1)

3- Changements climatiques et poissons d’eau douce

La distribution spatiale des espèces européennes d’eau douce a été sujette à de nombreuses fluctuations lors des périodes historiques et préhistoriques en réponse aux variations du climat (Cortey *et al.*, 2004; Kettle *et al.*, 2008; Turrero *et al.*, 2012). En particulier, la biogéographie des poissons de rivière est assez bien documentée, et fait état de l’élimination de la quasi-totalité de la faune présente au nord de l’Europe par les glaciations successives durant le Quaternaire puis à des expansions à partir de zones refuges situées au sud de l’Europe (côte méditerranéenne) ainsi qu’à des recolonisations à partir du bassin du Danube (Keith *et al.*, 2011). Compte tenu de la magnitude des changements climatiques survenus lors des dernières décennies, la question de la vulnérabilité des organismes d’eau douce, parmi lesquels les poissons de rivière, apparait donc cruciale.

3.1- Les caractéristiques des écosystèmes aquatiques d’eau douce

Les écosystèmes aquatiques d’eau douce couvrent moins de 1% de la surface de la Terre, mais sont parmi les milieux présentant les plus fortes diversités floristiques et faunistiques décrites à ce jour. Malgré leur valeur écologique et sociale, ces milieux sont pourtant soumis à de multiples pressions anthropiques et subissent des déclins de biodiversité qui excèdent souvent ceux documentés dans les écosystèmes terrestres (Dudgeon *et al.*, 2006). Dans les milieux aquatiques, le changement climatique est aujourd'hui reconnu comme une des principales menaces s'exerçant sur la biodiversité (Sala *et al.*, 2000; Heino *et al.*, 2009). En effet, la majorité des espèces d’eau douce, parmi lesquels les poissons, sont des organismes ectothermes, particulièrement sensibles aux conditions thermiques dont dépendent leur croissance et leur métabolisme, ainsi qu’aux effets indirects des températures sur les concentrations d’oxygène dissous nécessaires à leur survie (Elliott, 1981; Pörtner & Knust, 2007). L’augmentation des températures, couplée avec un dérèglement des conditions hydrologiques, pourrait également venir accélérer les extinctions locales aussi bien que globales en modifiant la structure et la disponibilité des habitats (Carpenter *et al.*, 1992; Leith & Whitfield, 1998). Par ailleurs, la distribution des espèces est hautement contrainte par la structure dendritique des réseaux hydrographiques, constituant ainsi un obstacle majeur à la dispersion (Matthews, 1998; Brown & Swan, 2010; Erős *et al.*, 2012; Peterson *et al.*, 2013). Cela pourrait par ailleurs être exacerbé par le fort niveau de fragmentation communément observé dans ces milieux, qu’il soit d’origine naturelle ou anthropique (Figure 8). Finalement, une autre particularité des écosystèmes d’eau douce réside dans l’importance des flux des masses d’eau qui conditionnent les déplacements des organismes. Ainsi, les déplacements des poissons de rivière sont soumis à la structure longitudinale des réseaux qui impose des changements unidirectionnels, qu'ils soient d’origine climatique ou non, ce qui pourrait renforcer la difficulté d’attribuer les changements observés aux changements climatiques seuls (Sorte, 2013).

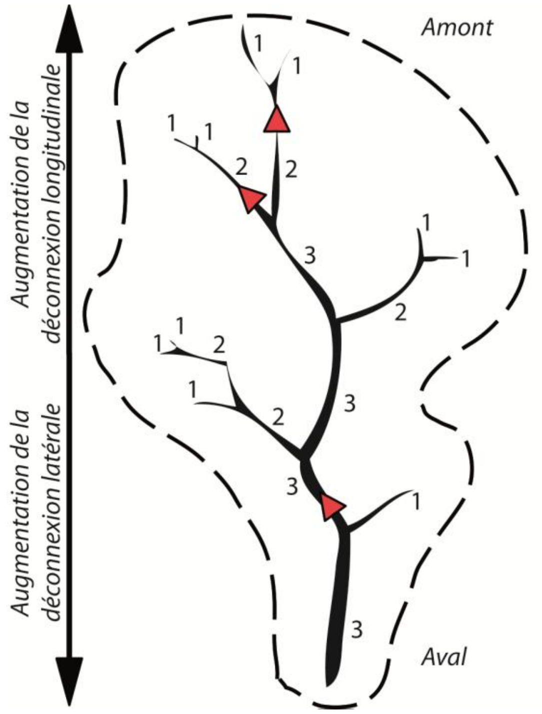


Figure 8 : Représentation schématique de la connectivité du réseau hydrographique d'un bassin versant présentant une structure dendritique typique. Les chiffres indiquent l'ordre de Strahler. La connectivité entre les habitats décroit généralement de manière latérale à l'aval et de manière longitudinale à l'amont, ce qui peut être renforcé par la présence d'obstacles (barrages : triangles rouges). La connexion entre bassins versants est généralement limitée, sauf si des canaux artificiels les relient.

3.2- Des lacunes dans les connaissances

Des études récentes ont confirmé qu'une augmentation de la température de l'eau pouvait avoir un effet significatif sur la croissance et le recrutement des poissons d'eau douce (Schindler *et al.*, 2005; Daufresne *et al.*, 2009; Nunn *et al.*, 2010) et conduire à des modifications de leur distribution spatiale (Hari *et al.*, 2006; Hickling *et al.*, 2006; Almodóvar *et al.*, 2012). Cependant, en passant en revue 77 articles publiés entre 1980 et 2011 traitant de changements de distribution récemment observés ou prédits pour le futur, il est apparu que malgré une longue histoire de recherche centrée sur les effets potentiels des changements climatiques, le nombre d'études s'étant focalisées sur les changements récents reste disproportionnellement faible (***P**$_I$*, Figure 9a). Par ailleurs, notre connaissance de l'influence des changements climatiques sur la distribution spatiale des poissons d'eau douce reste encore très fragmentaire, et ce particulièrement à cause de biais géographiques et taxonomiques. En effet, la majorité des études se sont intéressées à une seule ou un faible nombre d'espèces, appartenant majoritairement à une seule famille. Ainsi, 54% des études traitant de changements de distribution récents se sont intéressées à une espèce appartenant à la famille des salmonidés, tandis que la réponse de 91% des espèces étudiées n'a été décrite qu'au travers d'un seul article. Le manque d'études concernant les espèces menacées est également problématique (<10% du total des études), étant donné que ces dernières pourraient être les plus affectées par les changements climatiques, et pour lesquelles des mesures de conservation à court terme semblent prioritaires.

A ce jour, le travail d'Hickling *et al.* (2006) reste une des études clés quantifiant des changements de distribution chez des poissons d'eau douce, avec des déplacements moyens de 51 km vers le nord et de 32.7 m en altitude documentés pour 15 espèces en Grande Bretagne durant une période de 25 ans. La généralisation de ce patron est par ailleurs étayée par des travaux sur la truite (*Salmo trutta*) en Espagne et en Suisse, décrivant des contractions significatives de la distribution au cours des dernières décennies en lien avec une augmentation des températures (Hari *et al.*, 2006; Almodóvar *et al.*, 2012). Des expansions des distributions ont également été reportées de manière anecdotique dans diverses régions du monde (e.g. Babaluk *et al.*, 2000; Gómez *et al.,* 2004), malgré le fait que le lien avec les changements climatiques soit resté hypothétique dans la majorité des cas. Finalement, bien que ces études démontrent que les distributions spatiales des poissons d'eau douce se déplacent dans des directions en accord avec les changements climatiques récents, les liens de causalité restent difficiles à établir, et ce à cause de l'existence de nombreuses autres pressions (Figure 9b). Ainsi, les effets biologiques liés aux tendances climatiques seules ne représentent que 55% des articles, alors que les interactions avec d'autres facteurs liés à la dégradation de l'habitat (e.g. fragmentation), à l'introduction d'espèces exotiques ou au développement de pathogènes ou à d'autres activités anthropiques (e.g. pêche sportive) sont régulièrement citées comme facteurs explicatifs des tendances observées.

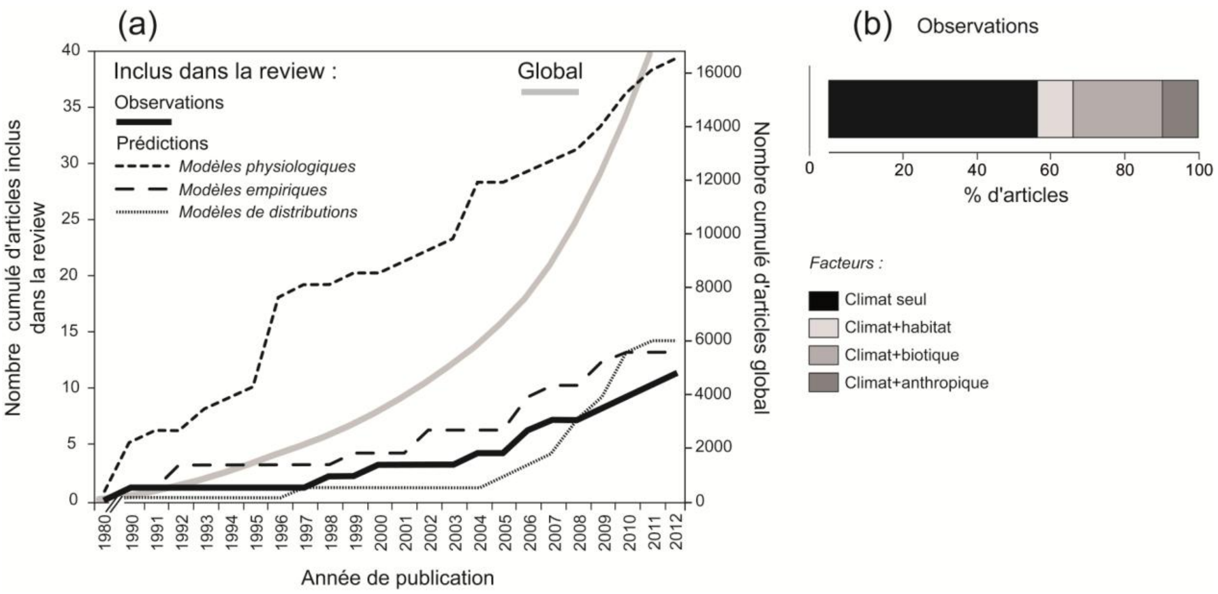


Figure 9 : (a) Nombre cumulé d'articles publiés de 1980 à 2012 (i) inclus dans la review et reportant des changements dans la distribution spatiale d'espèces de poissons d'eau douce (axe gauche, lignes noires), et (ii) résultant d'une recherche plus vaste de la littérature en écologie en utilisant comme termes de recherche *species* and *'climat* change*'* or *warming*. Les articles inclus dans la review ont été divisés entre ceux reportant des effets récents (Observations : ligne noire) et prédits pour le futur (Prédictions : lignes pointillées), ces derniers étant classifiés en fonction de l'approche de modélisation utilisée ; (b) proportion d'articles classés en fonction des facteurs explicatifs présumés des effets observés : climat seul (e.g. température ou précipitation), habitat pour la dégradation de l'habitat (e.g. pollution, fragmentation, prise d'eau), biotique pour les introduction d'espèces exotiques et les interactions biotiques (e.g. parasitisme, prédation) et anthropique pour les activités humaines directes (e.g. soutient de population, pêche). (Modifiée d'après **P_I**, Figure 1)

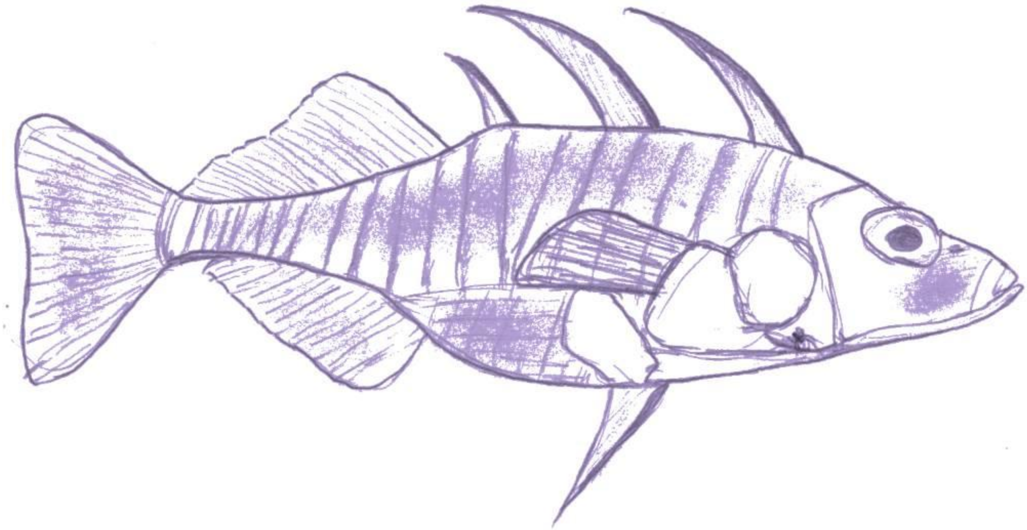
Par conséquent, alors que l'empreinte des changements climatiques actuels est supportée par des évidences empiriques substantielles chez de nombreux groupes taxonomiques (papillons : Hill *et al.*, 2002; poissons marins : Perry *et al.*, 2005; oiseaux : La Sorte & Thompson, 2007; plantes ligneuses : Lenoir *et al.*, 2008; mammifères : Moritz *et al.*, 2008; bryophytes : Bergamini *et al.*, 2009), la capacité des poissons d’eau douce à se déplacer pour suivre les modifications du climat reste largement inconnue.

4- Objectifs de la thèse

Les objectifs de cette thèse ont été d’évaluer les impacts des changements climatiques récents sur la distribution spatiale des poissons d’eau douce ainsi que d’identifier les mécanismes responsables, qu’il s’agisse de mécanismes intrinsèques ou extrinsèques. Dans une première partie, je me suis attachée à décrire les modifications de distribution spatiale des poissons des rivières françaises qui se sont produites lors des dernières décennies (**P_{III}**), en portant une attention particulière aux méthodes nécessaires pour détecter ces changements (**P_{II}**). Dans une seconde partie, l’accent principal a été mis sur la cohérence entre les changements de distribution et les changements climatiques observés. Cette question a été abordée de manière spécifique en analysant la réponse des poissons des rivières françaises (**P_{III}**, **P_{IV}**), puis au travers d’une méta-analyse de la littérature reportant des effets des changements climatiques récents sur la distribution spatiale des poissons d’eau douce (**P_{I}**). Dans une troisième partie, je me suis intéressée aux caractéristiques des espèces qui sous-tendent leur vulnérabilité face aux changements climatiques, et en particulier à l’influence de leur histoire évolutive et de leurs traits biologiques et écologiques (**P_{IV}**, **P_{V}**).

MATERIEL

Les données piscicoles et environnementales



"Who hears the fish when they cry?"

Henry David Thoreau (1849)

Les données de suivis nationaux de populations, les inventaires d'atlas, ou les collections des muséums d'histoire naturelle sont des données inestimables pour évaluer l'impact des changements climatiques récents sur la distribution spatiale des espèces (Shaffer *et al.*, 1998; Shoo *et al.*, 2006; Tingley & Beissinger, 2009). En particulier, suite à l'implémentation ces dernières décennies de politiques environnementales pour la protection et la gestion des milieux aquatiques (e.g. Directive cadre sur l'eau), des chroniques long-terme de suivis des organismes aquatiques d'eau douce sont maintenant disponibles. Cependant, ces données n'ayant pas été collectées dans le but explicite de détecter des modifications de distributions spatiales, il convient de leur appliquer une méthodologie adaptée afin d'éviter des biais d'échantillonnage potentiels (détaillé dans Partie II).

1- Les données piscicoles

Le programme de suivis des populations de poissons d'eau douce est assuré en France par l'Onema (Office National de l'Eau et des Milieux Aquatiques), qui a pour but de préserver la qualité de l'eau et le bon état écologique des systèmes aquatiques.

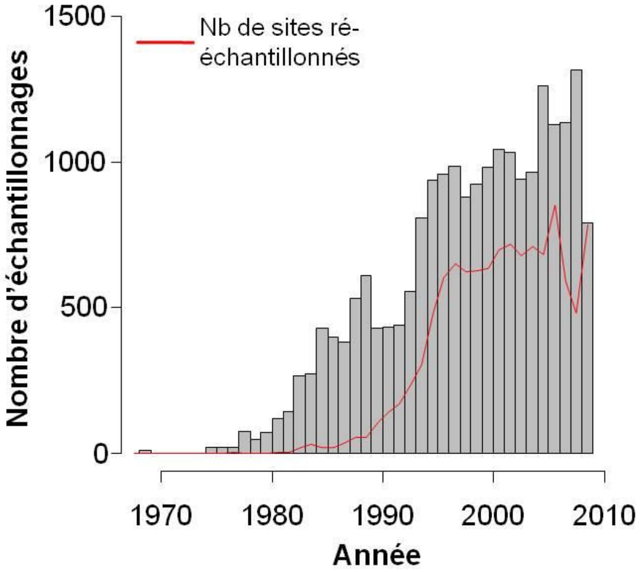


Figure 10 : Evolution du nombre d'échantillonnages et du nombre de sites ré-échantillonnés au cours du temps.

Les données ayant permis la réalisation de cette thèse ont été extraites depuis la Banque de Données Milieux Aquatiques et Poissons (BDMAP), et comprennent des échantillonnages spatialement et temporellement extensifs des assemblages de poissons d'eau douce à l'échelle nationale : 9014 stations échantillonnées et 21395 pêches réalisées à l'échelle de la France sur la période 1968-2009 (Figure 10). Les sites d'échantillonnages correspondent à des sections de cours d'eau où les échantillonnages sont réalisés suivant un protocole de pêche électrique standardisé durant les périodes de basses eaux (essentiellement de mai à octobre). Plusieurs procédures sont utilisées en fonction de la profondeur et de la largeur du cours d'eau. Les rivières peu profondes sont échantillonnées à pied, avec un seul ou plusieurs passages, et les rivières plus larges en bateau ou par des méthodes de prospection combinées (i.e. en bateau plus à pied), en général au moyen d'un seul passage. Différentes stratégies d'échantillonnage sont également employées, et impliquent soit une prospection complète de la section du cours d'eau, soit une prospection partielle des différents mésohabitats présents, ou des sections attenantes aux berges et d'autres aires délimitées de l'habitat (Belliard *et al.*, 2008; Poulet *et al.*, 2011). Cependant, différentes méthodes ont été successivement employées jusqu'en 1995 où un protocole d'échantillonnage unifié a été mis en place.

Pour répondre aux objectifs de cette thèse, 35 espèces ont été considérées dans la comparaison de méthodes statistiques ($\boldsymbol{P_{II}}$), alors que les changements de distributions ont été analysés pour 32 espèces ($\boldsymbol{P_{III}}$, $\boldsymbol{P_{IV}}$, $\boldsymbol{P_{V}}$) (Tableau 1).

Tableau 1 : Liste des espèces étudiées.

Espèce	Famille	Nom vernaculaire	P_{II}	P_{III}, P_{IV}, P_{V}
Abramis brama	Cyprinidae	Brème commune	●	●
Alburnoides bipunctatus	Cyprinidae	Spirlin	●	●
Alburnus alburnus	Cyprinidae	Ablette	●	●
Ameiurus melas	Ictaluridae	Poisson chat	●	●
Anguilla anguilla	Anguillidae	Anguille	●	●
Barbatula barbatula	Balitoridae	Loche franche	●	●
Barbus barbus	Cyprinidae	Barbeau fluviatile	●	●
Barbus meridionalis	Cyprinidae	Barbeau méridional		●
Blicca bjoerkna	Cyprinidae	Brème bordelière	●	●
Carassius carassius	Cyprinidae	Carassin	●	
Chondrostoma nasus	Cyprinidae	Hotu	●	●
Cobitis taenia	Cobitidae	Loche de rivière	●	
Cottus gobio	Cottidae	Chabot	●	●
Cyprinus carpio	Cyprinidae	Carpe commune	●	●
Esox lucius	Esocidae	Brochet	●	●
Gasterosteus aculeatus	Gasterosteidae	Epinoche	●	●
Gobio gobio	Cyprinidae	Goujon	●	●
Gymnocephalus cernua	Percidae	Grémille	●	●
Lepomis gibbosus	Percidae	Perche soleil	●	●
Leuciscus leuciscus	Cyprinidae	Vandoise	●	●
Lota lota	Lotidae	Lotte de rivière		●
Micropterus salmoides	Centrarchidae	Black-bass à grande bouche	●	
Parachondrostoma toxostoma	Cyprinidae	Toxostome	●	●
Perca fluviatilis	Percidae	Perche	●	●
Phoxinus phoxinus	Cyprinidae	Vairon	●	●
Pseudorasbora parva	Cyprinidae	Pseudorasbora	●	
Pungitius pungitius	Gasterosteidae	Epinochette	●	●
Rhodeus amarus	Cyprinidae	Bouvière	●	
Rutilus rutilus	Cyprinidae	Gardon	●	●
Salmo salar	Salmonidae	Saumon atlantique	●	●
Salmo trutta	Salmonidae	Truite	●	●
Sander lucioperca	Percidae	Sandre	●	●
Scardinius erythrophthalmus	Cyprinidae	Rotangle	●	●
Silurus glanis	Siluridae	Silure glane	●	
Squalius cephalus	Cyprinidae	Chevesne	●	●
Telestes souffia	Cyprinidae	Blageon	●	●
Thymallus thymallus	Salmonidae	Ombre commun		●
Tinca tinca	Cyprinidae	Tanche	●	●

2- Les données environnementales

2.1- Le réseau hydrographique

Tout au long de cette thèse, les distributions spatiales ont été considérées à l'échelle du réseau hydrographique français. Ce dernier, extrait de la base de données CCM2 (Catchment Characterisation and Modelling River and Catchment ; Vogt *et al.*, 2007) décrivant le réseau hydrographique européen, est constitué pour la France de plus de 100 000 segments (2 km de long en moyenne) comportant des informations sur les caractéristiques morphologiques et topographiques des bassins versants.

Plusieurs variables environnementales, fortement reliées à la distribution spatiale des poissons d'eau douce (Buisson et al., 2008), ont ensuite été sélectionnées pour décrire les conditions climatiques et d'habitat présentes au sein du réseau hydrographique français. Ces variables ont été extraites sous Système d'Information Géographique (SIG) à partir des coordonnées des segments du réseau hydrographique ou calculées à partir des données extraites.

2.2- Les caractéristiques de l'habitat

L'altitude (m) a été extraite à partir d'un modèle numérique de terrain à une résolution de 50m, et la pente (‰) à partir du Réseau Hydrographique Théorique (RHT, Pella *et al.*, 2012). Les variables décrivant la position des segments au sein des bassins versants proviennent de CCM2 : la superficie du bassin drainé en amont du segment (km²) et la longueur de réseau cumulée en amont du segment (m). Ces deux variables ont été réduites en une seule variable synthétique en utilisant une Analyse en Composante Principale (ACP) décrivant le gradient amont-aval. La distance à la source (km) a également été calculée afin de caractériser les déplacements des espèces le long du gradient longitudinal.

2.3- Les caractéristiques climatiques

Plusieurs variables bioclimatiques de températures et de précipitations ont été calculées à partir de deux sources différentes :

- Des moyennes de températures et de précipitations durant la période 1961-1990 issues de couches WorldClim à une résolution de 30-arc-s (Hijmans, 2012).

- Des données journalières de températures et de précipitations durant la période 1968-2008 issues des données SAFRAN à une résolution de 8 km (Méto-France ; Le Moigne, 2002).

3- Les caractéristiques des espèces

3.1- Phylogénie

Pour les analyses phylogénétiques, une phylogénie reconstruite à partir de données moléculaires extraites de *GenBank* basée sur trois gènes mitochondriaux a été utilisée (décrite dans Grenouillet *et al.*, 2011; Encadré 4).

3.2- Traits

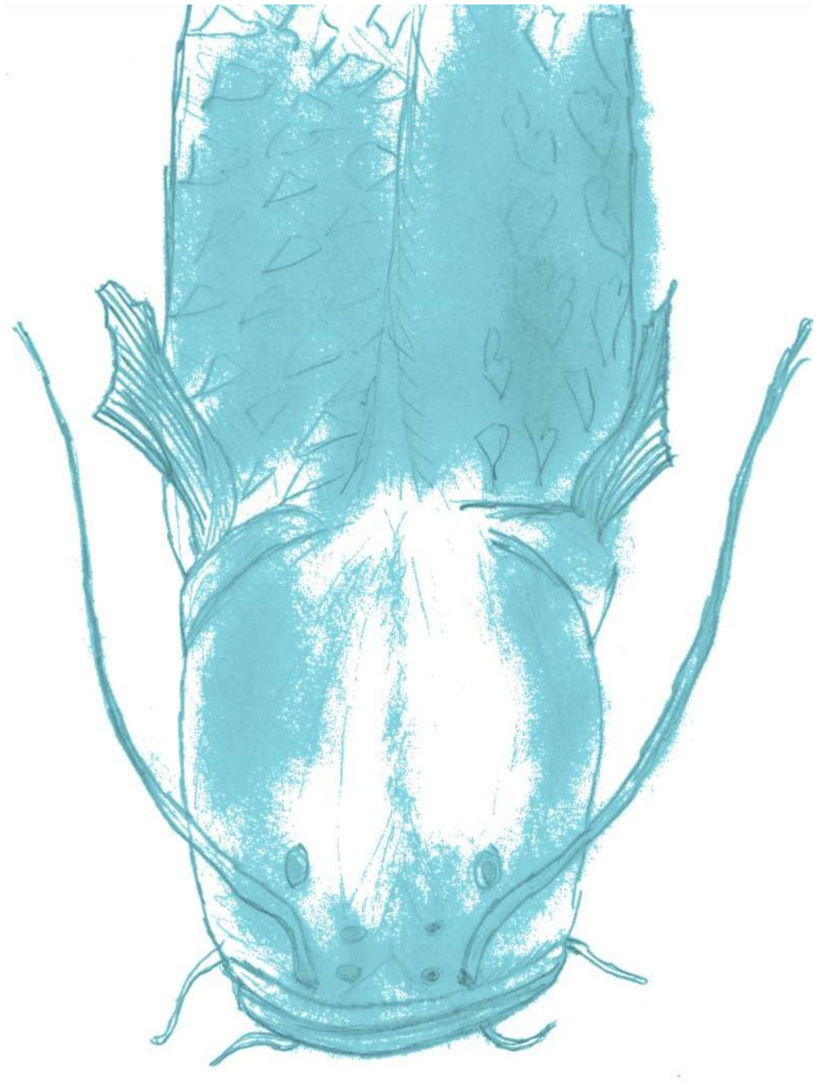
Pour identifier les caractéristiques intrinsèques de la vulnérabilité des espèces ($\boldsymbol{P_{IV}}$, $\boldsymbol{P_{V}}$), différents traits ont été considérés, principalement collectés dans la littérature (voir Supplementary information $\boldsymbol{P_{IV}}$, $\boldsymbol{P_{V}}$). Les traits ont été utilisés tels quel ou synthétisés par des axes issus d'Analyses en Coordonnées Principales (PCoA ; Gower, 1966) pour s'affranchir des problèmes de colinéarité.

- *Tolérance thermique* : la limite supérieure de la gamme de température optimale définie comme la gamme au sein de laquelle aucun signe de comportement anormal ne se produit, et la température optimale de ponte.
- *Position trophique* : classée des herbivores aux piscivores
- *Mobilité* : la mobilité larvaire et adulte obtenues à partir d'une PCoA basée sur 4 traits morphologiques.
- *Pression de propagule* : la durée du cycle de vie et la position de l'espèce le long du continuum r-K obtenues à partir d'une PCoA basée sur 7 traits d'histoire de vie.
- *Largeur de niche* : la tolérance environnementale calculée comme l'espace environnemental, incluant l'altitude, la pente, et la position le long du gradient amont-aval, utilisé par chaque espèce le long des axes principaux d'une analyse OMI (Outlying Mean Index, Doledec *et al.*, 2000).
- *Taille de la distribution :* exprimée en pourcentage du réseau hydrographique occupé par l'espèce.
- *Préférence altitudinale :* calculée d'après une classification hiérarchique basée sur différents descripteurs de la distribution des espèces le long du gradient altitudinal.

Toutes les analyses et les étapes de modélisation ont été effectuées à l'aide du logiciel R (R Development Core Team, 2011).

PARTIE I

Les changements de distribution récents



“Remember that all models are wrong; the practical question is how wrong do they have to be to not be useful.”

Box & Draper (1987)

1- Détecter des changements de distribution : quelles méthodes ?

Différentes approches ont été utilisées dans la littérature pour documenter des changements de distribution, basées principalement sur la comparaison de données de présence-absence entre une période historique et une période contemporaine :

- *Sites comme effet fixe* (Shaffer *et al.*, 1998)
  Impliquant le ré-échantillonnage d'un faible nombre de sites, généralement le long de gradients climatiques (e.g. transects altitudinaux : Chen *et al.*, 2010)
- *Sites comme effet aléatoire* (Shaffer *et al.*, 1998)
  Impliquant l'utilisation de données non-appareillées, venant principalement de données d'atlas mais présentant une couverture spatiale plus étendue (e.g. grille couvrant la Grande Bretagne : Hickling *et al.*, 2006).

Ces deux approches comprennent chacune leurs propres sources d'incertitude, qu'il convient de prendre en compte lors de l'interprétation des changements de distribution observés au cours du temps (Shaffer *et al.*, 1998). En effet, la comparaison entre données historiques et contemporaines présente généralement des biais inhérents plus importants que la comparaison de données collectées au sein d'une même période d'échantillonnage (Tingley & Beissinger, 2009). En particulier, la première approche repose sur le postulat que les données collectées sont directement comparables, et que les changements observés peuvent être attribués sans ambiguïté à des changements de distribution plutôt qu'à des changements d'abondances locales (Parmesan, 2006; Shoo *et al.*, 2006). Par ailleurs, l'étendue de la zone prospectée peut présenter d'importants biais environnementaux ou spatiaux, et ainsi procurer une vision incomplète de la distribution spatiale des espèces mais également de leur niche réalisée (Hortal *et al.*, 2008). Alors que la deuxième approche permet de surmonter ces difficultés en étendant l'échelle spatiale d'étude, elle requiert néanmoins un effort d'échantillonnage comparable entre les deux périodes temporelles, ce qui implique généralement des compromis entre la résolution et le niveau d'inférence de l'analyse (Shaffer *et al.*, 1998; Shoo *et al.*, 2006). Finalement, une source d'erreur potentielle, bien que souvent ignorée, vient de détectabilités variables des espèces suite à des changements de protocoles d'échantillonnages au cours du temps, qui peuvent venir simuler ou au contraire masquer des changements de distribution lors de comparaisons 'naïves' entre données historiques et contemporaines, et ce quel que soit le type d'approche utilisé (Tingley & Beissinger, 2009).

Dans cette thèse, les changements de distribution ont été inférés à partir de la comparaison de deux jeux de données non appareillés distribués à l'échelle de la France, entre deux périodes soumises à des régimes climatiques contrastés, la majorité des sites n'ayant pas été ré-échantillonnés avant la mise en place du Réseau Hydrobiologique et Piscicole (RHP) en 1995 (Figure 10).

La définition de ces deux périodes s'est basée sur trois critères de sélection :

(1) Les deux périodes doivent être suffisamment espacées dans le temps pour permettre de tester les effets de modifications climatiques.

(2) Chaque période doit être suffisamment courte pour permettre de décrire la distribution des espèces de poisson à un instant donné.

(3) Le nombre de sites pour chaque période doit être suffisant pour permettre une bonne couverture géographique du territoire et une bonne représentativité des conditions environnementales rencontrées à l'échelle du réseau hydrographique français.

Ainsi, ces critères nous ont amené à définir les deux périodes suivantes (Figure 11) :

- Une période ‘ancienne’ relativement froide : de 1980 à 1992, 3549 stations échantillonnées.
- Une période ‘récente’ relativement chaude : de 2003 à 2009, 3543 stations échantillonnées.

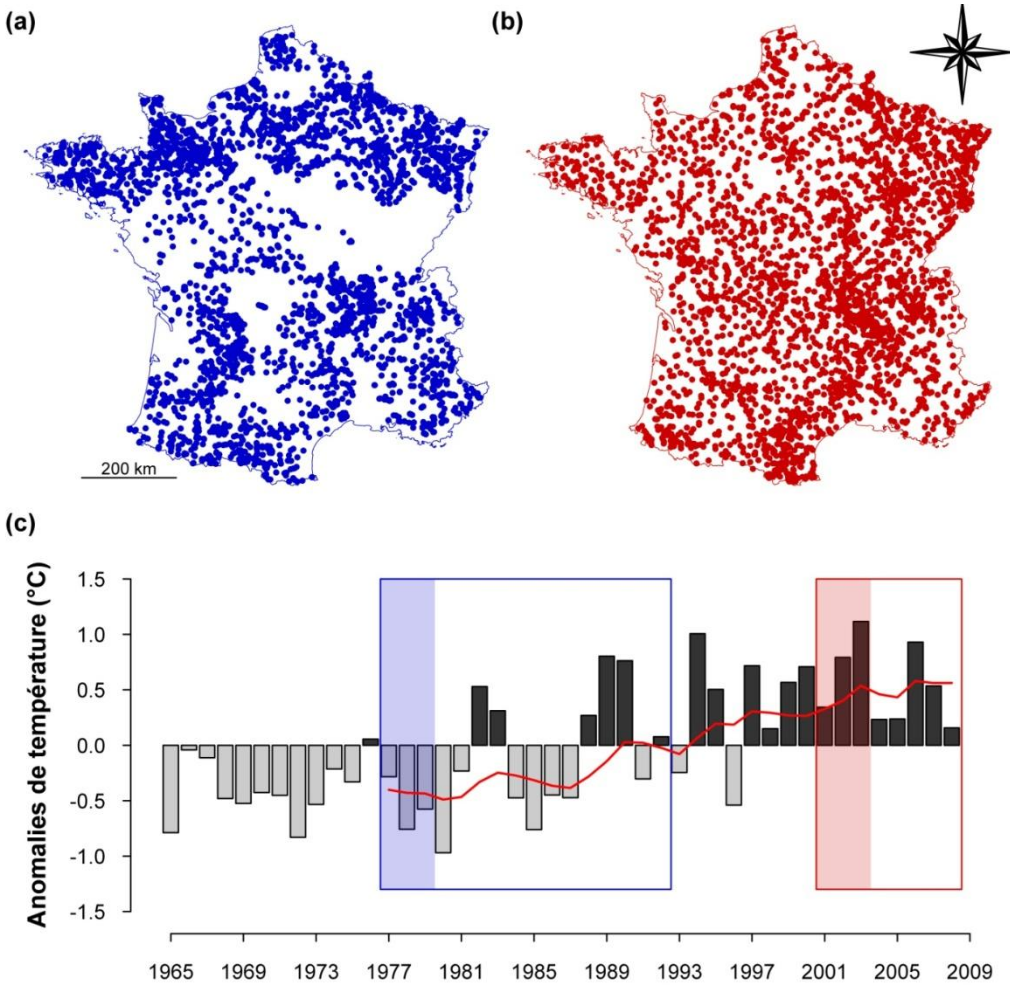


Figure 11 : Cartes représentant la position spatiale des sites sélectionnés pour détecter des changements de distribution entre (a) une période ‘ancienne’ et (b) une période ‘récente’ ; (c) anomalies de la température moyenne annuelle de 1965 à 2008 calculée à partir des données SAFRAN où la ligne rouge indique la moyenne mobile avec une fenêtre de 10 ans. Les rectangles font référence à la durée de chacune des périodes, en incluant les trois années précédentes (correspondant au cycle de vie moyen des espèces). La période initiale est composée majoritairement d’année ‘froides’ alors que la période contemporaine est constituée uniquement d’années ‘chaudes’. (Modifiée d’après $\boldsymbol{P}_{\boldsymbol{III}}$, Figure 1, S1)

1.1- Modélisation des distributions

Afin de surmonter le problème lié à la comparaison de données non-appariées, une approche couramment employée est l'utilisation de modèles de distribution d'espèces (*species distribution models,* SDMs). Ces méthodes, basées sur les relations corrélatives entre la présence de l'espèce et des variables environnementales, permettent de modéliser la distribution spatiale des espèces sur des zones géographiques plus étendues que les sites d'échantillonnage (Guisan & Zimmermann, 2000), et ainsi de détecter des changements potentiel des gammes de distribution par comparaison des relations établies entre l'espèce et son environnement (Crimmins *et al.*, 2011; Maggini *et al.*, 2011).

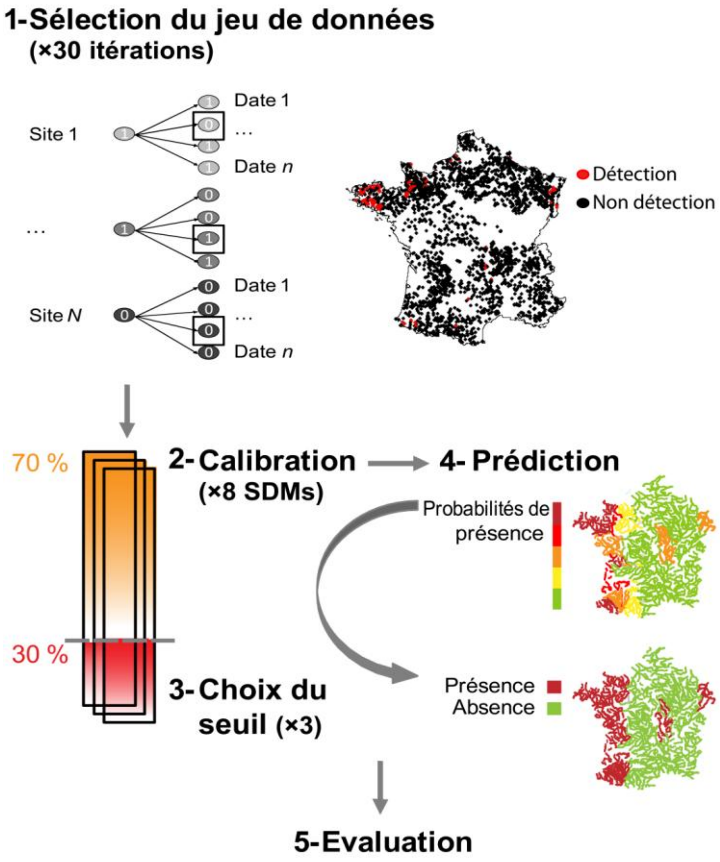
Encadré 1 : Méthodes statistiques utilisées dans l'approche consensuelle pour modéliser la distribution des espèces de poissons.

- **ANN** : basés sur des combinaisons pondérées de manière optimale et non linéaire des variables explicatives pour parfaire la prédiction de la réponse. Ici, le perceptron multicouche avec algorithme de rétropropagation a été utilisé.
- **CART** : méthode de classification non paramétrique basée sur un partitionnement récursif binaire des données en groupes homogènes de plus en plus petits.
- **GAM** : extensions non-paramétriques des GLM utilisant des fonctions de lissage non-linéaires.
- **GBT** : méthode basée sur la construction de séquences d'arbres de décision en combinant un algorithme de «boosting» et un algorithme d'arbre de régression.
- **GLM** : extensions des modèles linéaires capables de modéliser différentes formes de distribution en ajustant des termes paramétriques (ici, distribution binomiale).
- **MARS** : méthode d'ajustement adaptatif par régression non linéaire, basée sur un partitionnement des données en sous-groupes pour lesquels un ajustement local par lissage est effectué.
- **MDA** : méthode basée sur la construction de combinaisons des prédicteurs qui discriminent au mieux les groupes pré-définis (ici, les présences et absences).
- **RF** : méthode basée sur la construction d'un très grand nombre d'arbres de classification de façon aléatoire (tirage aléatoire des observations et des prédicteurs), qui sont ensuite agrégés par moyenne.

Cependant, alors que la plupart des études reposent sur l'analyse de courbes de réponse des espèces le long d'un gradient spatial unique (altitude : Lenoir *et al.,* 2008; e.g. latitude : Crimmins *et al.,* 2011; Maggini *et al.*, 2011), cette approche ne semblait pas adaptée aux poissons d'eau douce dont les distributions spatiales sont clairement influencées par une multitude de facteurs qui varient le long du réseau hydrographique (Matthews, 1998). Les distributions spatiales ont donc été modélisées en incorporant plusieurs variables climatiques et topographiques connues pour être fortement reliées à la distribution spatiale des espèces étudiées (voir Partie I : Données environnementales). Pour ce faire, des approches consensuelles intégrant la variabilité issue de différents choix méthodologiques ont été utilisées (Encadré 1). Par ailleurs, afin de prendre en compte la structure spatiale des rivières, les distributions spatiales ont été projetées non pas sur des mailles régulières couvrant le territoire comme couramment employés pour d'autres types d'organismes (e.g. Hill *et al.*, 2002), mais à l’échelle du réseau hydrographique français (voir Encadré 2 pour la description des différentes étapes du processus de modélisation).

Encadré 2 : Différentes étapes du processus de modélisation des distributions spatiales conduites indépendamment pour chacune des périodes et des espèces étudiées en utilisant une approche consensuelle.

La première étape consiste à sélectionner aléatoirement un événement de détection ou de non-détection de l’espèce pour chacun des sites d’étude, et ce afin d’éviter la pseudo-réplication (i.e. la non-indépendance des observations). La calibration est alors conduite sur 70% du jeu de données choisis aléatoirement, alors que le choix des seuils (selon trois méthodes différentes) et l’évaluation des performances prédictives se font sur les 30% restants. Les modèles calibrés sont alors utilisés pour modéliser la distribution de l’espèce sur les tronçons hydrographiques dont les caractéristiques environnementales sont comparables à celle des sites d’études. Les probabilités de présence sont obtenues en moyennant les prédictions issues des huit méthodes statiques (Marmion *et al.*, 2009), qui sont ensuite converties en présences-absences en utilisant les seuils précédemment identifiés (Liu *et al.*, 2005). Ces différentes étapes sont alors réitérées 30 fois, conduisant à l’obtention de 90 cartes de distribution par espèce pour chacune des périodes. Les prédictions sont alors agrégées, permettant ainsi de visualiser les zones d’agrément ou d’incertitudes issues des différents choix méthodologiques.

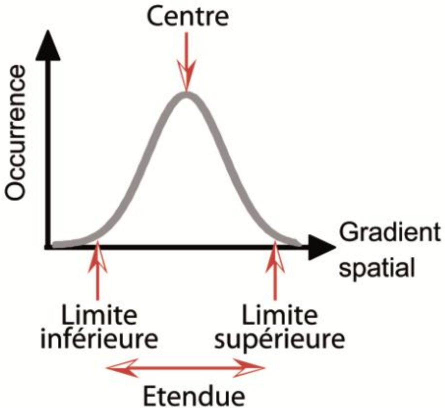


Le régime thermique des rivières dépendant principalement de leur position altitudinale et longitudinale au sein du bassin versant (Cassie, 2006), il a ainsi été possible de décrire des changements de distribution en lien avec les changements climatiques récents le long de gradients altitudinaux et longitudinaux (i.e. distance à la source) en utilisant plusieurs descripteurs (Encadré 3) (***P*$_{III}$**).

Encadré 3 : Description des patrons de distribution spatiale des espèces.

Le point de départ de n'importe quelle étude abordant la distribution spatiale d'une espèce repose sur la caractérisation précise des limites de distribution de cette dernière sur une carte (Holt & Keitt, 2005). A partir de la distribution le long du gradient des valeurs où l'espèce est présente (e.g. Zuckerberg *et al.*, 2009), il est possible de décrire la répartition spatiale de l'espèce à l'aide de différents descripteurs simples :

- Le **centre de la distribution** correspond à la valeur centrale (médiane) de la distribution.
- La **limite inférieure** correspond à la valeur en dessous de laquelle 2.5% des présences sont observées.
- La **limite supérieure** correspond à la valeur au dessus de laquelle 2.5% des présences sont observées
- L'**étendue** correspond à l'intervalle compris entre les deux limites.



1.2- La qualité des données : le problème de la détection imparfaite

Documenter les effets des changements climatiques requiert des analyses quantitatives capables de distinguer l'influence de ces derniers du bruit présent dans les données (Tingley & Beissinger, 2009; Brown *et al.*, 2011). Or, la fiabilité des distribution modélisées dépend de nombreux facteurs d'incertitude, incluant la qualité des données biologiques (Graham *et al.*, 1996), les décisions méthodologiques (Buisson *et al.*, 2010; Nenzén & Araùjo, 2011), et en particulier le choix de la méthode statistique (Thuiller, 2003; Thuiller, 2004). Ces dernières années, les méthodes consensuelles, en combinant un ensemble de prédictions provenant de différentes méthodes statistiques, ont démontré leur capacité à intégrer le problème inhérent à la variabilité entre prédictions, augmentant ainsi la capacité prédictive des modèles pris isolément (Marmion *et al.*, 2009; Grenouillet *et al.*, 2011).

Cependant, comme précédemment souligné, les incertitudes dues aux fausses absences résultant de détection 'imparfaite' peuvent être un problème fondamental dans l'estimation de la distribution spatiale d'une espèce, et plus encore dans la détection de changements de cette dernière au cours du temps (Tingley & Beissinger, 2009; Kéry, 2012). Pourtant, alors que les question d'incertitudes et d'erreurs issues des modèles de distribution d'espèces reçoivent une attention croissante (Grenouillet *et al.*, 2011; Hanspach *et al.*, 2011; Rocchini *et al.*, 2011), les conséquences liées à la détection imparfaite restent encore peu abordées (Kéry, 2012). Une fausse absence est le résultat d'une espèce considérée comme absente sur un site d'étude alors qu'elle était en réalité présente mais qui n'a pas été détectée lors de l'échantillonnage. Or, à l'heure actuelle, la majorité des méthodes statistiques utilisées, parmi lesquelles les méthodes consensuelles (e.g. BIOMOD, Thuiller, 2003), ignorent les problèmes de détection des espèces, et considèrent donc implicitement que la chance de détecter une espèce présente à un site donné est de 100%. Etant donné que la détection des espèces est généralement loin d'être parfaite, en particulier pour les espèces rares (MacKenzie *et al.*, 2002; Kéry & Plattner, 2007; Gibson, 2011; Meyer *et al.*, 2011), ce postulat peut avoir des conséquences importantes sur les performances des modèles (Rota *et al.*, 2011), et introduire des biais dans les relations établies entre l'espèce et son environnement (Tyre *et al.*, 2003; Gu & Swihart, 2004).

Les méthodes dites 'occupancy' ont été proposées il y a quelques années, indépendamment par MacKenzie *et al.* (2002) et Tyre *et al.* (2003), pour palier à ce problème. Basées sur la réplication des observations, ces méthodes prennent en compte de manière explicite la détectabilité des espèces en modélisant de manière imbriquée les événements d'occurrence (présence ou absence de l'espèce) et de détection (détection ou non-détection sachant que l'espèce était présente). Bien que leur potentiel ait été sous-exploité en raison de la difficulté à obtenir les données adéquates (impliquant la réplication des échantillonnages dans le temps et dans l'espace), ces modèles ont récemment eu un regain de popularité pour estimer les impacts des changements climatiques sur la distribution spatiale des espèces (Altwegg *et al.*, 2008; Moritz *et al.*, 2008; Tingley *et al.*, 2009; Tingley *et al.*, 2012). Cependant, l'évaluation des bénéfices apportés par ces méthodes par rapport à des méthodes 'conventionnelles' ne prenant pas en compte les problèmes de détection a rarement été menée (Kéry *et al.*, 2010; Lobo *et al.*, 2010; Rota *et al.*, 2011), et jamais par rapport à des méthodes consensuelles. Nous avons donc investigué l'influence que les fausses absences pouvaient avoir sur notre capacité à modéliser la distribution des espèces en confrontant deux approches statistiques différentes : une approche prenant en compte de manière explicite les problèmes de détection (modèles 'occupancy') et une approche consensuelle basée sur huit méthodes statistiques ne les prenant pas en compte (modèles 'consensus') ($\boldsymbol{P_{II}}$). Plus spécifiquement, nous avons comparé les performances prédictives ainsi que les aires de répartition modélisées avec des modèles 'consensus' et 'occupancy' pour 35 espèces de poissons présentant des degrés de détectabilité variables pour la période 2007 – 2009.

2- La détection imparfaite : quelles conséquences ?

La comparaison des méthodes statistiques prenant ou non en compte la détection des espèces ($\boldsymbol{P_{II}}$) nous a permis en premier lieu d'établir que les modèles 'occupancy' n'apportaient pas toujours des bénéfices conséquents pour modéliser la distribution spatiale des espèces (Figure 12). En effet, par rapport à des méthodes consensuelles, l'utilisation de modèles 'occupancy' améliorait peu les performances prédictives pour les espèces mal détectées, et au contraire conduisait à une réduction des performances pour les espèces bien détectées. Néanmoins, comparés à des méthodes conventionnelles 'simples', tels que les GLM, les modèles 'occupancy' produisaient de meilleurs résultats, démontrant ainsi, en accord avec les études précédentes, l'utilité de ce type d'approche pour modéliser la *vraie* plutôt que l'*apparente* distribution d'une espèce (Kéry *et al.*, 2010; Rota *et al.*, 2011). D'un autre côté, malgré les faibles différences de performances prédictives existant entre les méthodes consensuelles et 'occupancy', il est apparu que les distributions spatiales étaient affectées de manière importante par le choix du modèle (Figure 13). Alors que ces résultats soulèvent des interrogations quant à la validité des mesures de performances couramment employées (Lobo, 2008; Lobo *et al.*, 2010), ils semblent également indiquer que les approches consensuelles, en combinant plusieurs facettes de la distribution d'une espèce capturées par les différents algorithmes (Marmion *et al.*, 2009), permettraient de compenser, au moins partiellement, la perte d'information dans les données due aux fausses absences. De cette manière, la *vraie* distribution des espèces pourrait être une combinaison des prédictions issues des modèles 'occupancy' et celles issues des modèles 'consensus', chaque méthode présentant des avantages et des inconvénients.

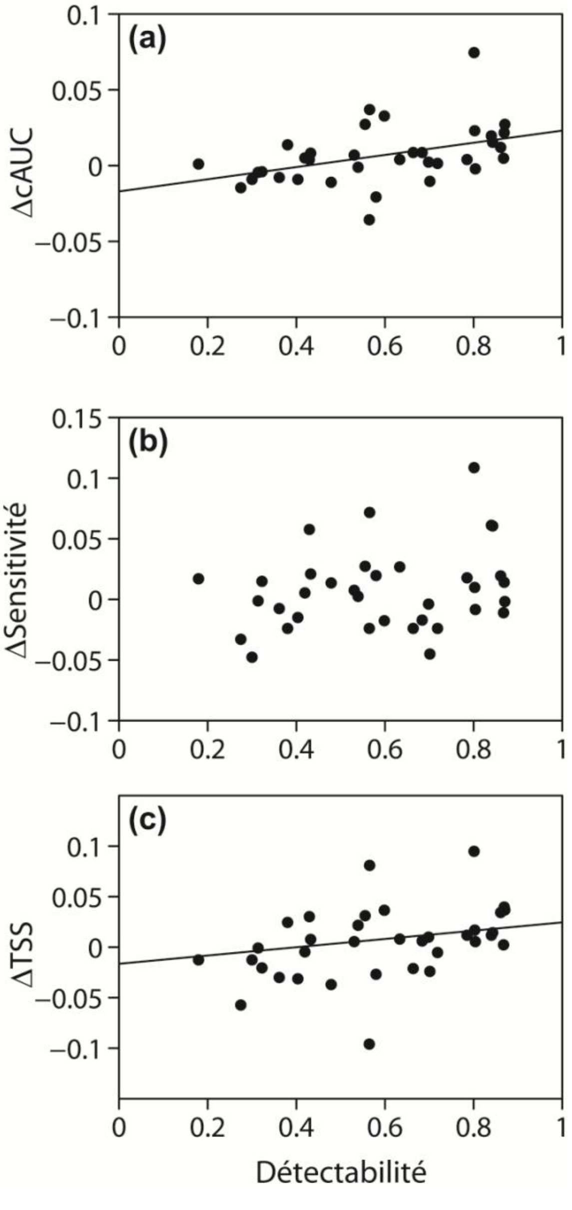


Figure 12 : Effet de la détectabilité des espèces sur les différences de performances prédictives entre les modèles consensus et occupancy (CONS – OCCU) : (a) cAUC, (b) sensitivité et (c) TSS. Les lignes indiquent des relations linéaires significatives ($p < 0.05$). (Modifiée d'après $\boldsymbol{P_{II}}$, Figure 2)

Concernant la poursuite des analyses, les résultats de cette étude ont permis d'établir que malgré le fait que les méthodes 'occupancy' soient une voie de modélisation attractive, les méthodes consensuelles présentaient un compromis acceptable entre les données disponibles et le niveau de fiabilité des prédictions, en particulier pour les espèces bien détectées. Au-delà de considérations méthodologiques, ces résultats ont également permis de démontrer que les problèmes inhérents à la qualité des données peuvent donner lieu à des incertitudes importantes dans l'estimation de la position d'une espèce le long d'un gradient spatial. Etant donné que cette variabilité pourrait être de la même magnitude que les changements de distribution attribués aux changements climatiques récents (Lenoir *et al.*, 2008; Moritz *et al.*, 2008; Crimmins *et al.*, 2011), il a donc semblé primordial d'accorder une attention particulière à d'éventuels changements de détection ayant eu lieu au cours de la période d'étude visant à détecter d'éventuelles modifications de répartition des espèces de poissons, sachant de surcroit que les protocoles d'échantillonnages avaient évolué au cours des dernières décennies.

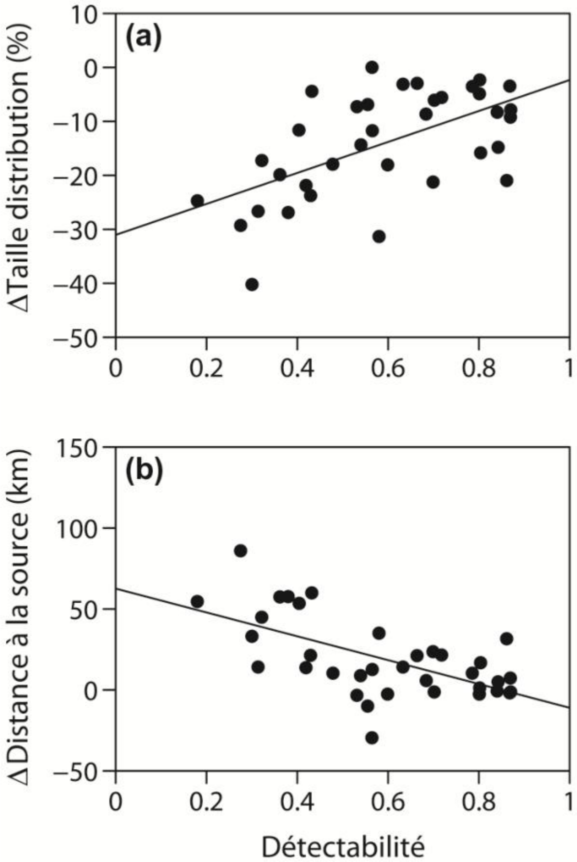


Figure 13 : Effet de la détectabilité des espèces sur les différences (a) de la taille de la distribution et (b) de la position du centre de la distribution le long de la distance à la source entre les modèles consensus et occupancy (CONS – OCCU). Les lignes indiquent des relations linéaires significatives ($p < 0.05$). (Modifiée d'après $\boldsymbol{P_{II}}$, Figure 4)

De ce fait, en marge des analyses visant à détecter des changements de distributions, nous avons cherché à déterminer si les succès de capture et la détectabilité des espèces avaient variés entre la période 'ancienne' et la période 'récente' ($\boldsymbol{P_{III}}$). Il est apparu que la méthode d'échantillonnage avait eu un effet significatif sur le nombre d'espèces détectées lors des échantillonnages, les succès de capture en bateau (i.e. dans les cours d'eau les plus larges) ayant augmenté au cours du temps. Cela a eu pour conséquence d'accroitre la détection des espèces dans les zones les plus à l'aval (>200 km de la source), alors qu'aucune relation n'a été trouvée avec l'altitude. Des différences de détectabilité ont également été mises en évidence pour plusieurs espèces, mais d'une ampleur relativement faible (moyenne = 0.05).

Par ailleurs ces différences n'avaient pas de lien avec les variations de performances prédictives entre les périodes d'étude ($p > 0.05$), ce qui semblait indiquer qu'elles étaient plus à même de refléter l'augmentation d'abondance de certaines espèces précédemment documentées dans certains fleuves français (Daufresne & Boët, 2007; Poulet *et al.*, 2011), plutôt que de réels biais d'échantillonnage.

3- Assemblages des poissons de rivières françaises : quels changements ?

L'analyse des patrons de distribution spatiale des 32 espèces de poissons de rivière les plus communes entre la période 'ancienne' (1980-1992) et la période 'récente' (2003-2009) (***P***P_{III}) ont permis de mettre en évidence des changements marqués pour la majorité des espèces. Cependant, des modifications contrastées ont été observées entre les différentes espèces, certaines présentant des changements au sein de toute leur aire de répartition (Figure 14), alors que d'autres présentent des changements nettement plus spatialisés, et ce qu'il s'agisse de gain ou de perte d'habitat (Figure 15).

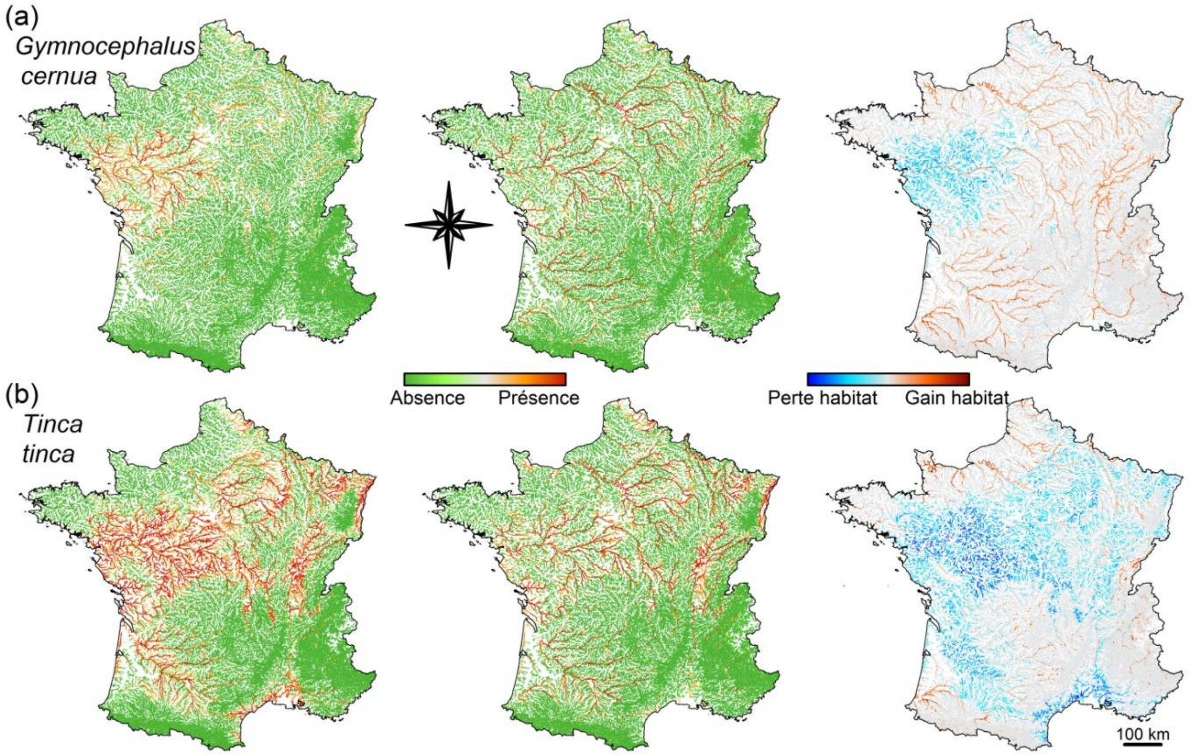


Figure 14 : Cartes montrant des exemples de changements de distribution (panel de droite) entre une période 'froide' (panel de gauche) et une période 'chaude' (panel du milieu) pour (a) une espèce dont la distribution s'est étendue, (b) une espèce dont la distribution s'est contractée.

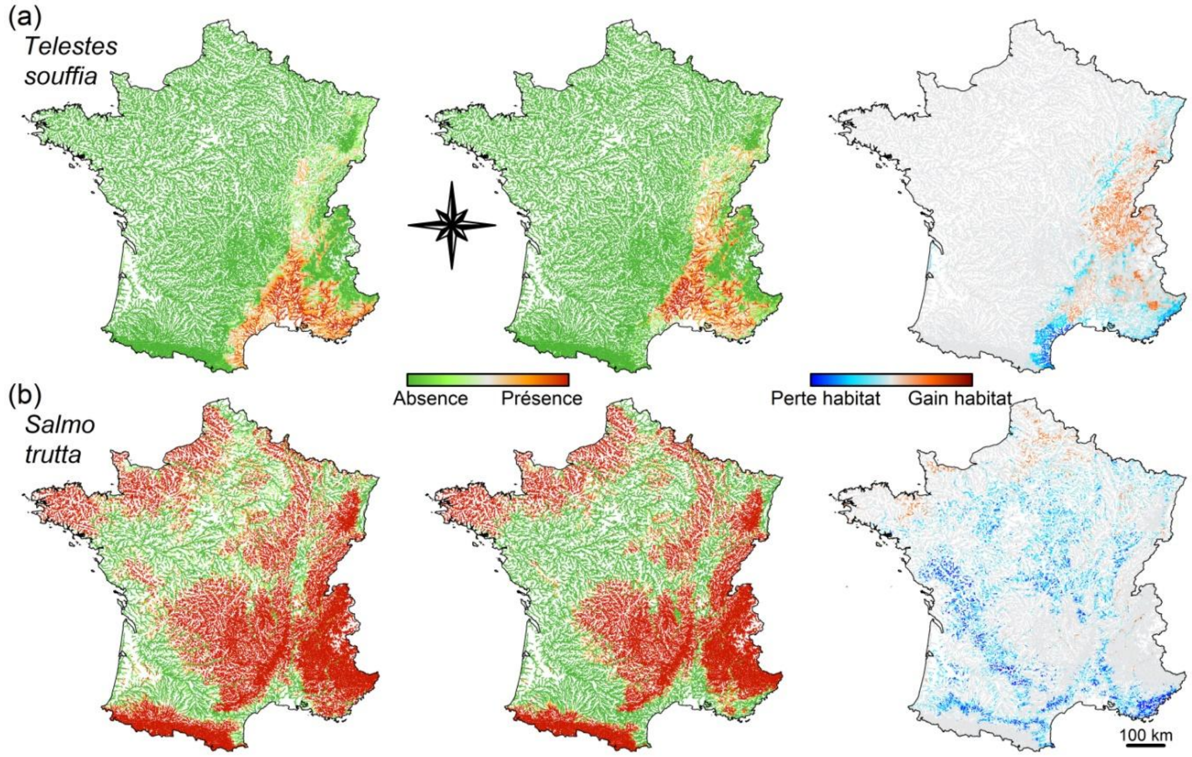


Figure 15 : Cartes montrant des exemples de changements de distribution (panel de droite) entre une période ‘froide’ (panel de gauche) et une période ‘chaude’ (panel du milieu) pour deux espèces présentant des patrons de remontée en altitudes contrastés.

Par exemple, alors que la grémille (*Gymnocephalus cernua*) semble être maintenant beaucoup plus commune dans la majorité des grands cours d’eau français qu’elle ne l’était il y a 20 ans, la tanche (*Tinca tinca*) semble au contraire être en nette régression au sein de tout le territoire français (Figure 14), des observations corroborées par l’analyse de tendances temporelles issues d’autre études (Daufresne & Boët, 2007; Poulet *et al.*, 2011). En comparaison, la truite (*Salmo trutta*) semble avoir subi des nets déclins aux marges de sa distribution initiale, correspondant à des zones de faibles altitudes (Figure 15a), un phénomène précédemment décrit pour cette espèce en Espagne et en Suisse (Hari *et al.*, 2006; Almodóvar *et al.*, 2012). Enfin, d’autres espèces présentent des patrons de changements plus complexes, comme le blageon (*Telestes souffia*), qui semble être en régression dans le sud de la France, et notamment dans les bassins côtiers méditerranéens, mais en expansion dans le haut du bassin du Rhône (Figure 15b). Ainsi, sur les 32 espèces étudiées, 12 montrent des réductions de leur aire de distribution, alors que 20 montrent des augmentations, les changements allant de -28.2% de leur distribution initiale à +58.1% (moyenne = +10.4% ± 0.19SD).

Malgré leur diversité, ces changements se traduisent par une remontée cohérente de la majorité des espèces le long des gradients altitudinaux et longitudinaux, en accord avec la réponse attendue des espèces aux changements climatiques récents (Figure 16). De manière générale, les espèces semblent avoir subi des changements plus importants à la limite de leur distribution qu'en leur sein, où les populations pourraient être plus stables et résistantes aux modifications environnementales (Brown *et al.*, 1996). Cela se traduit donc non pas par des déplacements complets de leur distribution mais plutôt par des remontées asymétriques d'une des limites. Alors que ce résultat indique que deux mécanismes différents pourraient être impliqués aux deux extrêmes de la distribution, il pourrait également avoir des répercussions importantes en termes de conservation des espèces, et en particulier pour l'identification des zones où les mesures de gestion devraient prioritairement être dirigées (Hannah *et al.*, 2007; Anderson *et al.*, 2009).

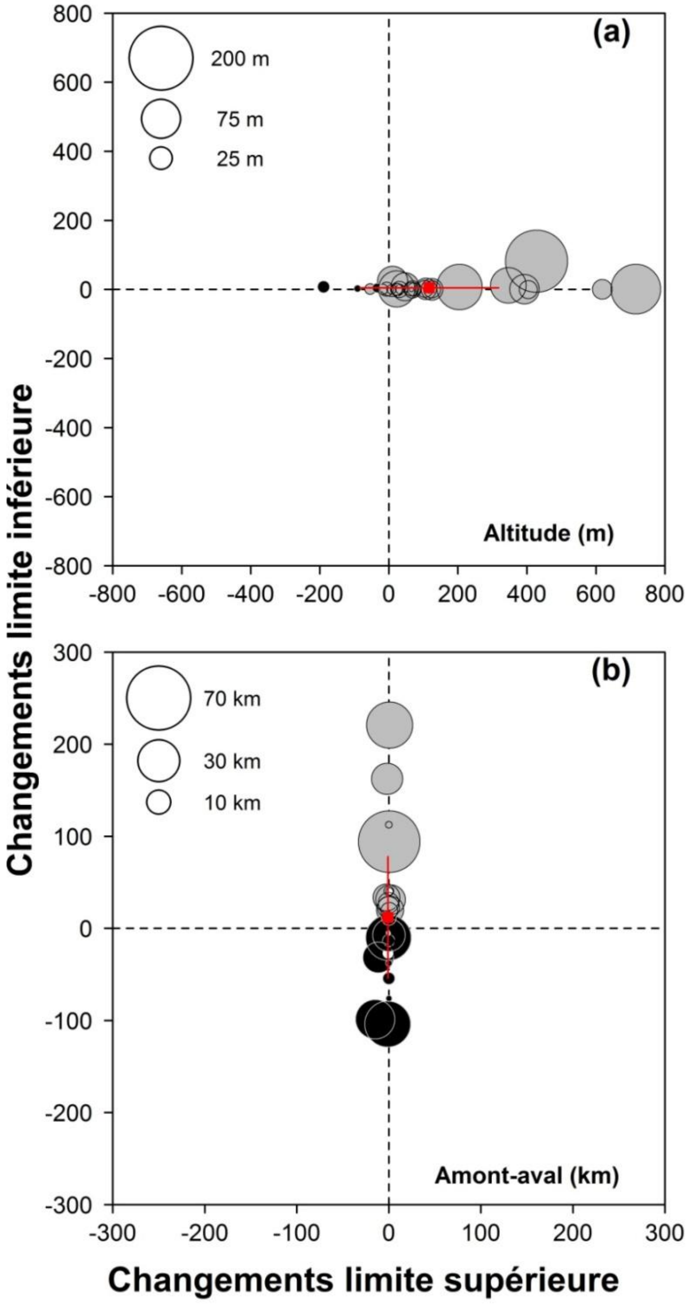


Figure 16 : Changements des limites supérieure et inférieure de la distribution entre une période 'froide' et une période 'chaude' le long des gradients (a) d'altitude et (b) de distance à la source. Les limites supérieures correspondent aux altitudes élevées et à l'amont. Chaque cercle représente une espèce pour laquelle la taille du cercle correspond au changement du centre de sa distribution. Les changements significatifs ($p < 0.05$) sont indiqués en noir pour les redescentes et en gris pour les remontées. Les carrés rouges et les barres associées indiquent les valeurs moyennes de changements des bornes inférieures et supérieures (± SD) pour toutes les espèces. (Modifiée d'après ***P_{III}***, Figure 3)

Plus spécifiquement, les remontées en altitude sont majoritairement dues à des colonisations par les populations vivant en limite supérieure de leur distribution (Figure 16a), notamment pour les espèces de basses altitudes, ce qui demeure le patron le plus communément observé à ce jour (Parmesan *et al.*, 2005; Wilson *et al.*, 2005). Cependant, alors que les vitesses de déplacements au centre de la distribution (13.7 m.décennie^{-1}) sont remarquablement concordantes avec celles estimées pour des poissons d'eau douce en Grande-Bretagne (13.1 m.décennie^{-1}; Hickling *et al.*, 2006), les vitesses d'expansion de la limite supérieure (61.5 m.décennie^{-1}) semblent nettement supérieures à celles précédemment estimées au travers de nombreux organismes, majoritairement terrestres (6.1 m.décennie^{-1} : Parmesan & Yohe, 2003; 11.0 m.décennie^{-1} : Chen *et al.*, 2011). Ainsi, les poissons de rivière pourraient être plus sensibles au réchauffement climatique que d'autres groupes taxonomiques. Cela pourrait s'expliquer non seulement par leur physiologie ectotherme et leur dépendance vis-à vis des concentrations d'oxygène dissous (Pörtner & Knust, 2007), mais également par la structure des réseaux hydrographiques ne leur procurant pas de refuges climatiques facilement atteignables par des déplacements à courte distance.

Au contraire, les modifications observées le long du gradient longitudinal résultent majoritairement de contractions des distributions vers l'amont suite à l'extinction des populations situées les plus à l'aval à une vitesse de 6.3 km.décennie^{-1} contre 0.6 km.décennie^{-1} au centre de la distribution (Figure 16b). Cela semble indiquer une plus grande vulnérabilité des populations vivant à la limite chaude de leur distribution, où les performances physiologiques sont plus sensibles à une augmentation des températures (Deutsch *et al.*, 2008; Huey *et al.*, 2012), ce qui pourrait également être amplifié par des phénomènes de magnifications dues à d'autres activités anthropiques (Isaak & Rieman, 2013). Certains auteurs ont avancé l'idée que les expansions étaient plus souvent documentées que les contractions à cause de la difficulté d'identifier les phénomènes d'extinction dans les populations fragmentées en limite de distribution (Thomas *et al.*, 2006). Etant donné que les succès de capture ont augmenté dans ces zones entre les deux périodes d'étude (voir 1.1- La détection imparfaite : quelles conséquences ?), les extinctions documentées ici ne semblent donc pas être liées à des biais d'échantillonnages.

Néanmoins, une forte variabilité est décelable dans les déplacements documentés pour les différentes espèces, ce qui suggère que malgré une réponse globalement consistante, des mécanismes dépendants des caractéristiques des espèces ou de l'environnent dans lequel elles évoluent pourraient être impliqués. Ainsi, alors que cette partie s'est attachée à décrire les changements observés, les questions de l'adéquation avec les changements climatiques récents et de l'influence des caractéristiques intrinsèques aux espèces seront abordées dans les parties deux et trois.

Cette première partie a permis d’établir que :

- La qualité des données, et en particulier les fausses absences, peuvent avoir des conséquences importantes sur notre capacité à estimer la distribution spatiale des espèces.

- Les approches consensuelles procurent une voie relativement efficace pour modéliser la distribution spatiale des espèces, en particulier pour les espèces les mieux détectées.

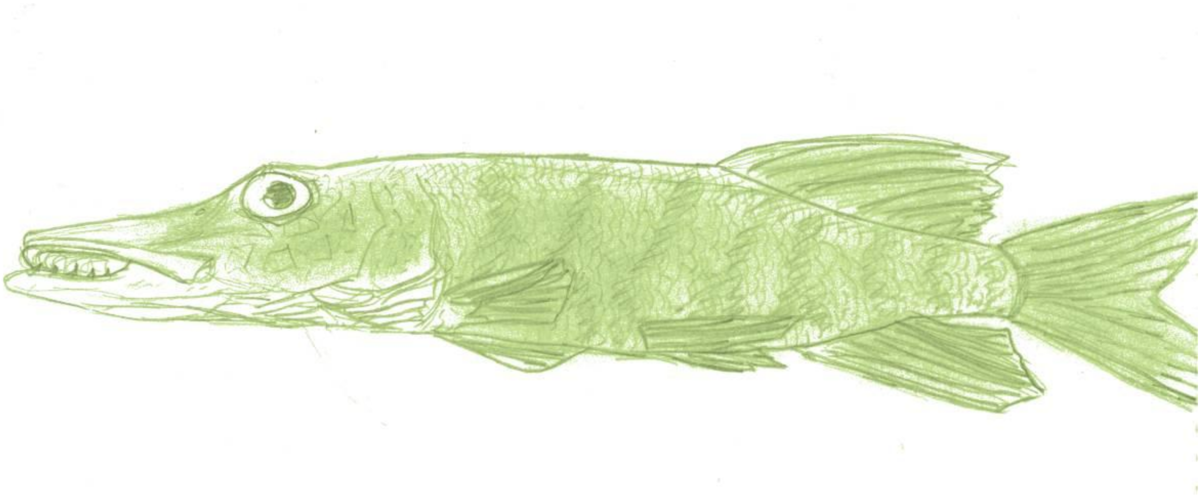
- Les poissons des rivières françaises montrent des modifications marquées de leurs distributions spatiales qui sont hautement spatialisées et idiosyncratiques.

- Ces modifications sont cohérentes avec une remontée de la majorité des espèces en altitude et vers les sources en lien avec des changements de leurs limites de distribution.

- Les réponses sont majoritairement asymétriques ce qui suggère l’existence de différents mécanismes agissant aux deux extrêmes de la distribution.

PARTIE II

La cohérence avec les changements climatiques



> *"Environments are forever changing… with relative rapidity they circulate about over the surface of the earth, and the species occupying them are thrust or pushed about, herded as it were, hither and thither."*
>
> *Joseph Grinnell (1924)*

1- La vélocité des changements climatiques

Afin de déterminer si les modifications des distributions spatiales étaient cohérentes avec le réchauffement climatique récent et de quantifier d'éventuels délais dans la réponse des poissons, nous avons comparé les vitesses de déplacement des espèces aux vitesses de déplacement des isothermes le long de gradients spatiaux (***P***$\boldsymbol{P_{III}}$). Plus spécifiquement, alors que la vélocité des changements climatiques est généralement exprimée le long du gradient latitudinal (Loarie *et al.*, 2009), nous avons considéré ici les déplacements le long des gradients altitudinaux et longitudinaux (Encadré 3).

Encadré 3 : Calcul de la vélocité des changements climatiques le long du gradient longitudinal (d'après Isaak & Rieman, 2013).

La première étape consiste à calculer le déplacement vertical (*a*) des isothermes le long du gradient altitudinal (m.décennie^{-1}) en divisant le taux de réchauffement observé sur le long-terme par le gradient thermique vertical (i.e. le changement de température le long du gradient d'altitude) :

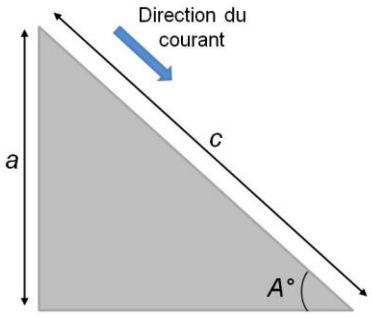
$$a = \frac{°\text{C.décennie}^{-1}}{°\text{C.100m}^{-1}} \quad (1)$$

où le réchauffement à long-terme a été calculé comme le coefficient de régression de la relation linéaire établie entre les températures annuelles moyennes et le temps durant la période 1968-2008, indépendamment pour chaque tronçon hydrographique. Le gradient thermique vertical a été quant à lui estimé indépendamment au sein de 54 bassins hydrographiques par des relations linéaires reliant la température avec l'altitude de tous les tronçons appartenant au bassin. La température de l'air a été utilisée comme un proxy de la température de l'eau en appliquant un facteur de transformation de 0.8°C

La deuxième étape permet de transformer le déplacement vertical *a* en distance de rivière (*c*, m.décennie^{-1}) en utilisant la relation trigonométrique du triangle rectangle :

$$c = \frac{a}{\sin(A°)} \quad (2)$$

où l'hypoténuse représente la longueur de cours d'eau *c*, et *A* la pente en degré.



De manière similaire aux estimations concernant les rivières nord-américaines, les isothermes de température se sont déplacées ces dernières décennies en France à un rythme compris majoritairement entre 40.6 et 74.3 m.décennie^{-1} vers de plus hautes altitudes, et entre 1.1 et 17.3 km.décennie-^{1} vers les sources, pour un réchauffement moyen observé de 0.24°C par décennie (Figure 17). Néanmoins, ces changements sont également très hétérogènes au sein des réseaux hydrographiques, les isothermes étant redescendus dans plusieurs zones géographiques (valeurs négatives ; Figure 17). De manière générale, les zones les plus à l'aval sont également celles présentant les vélocités les plus importantes à cause de la concavité des profils des rivières (Isaak & Rieman, 2013). Les patrons de contractions observés semblent donc au premier abord être en accord avec des extinctions induites par le climat. De la même manière, les expansions d'espèces vivant à basse altitude concordent avec l'hypothèse selon laquelle les espèces de plaine ont à parcourir de plus grandes distances pour suivre les modifications du climat que les espèces de montagne (Loarie *et al.*, 2009). Pourtant, alors que les vitesses de déplacements des espèces à leurs limites semblent concordantes avec les fourchettes de valeurs estimées pour la vitesse de déplacement des isothermes, les vitesses observées au centre de leur distribution semblent insuffisantes pour 'suivre' le changement climatique (Figure 18).

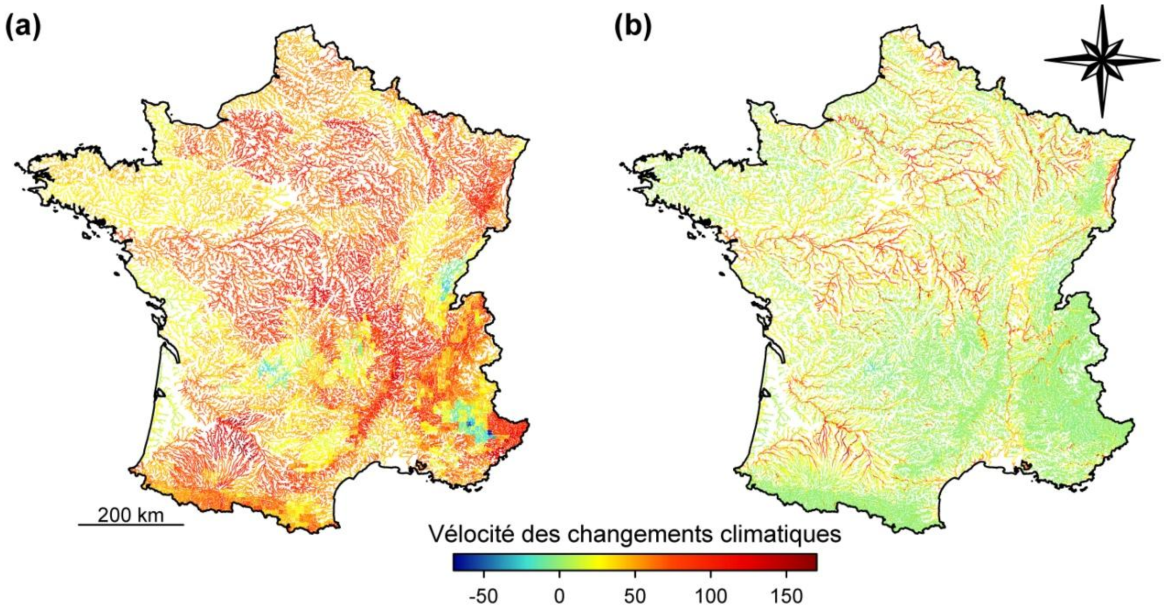


Figure 17: Vélocité des changements climatiques au sein du réseau hydrographique français exprimée en (a) distance altitudinale (m.décennie^{-1}) et (b) en distance longitudinale (km.décennie^{-1}). Des vélocités positives indiquent un déplacement des isothermes vers des altitudes plus hautes et vers les sources, alors que des vélocités négatives indiquent des déplacements vers des altitudes plus basses et vers l'aval. (Modifiée d'après ***P**$_{III}$*, Figure 1)

En effet, alors que la plupart des espèces se sont déplacées dans la direction attendue, la vélocité des changements climatiques est d'une magnitude bien supérieure aux déplacements observés. Cela indique qu'alors que les poissons semblent suivre leur niche climatique par des modifications complexes de leur distribution, ils ont en réalité accumulé un retard important dans leurs réponses (altitude = 46.8 m.décennie^{-1} ; amont = 15.0 km.décennie^{-1}), Etant donné que les températures pourraient se déplacer de plus de 100 km le long des cours d'eau dans les prochaines décennies (Isaak & Rieman, 2013), ces espèces pourraient, malgré leur capacités de dispersion relativement élevées, être incapables de se déplacer à une vitesse suffisante pour faire face aux changements futurs et accumuler à long terme un retard climatique important (Devictor *et al.*, 2008; Devictor *et al.*, 2012). Alors que les écosystèmes d'eau douce sont considérés à l'heure actuelle comme parmi les plus vulnérables aux changements climatiques (Sala *et al.*, 2000; Heino *et al.*, 2009), l'apparente inertie des poissons d'eau douce mérite donc une attention particulière, étant donné qu'elle pourrait conduire à des attritions biotiques différées dans le temps (Dullinger *et al.*, 2012). Il semble donc crucial de distinguer la part relative à la tolérance des espèces quant aux augmentations des températures, qu'il s'agisse de sensibilité ou d'adaptation thermique, de réels retards liés à leur incapacité à se déplacer suffisamment vite pour suivre les mouvements du climat. Néanmoins, là encore les retards observés sont très variables d'une espèce à l'autre, certaines espèces comme l'ombre commun (*Thymallus thymallus*) présentant même des vitesses de déplacements supérieures aux déplacements des isothermes. Alors que la sensibilité des poissons aux températures extrêmes plutôt qu'aux valeurs moyennes pourrait être un élément d'explication (Elliott, 1981; Matthews, 1998), tout comme l'interaction de multiples variables climatiques (Tingley *et al.*, 2012; Dobrowski *et al.*, 2013; VanDerWal *et al.*, 2013), l'influence d'autres facteurs interagissant avec le climat ne peut pas être exclue.

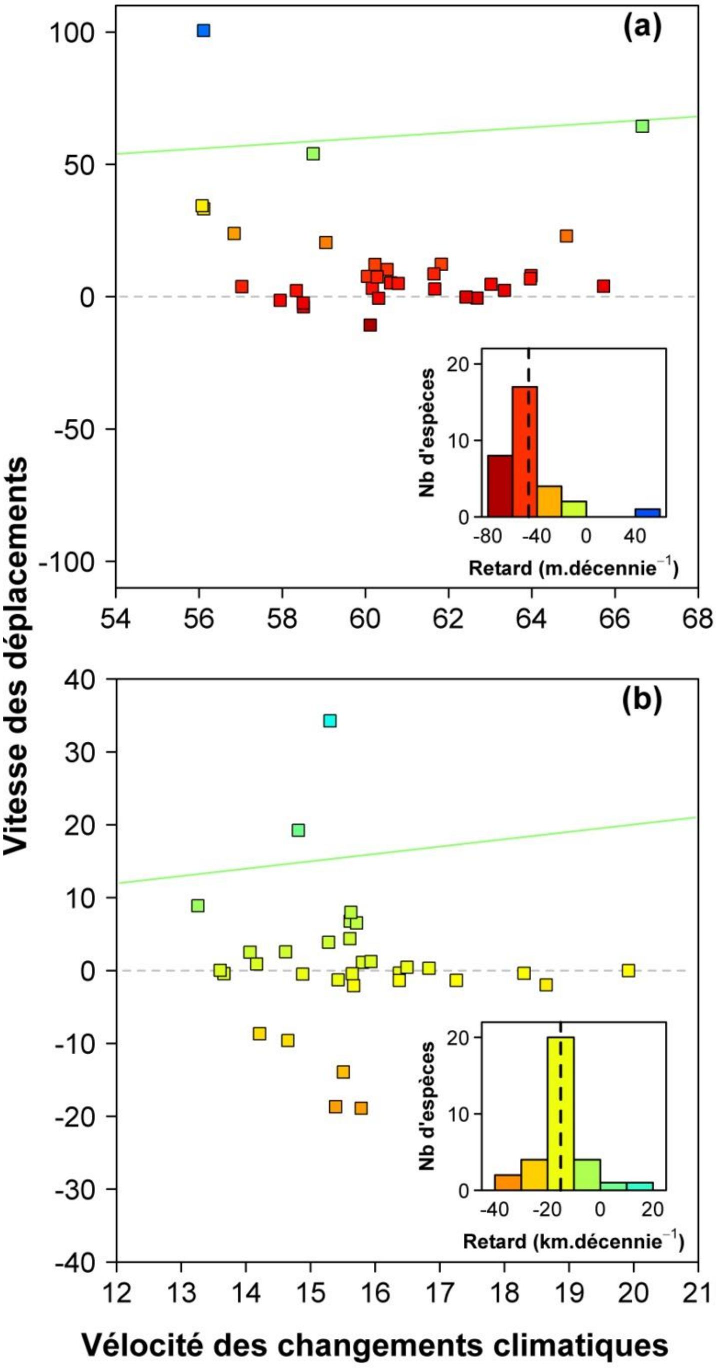


Figure 18: Comparaison de la vitesse de déplacements des espèces au centre de leur distribution et de la vélocité des changements climatiques le long des gradients (a) d'altitude (m.décennie^{-1}) et (b) de distance à la source (km.décennie^{-1}). Les changements de distribution positifs indiquent des remontées en altitude ou vers la source et les valeurs négatives des redescentes vers des altitudes plus basses ou vers l'aval. La ligne pleine indique la vitesse nécessaire pour que les espèces suivent parfaitement leur niche climatique. Les histogrammes montrent les retards entre les changements de distribution et la vélocité des changements climatiques (les valeurs négatives indiquent que les espèces sont en retard sur les changements climatiques). (Modifiée d'après ***P**$_{III}$*, Figure 5)

En particulier, sachant que les espèces menacées (*sensu* IUCN) sont probablement également celles les plus vulnérables aux changements climatiques (Foden *et al.*, 2008), les contractions observées pourraient être la résultante de la magnification des changements climatiques par d'autres pressions anthropiques (Brook *et al.*, 2008; Hockey *et al.*, 2011). De la même manière, le fait que la qualité de l'eau se soit améliorée dans les zones les plus aval des rivières européennes au cours des dernières décennies (Glennie *et al.*, 2002) pourrait expliquer les redescentes observées pour certaines espèces, même si une augmentation des surfaces artificialisées a également eu lieu durant cette même période. Finalement, étant donné l'intérêt économique des poissons de rivière, certaines espèces auraient pu bénéficier d'activités commerciales ou récréatives (e.g. introduction pour la pêche sportive, soutient de population) et étendre leur distribution dans des zones autrement non-favorables, alors que d'autres auraient pu au contraire être impactées négativement par ces activités, conduisant de ce fait à une contraction de leur distribution dans des zones qui leur sont pourtant climatiquement favorables (Leprieur *et al.*, 2008a).

2- Les différentes facettes des changements de distribution

Afin de quantifier les différentes facettes des changements de distribution et ainsi d'intégrer une dimension spatiale à nos mesures, nous avons étendu l'approche développée en $\boldsymbol{P_{III}}$ en comparant les changements de distribution observés avec les changements de distribution attendus de l'habitat climatiquement favorable à l'espèce (Figure 19). Cela a nécessité l'ajout d'une troisième étape consistant à projeter la distribution des espèces en utilisant les données climatiques de la période 'récente' à partir des modèles calibrés pour la période 'ancienne'. La distribution projetée représente ainsi l'espace climatiquement favorable à l'espèce dans la période la plus récente, et la comparaison des trois distributions spatiales permet alors d'identifier les aires géographiques correspondant à des événements de persistance, de colonisation, ou d'extinction, à la fois dans l'espace climatiquement favorable et dans l'espace climatiquement non favorable, mais également les aires géographiques correspondant aux zones nouvellement favorables d'un point du vue climatique mais qui n'ont pas été colonisées. Grace à cette approche, il nous a ainsi été possible d'étudier la spatialisation des changements observés, et de les attribuer à l'influence ou non des changements climatiques récents ($\boldsymbol{P_{IV}}$).

En effet, ces analyses nous ont permis de mettre en évidence que les changements de distribution, qu'il s'agisse de colonisation ou d'extinction, dus à des facteurs non-climatiques sont significativement plus importants que les changements liés au climat (Figure 20 ; $p < 0.001$). En premier lieu, ce résultat indique que l'attribution systématique des changements de distribution observés aux changements climatiques récents conduit vraisemblablement à une surestimation de leur empreinte sur le monde vivant (Parmesan *et al.*, 2011), et appelle à une meilleure prise en compte de facteurs non-climatiques dans l'évaluation de leurs conséquences futures sur la biodiversité (e.g. Thomas *et al.*, 2004; Xenopoulos *et al.*, 2005). D'un autre côté, il apparait également qu'alors que les changements climatiques récents ont eu une influence notable sur l'habitat climatiquement favorable de la majorité des espèces, il existe des délais importants dans leur réponse. En effet, de nombreuses espèces semblent avoir persisté dans des habitats qui ne leur sont plus climatiquement favorables puisque ces zones couvrent en moyenne 8.9% de leur distribution initiale (min : 0.1 ; max : 54.9%), alors que les extinctions dues au climat en représentent seulement 5.8% (min : 0.0 ; max : 17.1%).

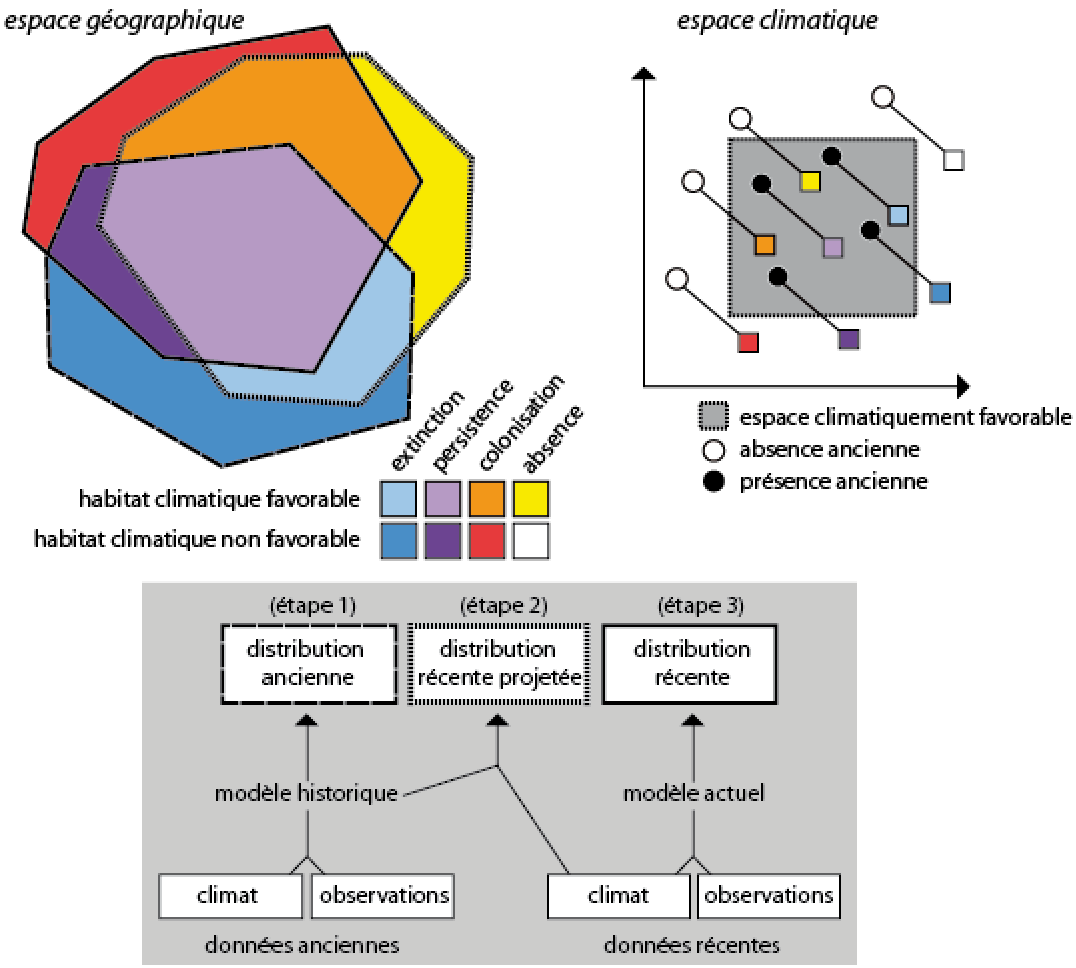


Figure 19 : Cadre théorique développé pour analyser les changements de distribution des espèces en lien avec les changements climatiques récents. La comparaison entre les distributions modélisées entre une période 'ancienne' (trait tireté) et une période 'récente' (trait plein), et l'habitat climatique favorable projeté pour la période 'récente' (trait pointillé) permet d'identifier les différentes facettes des changements de distribution, illustrés ici dans l'espace géographique (panel de gauche) et l'espace climatique (panel de droite). Les extinctions sont représentées en bleu : bleu foncé pour les extinctions dues au climat et bleu clair pour les extinctions dues à d'autres facteurs. La persistance est indiquée par du violet : violet clair pour la persistance dans un habitat climatiquement favorable et violet foncé pour la persistance dans un habitat qui n'est plus climatiquement favorable (i.e. zones où l'espèce pourrait être le plus à risque). Les colonisations sont indiquées en rouge : rouge foncé pour les colonisations en dehors de l'espace climatiquement favorable (e.g. introduction de l'espèce), et rouge clair pour les colonisations dues au climat (i.e. conservation de la niche climatique). Finalement, les habitats nouvellement favorables mais qui n'ont pas été colonisés (i.e. zones où l'espèce est en retard sur les changements climatiques) sont indiqués en jaune. (Modifiée d'après $\boldsymbol{P}_{IV}$, Figure 1)

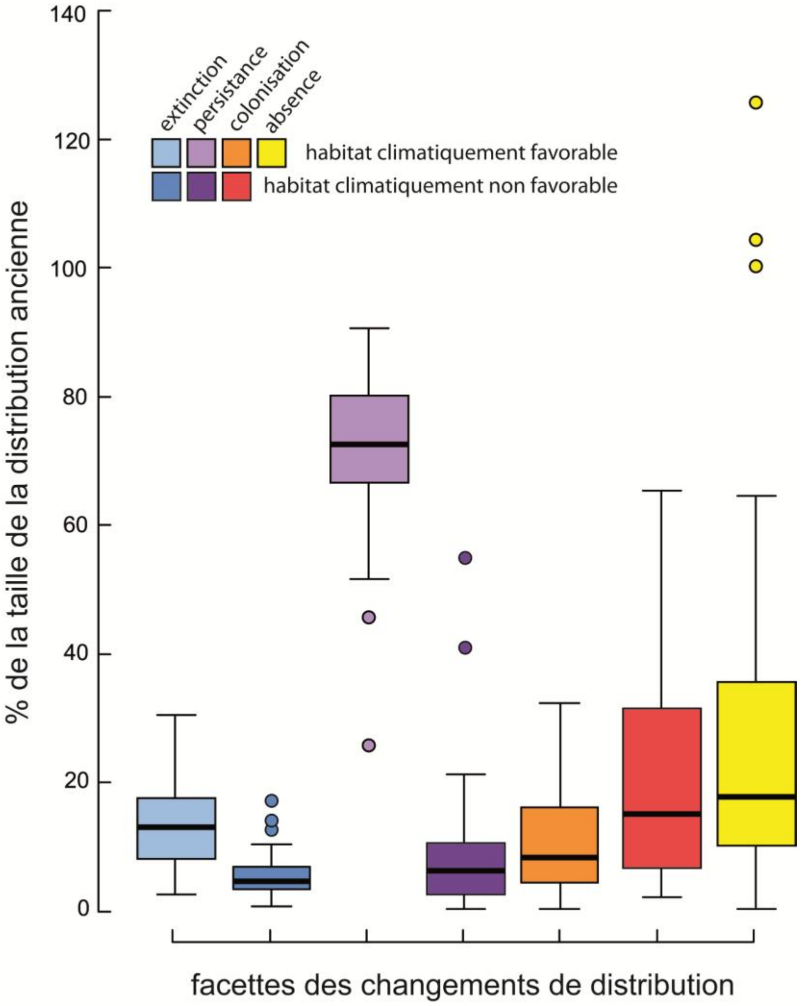


Figure 20: Différentes facettes des changements de distribution entre la période 'ancienne' et la période 'récente' pour les 32 espèces de poissons étudiées, exprimées en pourcentage de changements par rapport à la taille de la distribution initiale. La légende de couleur fait référence à la Figure 19. (Modifiée d'après ***P_{IV}***, Figure 2)

Par exemple, pour la truite (Figure 21), une espèce typique d'eau froide, les zones où les populations ont persisté malgré un climat défavorable sont situées en limite de distribution, qui sont également celles ayant subies le plus d'érosions climatiques. Ces zones pouvant être considérées comme des puits puisqu'elles contiennent les populations les plus exposées, cela suggère que les impacts réalisés des changements climatiques pourraient être différés dans le temps, et potentiellement conduire à des délais d'extinction (Kuussaari *et al.*, 2009; Dullinger *et al.*, 2012). De manière similaire, la capacité des espèces à suivre les mouvements du climat est également très hétérogène, les colonisations d'habitats devenus climatiquement favorables représentant en moyenne des expansions de seulement 10.6% (min : 0.1 ; max : 32.4%) de la distribution initiale, alors que les zones non encore colonisées varient de 0.1 à 125.7%. Les changements modérés documentés ici ne devraient donc pas être interprétés pour conclure de manière optimiste sur l'apparente résilience des poissons de rivière face à l'augmentation récente des températures puisqu'ils pourraient donner une vision erronée des effets à long-terme du changement climatique. Alors que la vulnérabilité actuelle des espèces pourrait être majoritairement influencée par des facteurs non-climatiques, leur rôle prédominant pourrait être altéré dans le futur proche au profil des altérations purement climatiques (Beever *et al.*, 2011; Zhu *et al.*, 2012). Les retards observés dans la réponse des espèces pourraient se traduire par des extinctions et des colonisations différées, dont la dynamique transitoire est un réel défi en terme de conservation et de préservation des processus écosystémiques au regard de la complexité des forces extrinsèques s'exerçant sur les écosystèmes (Jackson & Sax, 2013). Ces résultats témoignent néanmoins de l'existence de mécanismes qui permettent aux espèces de s'adapter aux modifications du climat en persistant *in situ* ou en suivant leur niche climatique, mécanismes dont la nature et le déterminisme sont à l'heure actuelle, largement spéculatifs.

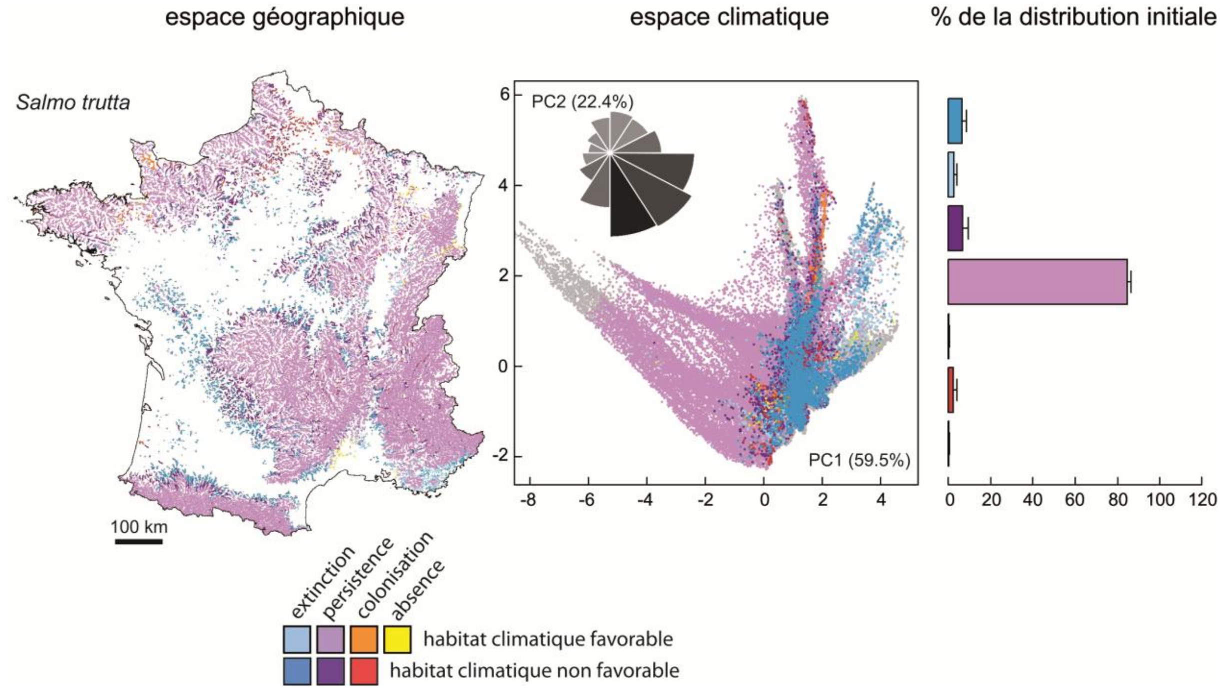


Figure 21: Exemple de spatialisation des différentes facettes des changements de distribution entre la période 'ancienne' et la période 'récente' pour la truite, dans l'espace géographique et climatique et exprimées en pourcentage de changements par rapport à la taille de la distribution initiale. Les changements dans l'espace climatique sont obtenus en projetant les tronçons hydrographiques décrivant les différentes facettes des changements dans une ACP basée sur 6 variables climatiques. L'axe 1 représente un gradient allant de zones chaudes et sèches (valeurs positives) à des zones froides et humides (valeurs négatives). L'axe 2 est quant à lui associé à un gradient de variabilité des températures allant de zones présentant des conditions stables (valeurs positives) à des zones présentant de fortes variabilités des régimes thermiques (valeurs négatives). Le diagramme polaire indique les fréquences d'occurrence et les directions des changements climatiques entre les deux périodes, la couleur grise étant proportionnelle à l'amplitude des changements observés dans chacune des directions. Les barres d'erreurs indiquent l'écart-type pour les 30 itérations. (Modifiée d'après **P_{IV}**, Figure 3)

3- Les rivières françaises : un cas isolé ?

Finalement, la généralisation des résultats concernant les poissons des rivières françaises est soutenue par les résultats issus d'une méta-analyse menée sur la littérature reportant des changements de l'habitat favorable récemment observés et prédits pour le futur, principalement dans l'hémisphère nord (***P_I***). En effet, cette méta-analyse confirme que les poissons d'eau douce pourraient être sévèrement affectés par les altérations du climat, et supporte la vision de potentiels gagnants et perdants du changement climatique (Rosset & Oertli, 2011). Cependant, elle révèle également qu'alors que les prédictions sont étayées par des évidences empiriques, comme en témoigne la corrélation entre les effets observés et prédits (Figure 22), la magnitude et la variabilité des observations excèdent de loin celles des prédictions, et ce qu'il s'agisse d'impacts positifs ou négatifs. Cela confirme non seulement un synergisme entre les changements climatiques et d'autres facteurs non-climatiques, mais également l'existence de réponses fortement espèce-dépendantes dont les caractéristiques sous-jacentes ne sont pas prises en compte dans les modèles prédictifs. Ainsi, les effets des changements climatiques pourraient être plus sévères que ce qui est généralement reconnu, en venant interagir et amplifier les menaces actuelles pesant sur la biodiversité. De ce fait, les stratégies de conservation ne se focalisant que sur un unique facteur de risque pourraient être inadéquates à cause des effets en cascade issus des synergies entre les différentes pressions anthropiques (Brook *et al.*, 2008).

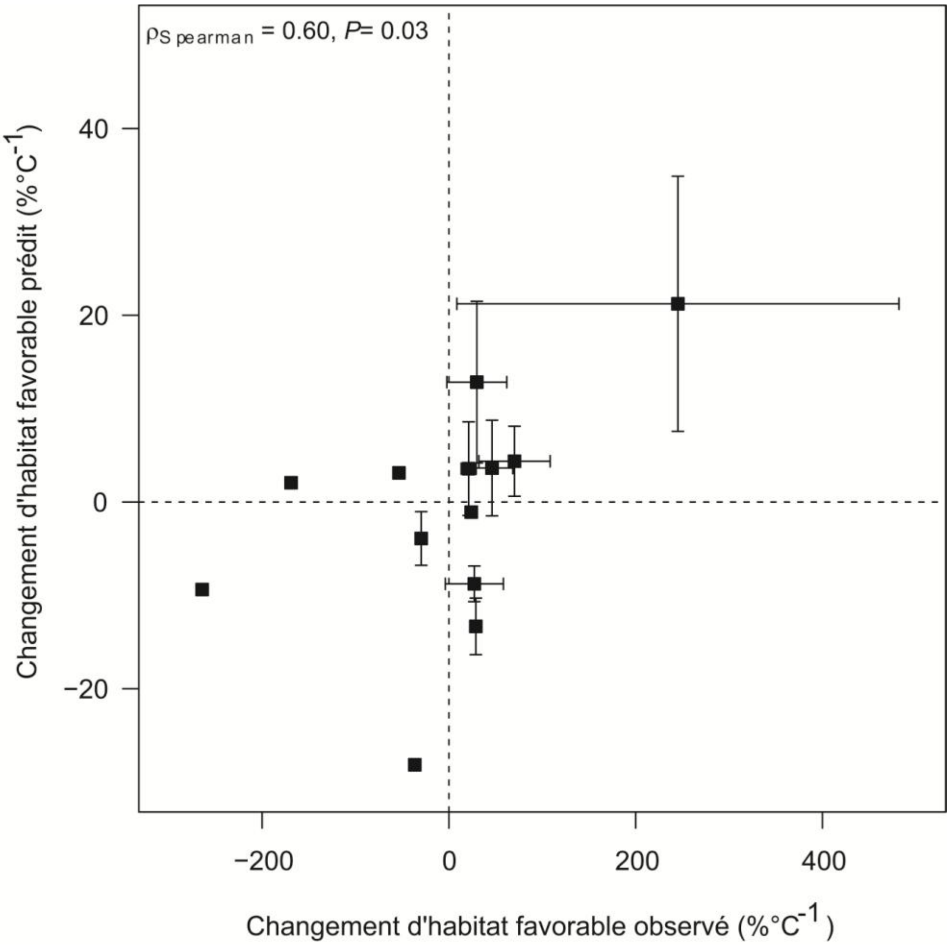


Figure 22: Comparaison des changements d'habitat favorables récemment observés et prédits pour le futur exprimé en pourcentage de changement par degré de réchauffement pour 16 familles de poissons d'eau douce issus d'une méta-analyse comprenant 50 effets observés et 277 effets prédits. Chaque rectangle représente la valeur moyenne pour une famille et les barres l'erreur standard (Modifiée d'après ***P_I***, Figure 6)

Cette deuxième partie a permis d’établir que :

- Les poissons de rivière ont répondu au réchauffement récent des températures de manière cohérente avec les variations géographiques de l’exposition aux changements climatiques.

- Des facteurs non-climatiques ont majoritairement participé aux modifications observées.

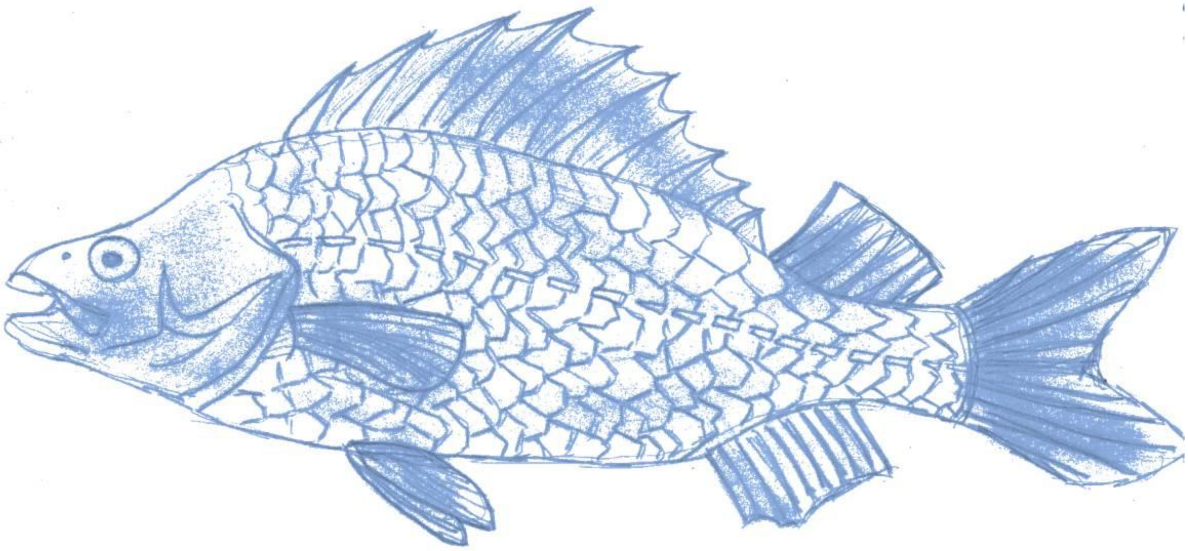
- Il existe des délais importants dans la réponse des espèces qui suggèrent :

    1) Que les poissons d’eau douce pourraient être particulièrement vulnérables aux changements climatiques futurs.

    2) L’existence de mécanismes intrinsèques permettant aux espèces de limiter les impacts liés aux changements climatiques en persistant *in situ* ou en suivant leur niche climatique.

PARTIE III

La vulnérabilité intrinsèque des espèces



"I have my own views about Nature's methods, though I feel that it is rather like a beetle giving his opinions upon the Milky Way."

Arthur Conan Doyle (1895)

Comme nous l'avons vu dans la partie précédente, les changements de distribution sont généralement complexes et multi-facettes (Parmesan *et al.*, 2005; Rabasa *et al.*, 2013), ce qui rend laborieuse la distinction des différents mécanismes impliqués. Alors que nous avons précédemment établi l'influence des facteurs extrinsèques, climatiques et non-climatiques, dans les changements observés, dans cette troisième partie, nous nous sommes intéressés aux caractéristiques intrinsèques aux espèces.

1- Les contraintes évolutives

Les effets des contraintes évolutives sur la capacité des espèces à suivre les changements climatiques récents ont été abordés séparément aux limites supérieure et inférieure de la distribution le long du gradient altitudinal d'après les modifications documentées en $\boldsymbol{P_{III}}$. Pour cela, les réponses des espèces ont été étudiées dans un cadre phylogénétique comprenant deux étapes ($\boldsymbol{P_{V}}$) (voir Encadré 4 pour les détails sur la méthodologie utilisée) :

(1) Nous avons tout d'abord testé les patrons de corrélation phylogénétique des changements de distribution aux limites altitudinales inférieures et supérieures de la distribution afin de déterminer si les espèces qui s'étaient déplacées étaient plus proches d'un point de vue évolutif que ce qu'on aurait pu attendre du au hasard seul.

(2) Nous avons ensuite cherché à savoir quelles étaient les caractéristiques des espèces qui étaient responsables des patrons de corrélation phylogénétique observés en confrontant plusieurs hypothèses non-exclusives sur le lien entre les traits des espèces et la magnitude des changements de distribution des limites altitudinales.

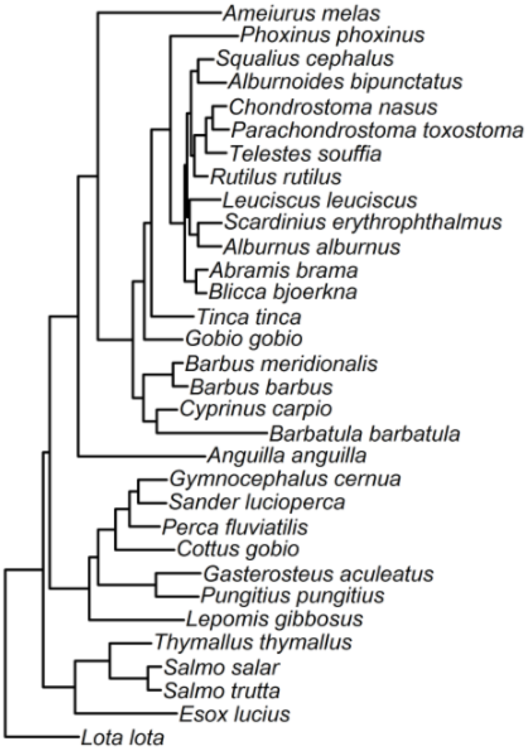
Conformément aux attentes théoriques, nous avons mis en évidence que les changements de distribution étaient bel et bien en lien avec des caractéristiques biologiques et écologiques clés des espèces (Thuiller *et al.*, 2005a; Williams *et al.*, 2008). Plus spécifiquement, en identifiant des traits corrélés aux changements de distribution et présentant des patrons phylogénétiques similaires, nous avons pu démontrer que les magnitudes de retraite et d'expansion des limites froides et chaudes de la distribution étaient influencées par des mécanismes différents. Nos résultats supportent l'hypothèse que les tolérances thermiques, qui présentent un fort signal phylogénétique, participent de manière prépondérante aux extinctions observées à la limite chaude (Figure 23 ; Tableau 2), ces contractions montrant également un fort conservatisme phylogénétique ($\lambda = 1.00$, $p < 0.05$). Les espèces d'eau froide (ayant une limite supérieure de température basse) ont ainsi subi des extinctions plus importantes à leur limite chaude que les espèces d'eau chaude (ayant une limite supérieure de température élevée). La généralité de ce résultat est par ailleurs étayé par des déclins similaires documentées pour des macroinvertébrés en Australie (Chessman, 2012), des lézards au Mexique (Sinervo *et al.*, 2010), ou encore des oiseaux en France (Jiguet *et al.*, 2007; Jiguet *et al.*, 2010). Cela semble suggérer que les espèces adaptées au froid ne pourront pas s'adapter aux changements climatiques à cause de contraintes génétiques fortes existant au niveau de leur tolérance vis-à-vis des températures, et pourraient donc subir un risque d’extinction accru (Sinervo *et al.*, 2010; Hoffmann *et al.*, 2013). Ce patron d’extinction sélectif d’un point de vue évolutif est par ailleurs concordant avec ce qui a été observé par le passé (McKinney, 1997; Roy *et al.*, 2009). Cela suggère donc que l’histoire évolutive des espèces pourrait être utilisée pour prédire leur vulnérabilité face aux changements futurs, tout en permettant de considérer leur originalité phylogénétique dans les stratégies de conservation (McKinney, 1997; Pau *et al.*, 2011; Thuiller *et al.*, 2011).

Encadré 4 : Cadre phylogénétique utilisé pour relier les traits des espèces aux changements de distribution observés

Le **signal phylogénétique**, c'est-à-dire la tendance pour des espèces phylogénétiquement proches à partager des valeurs plus similaires que des espèces prises de manière aléatoire le long de l’arbre phylogénétique (Losos, 2008), a été évalué en utilisant le λ de Pagel (Harvey & Purvis, 1991). Le λ de Pagel est un indice plus performant que d’autres outils existants pour mesurer le signal phylogénétique (Freckleton *et al.*, 2002; Münkemüller *et al.*, 2012), qui permet également de prendre en compte la non-indépendance des espèces dans les analyses corrélatives de manière relativement souple (Harvey & Purvis, 1991).

Les **relations entre les changements de distribution et les traits des espèces** ont été quant à elles testées en utilisant des **PGLS** (*Phylogenetic Generalized Least Squares*), permettant de prendre en compte la non-indépendance des données en ajustant la matrice de variance/covariance par rapport au degré de relation phylogénétique existant entre les espèces (Harvey & Purvis, 1991).

Abre phylogénétique des 32 espèces de poissons d’eau douce



Concerant les changements de limites altitudinales, une procédure d’inférence basée sur le critère d’information d’Akaike corrigé pour de faibles tailles échantillons (cAIC) a été menée afin d’identifier les modèles les plus vraisemblables (ΔAIC ≤ 2) parmi tous les modèles construits (avec un nombre de variables prédictives maximum incluant trois traits) et de construire un modèle final moyen (Burnham & Anderson, 2004). Cependant, afin de prendre en compte l’effet de facteurs confondants susceptibles d’influencer les changements de distribution observés, nous avons au préalable contrôlé la magnitude des déplacements altitudinaux pour les effets dus aux patrons d’exposition aux changements climatiques ainsi qu’au degré de manipulation anthropique des espèces du aux activités commerciales et récréatives. L’inférence multi-modèles a donc été menée sur les résidus de la régression reliant les changements de distribution observés aux facteurs potentiellement confondants.

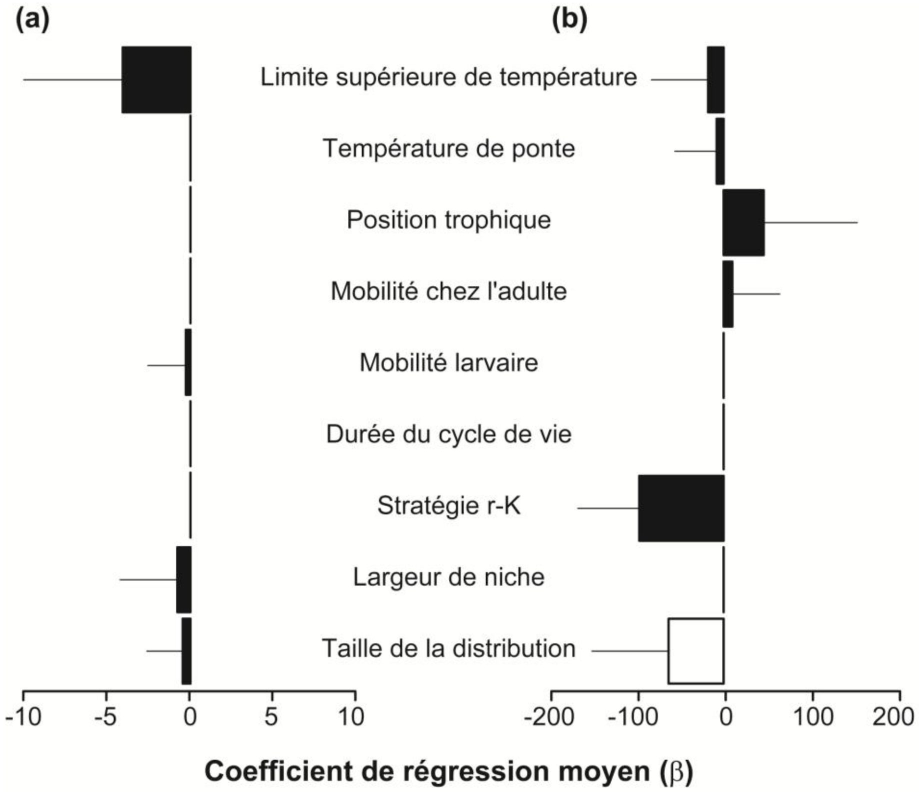


Figure 23: Coefficients de régression standardisés du modèle moyen reliant les changements de limites (a) chaude et (b) froide aux traits des espèces. Les barres sont les intervalles de confiance. Les couleurs indiquent si les résultats supportent les relations attendues : noir pour 'oui', blanc pour 'non. (Modifiée d'après $\boldsymbol{P_V}$, Figure 3)

Au contraire, les stratégies d'histoire de vie et la taille de la distribution, deux traits labiles d'un point de vue évolutif, sont les plus importants pour expliquer les expansions observées en limite froide de la distribution (Figure 23 ; Tableau 2), expansions qui ne montrent pas de conservatisme phylogénétique ($\lambda = 0.10$, $p = 0.78$). Cependant, nous avons également trouvé que les magnitudes d'expansion sont dépendantes, dans une moindre mesure, de la sensibilité directe (via les tolérances thermiques) et indirecte (via la position trophique) des espèces aux températures. Cela suggère qu'alors que la sensibilité des espèces est dépendante de leur histoire évolutive, des filtres environnementaux forts ont favorisé la convergence d'une suite de traits similaires chez des espèces éloignées phylogénétiquement, leur permettant de mieux suivre les déplacements du climat. En particulier, les espèces montrant les taux de colonisations les plus importants sont les espèces ayant les pressions de propagule les plus fortes (les espèces ayant une stratégie r), une caractéristique requise pour faire face aux instabilités de l'habitat (Southwood, 1977). Les stratégies d'histoire de vie des espèces pourraient ainsi être soumises à des pressions évolutives fortes, conduisant de ce fait à la sélection de capacités de dispersion élevées dans les populations vivant en front de colonisation (Lavergne *et al.*, 2010; Phillips *et al.*, 2010; Pauls *et al.*, 2013). De tels phénomènes ont d'ailleurs été observés chez de nombreux insectes (Hill *et al.*, 2012), suggérant un effet rétroactif entre l'expansion de la distribution et l'évolution de traits permettant son accélération, et ce qu'il s'agisse de sélection naturelle ou de sélection purement spatiale ('spatial sorting' ; Shine *et al.*, 2011). Néanmoins, comme précédemment suggéré pour expliquer les changements de distribution du Quaternaire, la colonisation des habitats nouvellement favorables d'un point de vue climatique est interdépendante d'autres mécanismes que la dispersion des propagules seule (Davis & Shaw, 2001). Par exemple, nous avons trouvé que les expansions les plus importantes étaient associées aux espèces ayant les distributions les plus restreintes, ce qui peut s'expliquer par le manque d'habitats disponibles pour les espèces cosmopolites ainsi que par la présence de micro-refuges potentiels au sein de leur aire de répartition (Hof *et al.*, 2011). Les espèces peu étendues géographiquement pourraient donc être les plus sensibles aux changements climatiques, indépendamment de leur capacité de colonisation (Thuiller *et al.*, 2005a). Finalement, bien que des évolutions adaptatives rapides puissent être partie intégrante des changements de distribution observés, les interactions entre dispersion et adaptation en réponse aux changements climatiques restent encore peu comprises (Lavergne *et al.*, 2010).

Tableau 2 Conservatisme phylogénétique (λ de Pagel) et sélection des modèles (PGLS) construits pour tester les relations entre les changements de distributions aux limites chaude (limite altitudinale inférieure) et froide (limite altitudinale supérieure) et les traits des espèces. ● indique un trait qui a été inclus dans un modèle. w_i représente le poids d'évidence du modèle. (Modifié d'après $\boldsymbol{P}_V$, Table 1)

	Conservatisme phylogénétique	Sélection de modèles									
		Limite chaude				Limite froide					
Trait	λ	M1	M2	M3	M4	M1	M2	M3	M4	M5	M6
Limite supérieure de température	0.85**	●*	●*		●*			●			●
Température de ponte	0.82**									●	
Position trophique	0.9***					●*			●*		●*
Mobilité larvaire	1***								●		
Mobilité chez l'adulte	0.83*				●						
Durée du cycle de vie	0										
Stratégie r-K	0.382					●**	●**	●**	●	●**	●*
Largeur de niche	0			●							
Taille de la distribution	0		●			●**	●**	●**		●**	
wi	-	0.39	0.25	0.21	0.15	0.20	0.18	0.17	0.14	0.14	0.1
R^2	-	0.14	0.18	0.11	0.16	0.47	0.42	0.44	0.31	0.46	0.31

$^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$

Etant donné que les extinctions locales sont reconnues pour entrainer des extinctions globales (McKinney, 1997), cette étude tend à démontrer que les espèces les plus vulnérables aux changements climatiques pourraient être les espèces adaptées au froid et présentant des stratégies K, pour lesquelles les taux de colonisation pourraient ne pas être en mesure de compenser les extinctions. Cependant, bien que les mécanismes identifiés ici fournissent des informations précieuses sur la manière dont les espèces répondent aux changements climatiques par des modifications de leur distribution spatiale, notre compréhension est encore très incomplète. En effet, de manière similaire à d'autres études abordant l'influence des traits des espèces (Angert *et al.*, 2011), les faibles performances prédictives des modèles suggèrent l'existence d'autres mécanismes largement répandus. Alors que d'autres mécanismes d'adaptation pourraient être impliqués (e.g. changements phénologiques ; Willis *et al.*, 2008), l'interaction avec d'autres facteurs non-climatiques peut également expliquer une large part de la variabilité non-expliquée (voir Partie II).

2- Les traits impliqués dans la vulnérabilité aux changements climatiques

Afin d'explorer plus spécifiquement les questions relatives à la capacité des espèces à faire face aux changements climatiques en s'abstrayant des modifications de distributions non liées au climat, nous avons testé les liens potentiels existant entre les différentes facettes des changements de distribution et certaines de leur caractéristiques clés (***P_{IV}***). Spécifiquement, nous avons considéré les caractéristiques des espèces sous-tendant :

(1) Le risque d'extinction lié aux changements climatiques.

(2) Le risque d'extinction lié à des facteurs non climatiques.

(3) La capacité à persister dans un habitat qui ne leur était plus climatiquement favorable.

(4) La capacité à coloniser des habitats qui leur sont devenus favorable d'un point de vue climatique.

En accord avec les résultats précédents, il est apparu que les espèces adaptées au froid avaient subi les extinctions les plus importantes (Tableau 3). Par contre, nous avons trouvé que la durée du cycle de vie avait un effet antagoniste sur l'extinction et la capacité de persistance dans les habitats climatiquement non-favorables. Bien que ce résultat semble contre-intuitif au premier abord, il pourrait indiquer qu'alors que l'extinction chez les espèces ayant un cycle de vie long serait moins facilement détectable à cause de l'existence de délais d'extinction (Kuussaari *et al.*, 2009), les espèces ayant un cycle de vie plus court seraient tout de même plus résilientes aux changements climatiques rapides. Sachant que la durée du cycle de vie est un bon proxy pour la plupart des taux démographiques, la fécondité plus élevée chez ces espèces pourrait leur permettre de compenser les extinctions locales en favorisant l'établissement d'individus dans les sites devenus inoccupés et en entretenant les flux de gènes au sein de métapopulations (Opdam & Wascher, 2004; Early & Sax, 2011). Concernant la capacité des espèces à coloniser des habitats nouvellement favorables, il est apparu que les espèces de basse altitude ayant des cycles de vie longs et des distributions restreintes montraient les plus grands retards. Alors que cela confirme que les espèces ayant des taux de renouvellement rapides seraient plus enclines à répondre rapidement aux changements climatiques (Perry *et al.*, 2005), ce résultat démontre que la dynamique de colonisation est également dépendante de la distribution spatiale des habitats qui est souvent inégale, ce qui peut conduire à des différences importantes dans les vitesses de déplacement des espèces (Chen *et al.*, 2011; Bennie *et al.*, 2013). La dispersion pourrait ainsi jouer des rôles différents dans l’adaptation et la persistance des populations vivants aux deux extrêmes de la distribution dans un contexte de changements climatiques rapides (Hampe & Petit, 2005).

Tableau 3 Résultats des modèles (PGLS) testant les relations entre les différentes facettes des changements de distribution et certaines caractéristiques clés des espèces : extinctions induites par le climat (i.e. taille de la distribution devenue non favorable d’un point de vue climatique où l’espèce s’est éteinte), extinctions induites par des facteurs non climatiques (i.e. taille de la distribution restée climatiquement favorable où l’espèce s’est éteinte), persistances dans des zones climatiquement non-favorables (i.e. rapport entre la taille de la distribution où l’espèce a persisté et celle qui est devenue non favorable climatiquement) et retards de colonisation dans des zones nouvellement favorables d’un point de vue climatique (i.e. la part de l'aire nouvellement favorable qui reste non colonisée). β indique le coefficient de pente du modèle et p la significativité (*ns*: non significatif). (Modifié d’après $\boldsymbol{P_{IV}}$, Table 1)

	Extinctions dues au climat		Extinctions dues à d’autres facteurs		Persistance		Retards de colonisation	
Traits	β	p	β	p	β	p	β	p
Mobilité chez l’adulte	-0.012	*ns*	-0.007	*ns*	-0.014	*ns*	0.023	*ns*
Durée du cycle de vie	-0.015	0.019	0.030	*ns*	-0.095	0.003	0.063	0.012
Limite supérieure de température	-0.016	0.026	-0.040	0.016	0.046	*ns*	-0.022	*ns*
Taille de la distribution	-0.002	*ns*	-0.050	0.002	0.059	*ns*	-0.070	0.003
Préférence altitudinale	0.003	*ns*	-0.029	*ns*	0.067	*ns*	-0.076	0.002

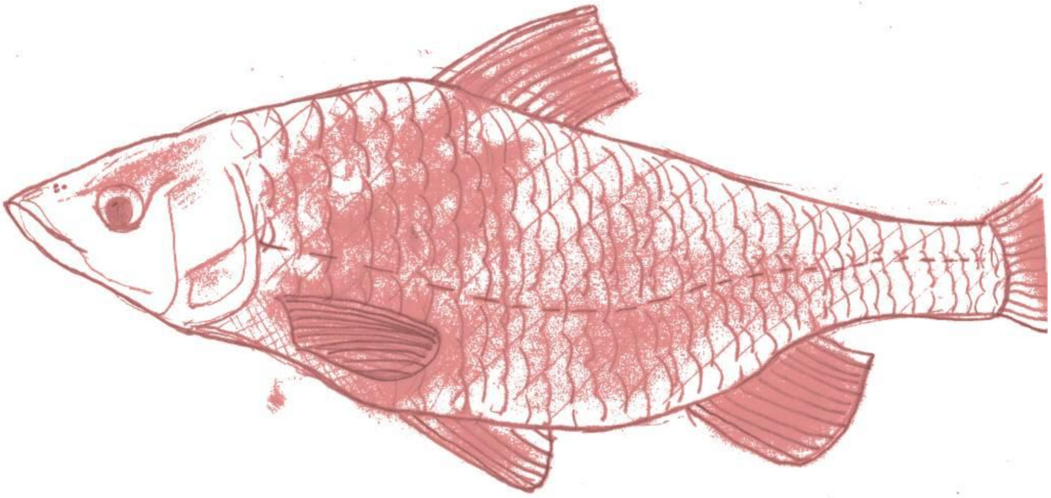
Finalement, il est également ressorti des analyses que les traits conditionnant les risques d’extinction vis-à-vis du climat par rapport à d’autres facteurs non climatiques pouvaient être en partie similaires (tolérances thermiques), démontrant ainsi que certaines espèces pourraient être particulièrement vulnérables à l’effet synergique des changements globaux. Cependant, malgré ce recoupement, la vulnérabilité des espèces semble également sous-tendue par des caractéristiques différentes, soulignant ainsi l’importance de distinguer l’effet du climat d’autres pressions anthropiques dans l’évaluation du risque d’extinction global des espèces. De cette manière, lorsque plusieurs facteurs interagissent, le contexte pourrait devenir primordial pour prédire la vulnérabilité des espèces, ce qui pourrait expliquer le manque de cohérence des études estimant les risques d’extinctions pour divers groupes taxonomiques et régions (Brook *et al.*, 2008). Ainsi, les traits qui sous-tendent la vulnérabilité des espèces pourraient être fondamentalement différents en fonction des menaces s’exerçant sur le milieu, indiquant de ce fait que les effets des traits impliqués dans les extinctions dues au climat pourraient avoir été précédemment surestimés ou non décelés à cause d’interactions avec d’autres facteurs confondants (e.g. Hockey *et al.*, 2011).

Cette troisième partie a permis d’établir que :

- Les caractéristiques biologiques et écologiques des espèces sont impliquées dans leur capacité à répondre aux changements climatiques.
- La vulnérabilité des espèces aux changements climatiques dépend de leur histoire évolutive.
- Les mécanismes de persistance et de colonisation sont induits par des mécanismes différents.
- Les caractéristiques prédisposant une espèce à des risques d’extinction climatiques peuvent être différentes de celles exercées par des facteurs non-climatiques.

CONCLUSIONS & PERSPECTIVES

Des réponses complexes…quelles implications ?



"The fairest thing we can experience is the mysterious. It is the fundamental emotion which stands at the cradle of true science."

Hans Selye (1958)

1- Conclusions générales

Les résultats de cette thèse ont permis de démontrer que la réponse d'une espèce soumise à des changements climatiques rapides n'est pas un phénomène aléatoire ou hautement déterministe mais dépend d'un ensemble de facteurs biologiques et environnementaux dont les effets sont difficiles à prédire. Cependant, nous avons pu mettre en évidence la nécessité de considérer les différentes facettes de la réponse des espèces dans l'évaluation de leur vulnérabilité face aux changements climatiques, ainsi que l'utilité de prendre en compte leur histoire évolutive dans la compréhension des mécanismes sous-jacents. Ainsi, l'analyse de chroniques 'anciennes' représente un des atouts majeurs pour l'écologie des changements climatiques, qui, couplée avec des outils adéquats, devrait permettre des avancées notables sur notre capacité à anticiper les conséquences des modifications futures sur la biodiversité.

Il ressort également de ces travaux que les changements de distribution pourraient avoir des conséquences écologiques importantes à différents niveaux d'organisation (Walther, 2010; Woodward *et al.*, 2010; Peñuelas *et al.*, 2013). En effet, les mouvements de populations résultant des variations récentes du climat pourraient induire des modifications fortes de la structure et de la diversité génétique des populations, suscitées par l'évolution de réponses adaptatives en front de colonisation ou par l'érosion génétique des populations les plus exposées (Lavergne *et al.*, 2010; Shine *et al.*, 2011; Rubidge *et al.*, 2012; Pauls *et al.*, 2013). Les patrons de diversité pourraient par ailleurs être profondément modifiés par la redistribution des assemblages dans l'espace, non seulement à cause de l'incursion de nombreuses espèces à de hautes altitudes, qui sont des zones comprenant généralement peu d'espèces, mais également à cause de la disparition systématique d'espèces présentant des combinaisons de traits favorisant l'extinction dans les habitats les plus exposés (McKinney & Lockwood, 1999). Cela pourrait conduire à une baisse de la diversité taxonomique mais également phylogénétique à la fois au sein (diversité α) mais également entre (diversité β) les régions où ces espèces sont uniques (Winter *et al.*, 2009). De plus, les menaces s'exerçant sur les espèces pourraient ne pas être limitées à la perte d'habitat, mais s'étendre également à des changements potentiels des interactions biotiques, tels que la compétition, la prédation ou le parasitisme, résultant de l'établissement de nouvelles communautés (Williams & Jackson, 2007; Stralberg *et al.*, 2009) et conduisant *in fine* à des altérations profondes du fonctionnement des écosystèmes et des services écosystémiques (Lovejoy & Hannah, 2005; Walther, 2010).

Enfin, en ayant permis une meilleure compréhension des mécanismes qui sous-tendent la réponse des espèces aux modifications de leur environnement, ces travaux pourraient avoir des implications importantes en termes de politiques de conservation (Berg *et al.*, 2010). En premier lieu, il ressort que les poissons d'eau douce ont déjà répondu à l'augmentation récente des températures, et qu'ils pourraient être fortement vulnérables aux changements climatiques futurs, en particulier à cause du synergisme avec d'autres pressions non-climatiques. Ces milieux étant soumis à de nombreuses altérations d'origine anthropique, des mesures de restauration d'habitat et de la connectivité écologique pourraient donc s'avérer nécessaires (Olden *et al.*, 2010). La transition des politiques centrées sur les espèces vers des politiques centrées sur le paysage devrait ainsi permettre aux populations de mieux répondre aux modifications engendrées par le climat à large échelle spatiale (Opdam & Wascher, 2004). Les stratégies de conservation pourraient évoluer d'une vision statique (e.g. aires protégées) à une vision plus dynamique intégrant des réseaux d'aires protégées interconnectés avec des zones intermédiaires assurant la connectivité entre les habitats, permettant aux espèces de se déplacer mais également de s'adapter aux perturbations de leur environnement (Opdam & Wascher, 2004). Par exemple, bien que le potentiel d'adaptation des espèces *in situ* via une évolution de leurs tolérances thermiques semble limité à cause de contraintes évolutives fortes, il apparait que leur capacité de persistance pourrait être augmentée par les échanges au sein de métapopulations. Ainsi, les efforts de conservation pourraient être dirigés de manière à prévenir la fragmentation et l'érosion génétique des populations vivant en limite de leur distribution (Hampe & Petit, 2005). Finalement, étant donné l'ampleur des vitesses des changements climatiques prédites pour le futur (Loarie *et al.*, 2009; Isaak & Rieman, 2013), et le fait que nombre d'espèces n'ont pas encore répondu à l'altération de leur habitat climatique, la question de l'adéquation entre les zones protégées et les routes de dispersion apparait également cruciale (Hannah *et al.*, 2007; Lawler *et al.*, 2013). Cependant, les politiques mises en place pour atténuer les pertes de biodiversité devront reconnaitre la nécessité de gérer de manière simultanée plusieurs facteurs de risque pesant sur les espèces, ainsi que leurs potentiels effets en cascade (Brook *et al.*, 2008).

2- Perspectives de recherche

Comprendre la nature multi-facette des changements de distribution requiert une approche réellement interdisciplinaire (Opdam & Wascher, 2004; Parmesan, 2006; Gaston, 2009; Thomas, 2010). En effet, le point de départ de n'importe quelle étude abordant la distribution spatiale d'une espèce repose sur la caractérisation précise des limites de distribution de cette dernière sur une carte (Fortin *et al.*, 2005; Holt & Keitt, 2005). La compréhension des changements de distribution ne se limite donc pas à l'identification seule de la niche écologique de l'espèce mais nécessite de s'intéresser à la dynamique des populations ainsi qu'aux adaptations locales et à l'évolution des capacités de dispersion, et devrait être étudié dans un contexte d'interactions biotiques multiples (e.g. communautés) (Parmesan, 2006; Anderson *et al.*, 2009; Berg *et al.*, 2010; Hill *et al.*, 2012). Cela pourrait permettre des avancées notables quant à notre capacité à anticiper les changements futurs, et aider à mettre en place des stratégies de gestions adaptées en parallèle des recherches en cours visant à comprendre la réponse actuelle des espèces (Williams *et al.*, 2008; Dawson *et al.*, 2011).

2.1- Prendre en compte la dynamique temporelle des distributions

Les changements documentés entre deux périodes d'études ne permettent ni une estimation de potentiels changements dans les vitesses de déplacement, ni une comparaison de l'influence relative de différents déterminants (Beever *et al.*, 2011). Par ailleurs, les changements de distribution documentés exclusivement à partir de mouvements des limites de distribution peuvent conduire à des conclusions biaisées en partie à cause de fluctuations d'abondance des populations (Parmesan *et al.*, 2005). En particulier, la variabilité démographique est généralement conditionnée par des variations climatiques spatiales et temporelles se produisant à des échelles fines, où les fluctuations interannuelles du climat peuvent venir se surimposer aux tendances climatiques à long-terme (Bennie *et al.*, 2013). Ainsi, la structure spatiale et la dynamique temporelle des mécanismes qui sous-tendent les changements de distribution n'ont pas été explorées en profondeur (La Sorte & Thompson, 2007). De nouvelles approches sont donc nécessaires pour comprendre comment la variabilité spatio-temporelle des changements climatiques influence les patrons et les vitesses de déplacements.

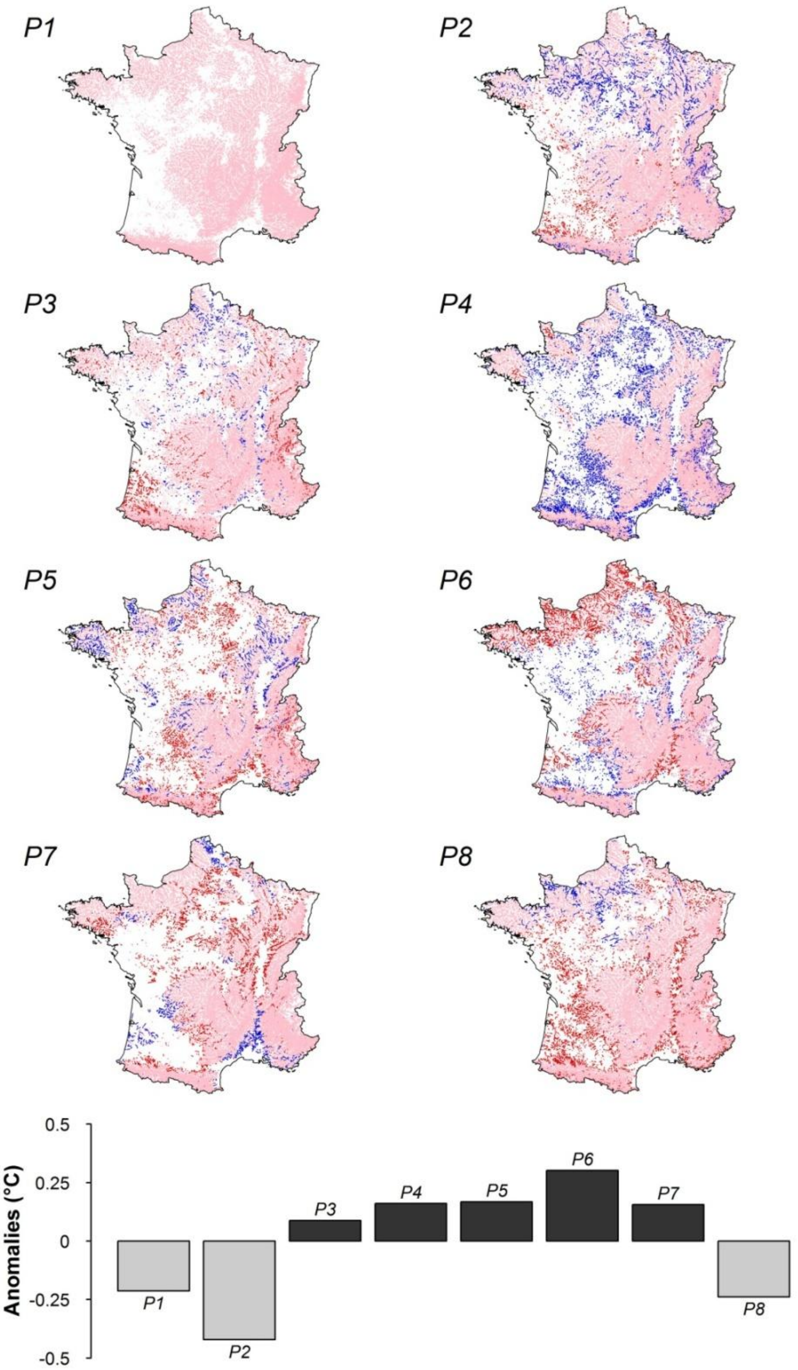


Figure 24: Exemple de la dynamique temporelle de la distribution spatiale de la truite modélisée à partir de modèles 'occupancy' pour 8 périodes temporelles successives : 1990-1994 ; 1995-1997 ; 1998-1999 ; 2000-2001 ; 2002-2003 ; 2440-2005 ; 2006-2008 ; 2009-2011. Le rose indique la présence de l'espèce, le rouge une colonisation et le bleue une extirpation. Les anomalies de températures font référence aux températures annuelles moyennes au sein de chacune des périodes, en incluant l'année précédente, par rapport à l'ensemble de la période d'étude (1990-2011).

Afin d'étudier ces questions, il serait intéressant d'étendre l'approche qui a été appliquée pour documenter les changements de distribution en intégrant une dimension dynamique aux analyses. Les changements de distribution pourraient être abordés non plus entre deux périodes temporelles mais entre plusieurs périodes successives, permettant ainsi d'examiner la dynamique temporelle des changements (extirpation ou colonisation ; Figure 24). Par exemple, en modélisant la distribution de la truite pour huit périodes distinctes, de fortes fluctuations dans la distribution spatiale apparaissent clairement, qui semblent en lien avec les variabilités des régimes thermiques (Figure 24). Les processus de colonisation et d'extirpation pourraient alors être étudiés séparément en les reliant à différents déterminants climatiques ou non et à leurs éventuelles interactions, tout en prenant en compte leur spatialisation.

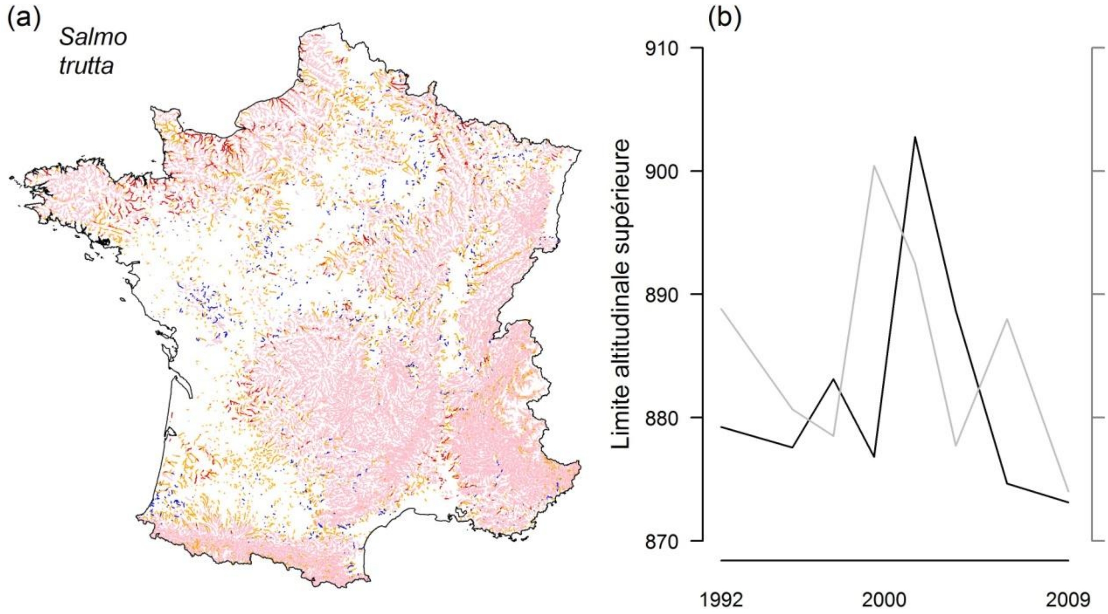


Figure 25 : Analyse de la dynamique temporelle de la distribution spatiale de la truite au sein des 8 périodes d'étude : (a) caractérisation des événements de turnover : Rouge : colonisation si l'espèce a colonisé le tronçon au cours de la période d'étude et s'y est maintenue de manière quasiment constante ; Bleu : extirpation si l'espèce a quasiment disparu alors qu'elle était présente au début de la période d'étude ; Rose : persistance si l'espèce a été majoritairement considéré comme présente au cours de la période d'étude ; Orange : dynamique si les patrons temporels ne correspondent à aucune des catégories précédemment décrites (d'après LaSorte & Thomson, 2007) ; (b) dynamiques des limites de distribution altitudinales inférieure et supérieure estimées pour chacune des périodes.

Par ailleurs, cette approche pourrait permettre de distinguer la nature épisodique des contractions et des expansions de distribution en catégorisant les différents événements potentiellement en lien avec la réponse des espèces aux tendances climatiques à long terme (i.e. colonisation, extirpation, persistance, dynamique) (Figure 25a). Ainsi, pour la truite, la contraction de la distribution documentée précédemment semble en réalité être beaucoup plus dynamique que ce que nous avions estimé, les populations vivant en limite chaude présentant une forte variabilité démographique (Figure 25a). D'autre part, cette approche pourrait permettre de ré-affiner les vitesses de déplacement estimées en $\boldsymbol{P_{III}}$ en prenant en compte la variabilité temporelle des trajectoires (Figure 25b), et ainsi d'évaluer avec plus de précision la vulnérabilité des poissons de rivière aux changements climatiques.

2.2- Evaluer les conséquences sur la diversité génétique des populations

Comprendre comment les micro-adaptations génétiques vont affecter la capacité des espèces à répondre aux changements climatiques reçoit aujourd'hui une attention grandissante (Bradshaw & Holzapfel, 2006; Gienapp *et al.*, 2008; Lavergne *et al.*, 2010; Pauls *et al.*, 2013). Le changement climatique et la subséquente réorganisation des communautés impliquent que, potentiellement, toutes les populations ont ou vont subir des changements de pression de sélection, processus pendant lesquels la diversité génétique pourrait jouer un rôle fondamental (Pauls *et al.*, 2013). Comme nous l'avons vu précédemment, de nombreux traits, tels que les stratégies de reproduction, pourraient évoluer en front de colonisation et influencer non seulement les taux d'expansion, mais également les patrons spatiaux d'adaptation locale et de potentiel adaptatif (Phillips *et al.*, 2010; Shine *et al.*, 2011; Hill *et al.*, 2012; Pauls *et al.*, 2013). Plus spécifiquement, l'évolution de phénotypes qui sous-tendent de plus grandes capacités de dispersion pourraient conduire à des réorganisations de la structure génétique de ces populations impliquant :

(1) la fixation de traits qui facilitent l'expansion et la survie

(2) une réduction de la diversité allélique et la fixation d'allèles délétères, et donc une baisse du potentiel adaptatif.

D'un autre côté, les populations vivant en limite chaude de la distribution pourraient subir une érosion génétique suite à une baisse de la taille effective des populations, et de ce fait voir leur potentiel adaptatif se réduire (Rubidge *et al.*, 2012; Pauls *et al.*, 2013).

Evaluer les conséquences des changements climatiques au niveau adaptatif requiert donc des approches intégratives visant à documenter non seulement l'évolution d'une caractéristique ou d'un gène unique mais également leurs conséquences en terme de fitness et de dynamique de population (Lavergne *et al.*, 2010). En effet, la mise en place de mesures de conservation efficaces requiert des informations à la fois sur le plan écologique et évolutif. Pourtant, la plupart des études n'ont procuré qu'une vision partielle du niveau de menace pesant sur les espèces en n'abordant qu'une seule facette du statut des populations (Frankham, 2010; Geist, 2011; Loss *et al.*, 2011). La combinaison d'analyses démographiques et génétiques comme celle développée en $\boldsymbol{A_I}$ pourrait ainsi représenter un outil essentiel pour prioriser et initier des mesures de gestion adaptées. L'identification de zones correspondant aux fronts de colonisation et d'extinction basée sur des analyses démographiques (voir 2.1- Prendre en compte la dynamique temporelle des distributions) pourrait permettre d'initier des suivis du statut génétique de ces différentes populations et ainsi étudier les patrons spatiaux d'adaptations locales et de potentiel adaptatif aux changements climatiques récents. Les comparaisons de mesures de différenciation génétique neutres (*Fst*) et de traits quantitatifs (*Qst*) devraient révéler si la sélection affecte réellement les populations de manière différente en limites ou au centre de la distribution, et indiquer des érosions potentielles de la diversité génétique et donc du potentiel adaptatif des espèces soumises aux plus forts stress climatiques.

2.3- Evaluer les conséquences sur les patrons de biodiversité

Alors que dans cette thèse les conséquences des changements climatiques ont été abordées au niveau spécifique, ces dernières doivent également être considérées dans un contexte d'interactions biotiques multiples (Williams & Jackson, 2007; Berg *et al.*, 2010; Woodward *et al.*, 2010). Il serait donc important d'évaluer les conséquences des changements de distribution à un niveau d'organisation supérieur, tels que les assemblages ou les réseaux trophiques. En particulier, et malgré les nombreux cas de remontées documentés en réponse aux changements climatiques récents, la généralisation de modifications de patrons de biodiversité (taxonomique, fonctionnelle et phylogénétique) le long de gradients altitudinaux ou latitudinaux reste rare (Forister *et al.*, 2010; Tingley & Beissinger, 2013). Par ailleurs, alors que les prédictions pour le futur font état de modifications fonctionnelles et phylogénétiques potentiellement importantes des assemblages (Thuiller *et al.*, 2011; Buisson *et al.*, 2013), les études concernant les modifications récentes se sont presque exclusivement focalisées sur des modifications de richesse spécifique (Wilson *et al.*, 2007; Moritz *et al.*, 2008; Forister *et al.*, 2010; Tingley & Beissinger, 2013). Comme nous l'avons vu précédemment, le changement climatique pourrait impacter non seulement le nombre d'espèces présentes sur un site, mais également causer des changements dans l'espace fonctionnel : certaines espèces pourraient disparaitre à cause d'une combinaison de traits les rendant vulnérables aux modifications environnementales ou suite à la compétition avec des espèces en pleine expansion et présentant des traits écologiques similaires, alors que certaines espèces plus adaptées pourraient s'établir. Bien que ces nouvelles communautés puissent assurer de nombreux services écosystémiques et continuer à supporter des réseaux trophiques complexes, elles pourraient pourtant représenter des assemblages fondamentalement différents d'un point de vue fonctionnel. L'analyse de changements potentiel de cet espace fonctionnel pourrait ainsi procurer une voix intéressante pour détecter l'influence des changements climatiques, indépendamment de la structure ou de la richesse taxonomique des communautés, qui pourrait être par ailleurs plus sensible que l'analyse des patrons d'extirpations et de colonisations seuls (Villéger *et al.*, 2008; Mouillot *et al.*, 2013). De la même manière, l'homogénéisation biotique est au cœur des préoccupations actuelles (McKinney & Lockwood, 1999; Villéger *et al.*, 2011). Il s'agit d'un processus temporel conduisant à une augmentation de la similarité des assemblages dans une région donnée, suite à l'expansion des espèces les plus cosmopolites et l'extirpation des espèces les plus rares. Alors que ce phénomène a été étudié majoritairement dans un contexte d'invasions biologiques (Olden, 2006; Leprieur *et al.*, 2008b), les conséquences des colonisations et des extinctions le long de gradients spatiaux suite aux changements climatiques en cours mériteraient une plus grande attention, en particulier au regard des résultats obtenus dans cette thèse concernant les caractéristiques phylogénétiques, fonctionnelles et écologiques des espèces présentant des modifications de leur répartition spatiale.

2.4- Anticiper les changements de distribution futurs

Un des défis dans l'analyse de données temporelles réside dans la difficulté de discerner les effets relatifs aux changements climatiques de ceux d'autre facteurs, et ce particulièrement à cause de leurs interactions potentielles (Brown *et al.*, 2011). L'approche développée en $\boldsymbol{P_{IV}}$ pourrait ainsi représenter une voie prometteuse pour guider des avances méthodologiques permettant de mieux anticiper les conséquences des changements climatiques à venir. En effet, la comparaison systématique des effets observés et attendus devrait permettre d'obtenir une connaissance plus approfondie de l'influence spécifique du changement climatique relativement à d'autres facteurs et des caractéristiques des espèces sur les changements de distribution observés, et ainsi permettre d'affiner la fiabilité des projections pour le futur. Ainsi, outre les avancées purement méthodologiques qui pourraient être apportées aux approches de modélisation prédictives, telles que le couplage de modèles statistiques et mécanistes (Kearney & Porter, 2009; Dormann *et al.*, 2012), il serait important de considérer l'inclusion de facteurs non-climatiques (e.g. obstacles à la dispersion) ou encore la prise en compte des caractéristiques clés des espèces (e.g. capacité de dispersion). Alors que de telles études ont déjà été conduites (Araújo *et al.*, 2006; Hein *et al.*, 2011), elles ont pour l'heure essentiellement permis de mettre en évidence la grande variabilité résultant des différents scénarios testés. La comparaison des trajectoires observées et futures pourrait ainsi apporter une précision supplémentaire, en permettant d'identifier les réponses les plus vraisemblables des espèces. De manière plus spécifique aux poissons d'eau douce, une des limitations majeures des projections futures réside dans le fait que les obstacles physiques pouvant entraver les déplacements des espèces et l'absence de connectivité entre les bassins hydrographiques ne sont pas pris en compte. Les modèles développés en $\boldsymbol{A_{II}}$ pour l'horizon 2080 sous différents scénarios climatiques pourraient ainsi être utilisés pour tester l'influence de la présence d'obstacles (barrages) et du phénomène d'insularité des réseaux hydrographiques sur les distributions potentielles des espèces dans le futur. La comparaison avec les trajectoires observées durant les dernières décennies de changements climatiques pourrait ainsi apporter des éléments de réponse concernant l'influence de la fragmentation des réseaux hydrographiques sur la capacité des poissons de rivière à se déplacer en réponse aux changements climatiques futurs. La prise en compte de la structure dendritique des réseaux pourrait également permettre, en utilisant des modèles spatiaux, d'évaluer le rôle de la connectivité hydrographique dans les patrons de colonisation et ainsi de déterminer les routes de dispersion offertes au espèces de manière plus réaliste (Erős *et al.*, 2012; Gil-Tena *et al.*, 2013; Peterson *et al.*, 2013).

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“If you copy from one author, it's plagiarism. If you copy from two, it's research.”

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ARTICLE I (P_I)

Comte L., Buisson L., Daufresne M. & Grenouillet G. (2013**)**. Climate-induced changes in the distribution of freshwater fish: observed and predicted trends. ***Freshwater Biology*** 58: 625–639.

Climate-induced changes in the distribution of freshwater fish: observed and predicted trends

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ABSTRACT

1. Climate change could be one of the main threats faced by aquatic ecosystems and freshwater biodiversity. Improved understanding, monitoring and forecasting of its effects is thus crucial for researchers, policy makers and biodiversity managers.
2. Here, we provide a review and some meta-analyses of the literature reporting both observed and predicted climate-induced effects on the distribution of freshwater fish. After reviewing three decades of research, we summarize how methods in assessing the effects of climate change have evolved, and whether current knowledge is geographically or taxonomically biased. We conducted multispecies qualitative and quantitative analyses to find out whether the observed responses of freshwater fish to recent changes in climate are consistent with those predicted under future climate scenarios.
3. We highlight the fact that, in recent years, freshwater fish distributions have already been affected by contemporary climate change in ways consistent with anticipated responses under future climate change scenarios: the range of most cold-water species could be reduced or shift to higher altitude or latitude, whereas that of cool- and warm-water species could expand or contract.
4. Most evidence about the effects of climate change is underpinned by the large number of studies devoted to cold-water fish species (mainly salmonids). Our knowledge is still incomplete, however, particularly due to taxonomic and geographic biases.
5. Observed and expected responses are well correlated among families, suggesting that model predictions are supported by empirical evidence. The observed effects are of greater magnitude and show higher variability than the predicted effects, however, indicating that other drivers of changes may be interacting with climate and seriously affecting freshwater fish.
6. Finally, we suggest avenues of research required to address current gaps in what we know about the climate-induced effects on freshwater fish distribution, including (i) the need for more long-term data analyses, (ii) the assessment of climate-induced effects at higher levels of organisation (e.g. assemblages), (iii) methodological improvements (e.g. accounting for uncertainty among projections and species' dispersal abilities, combining both distributional and empirical approaches and including multiple non-climatic stressors) and (iv) systematic confrontation of observed versus predicted effects across multi-species assemblages and at several levels of biological organisation (i.e. populations and assemblages).

Keywords: species distribution, range shift, empirical data, predictive modelling

INTRODUCTION

Knowledge of the biodiversity of freshwater ecosystems is still very incomplete, but declines in biodiversity are thought to be far greater in fresh water than in the most affected terrestrial ecosystems (Dudgeon *et al.*, 2006). It is suggested that the most influential drivers are related to climate-induced stress (Sala *et al.*, 2000; Heino *et al.*, 2009). Freshwater ecosystems may thus be those most threatened by the effect of future climate change (Millenium Ecosystem Assessment, 2005). Therefore, a better understanding, monitoring and ability to predict these effects on biodiversity are crucial for researchers, policy makers and biodiversity managers.

There is a long history of research addressing the effect of climate change on freshwater fish, with particular attention being devoted to changes in species distribution (Heino *et al.*, 2009). Indeed, forecasting potential distributional shifts in freshwater fish in response to projected climate scenarios has become a popular conservation tool, favoured by the recent development of many statistical methods that are now applied routinely (e.g. Thuiller, 2003). Changes in species distribution based on current and historical records have also been documented. As this literature has accumulated recently, both the observed and predicted effects of climate change on fish species distribution have already been reviewed (e.g. Reist *et al.*, 2006; Heino *et al.*, 2009; Booth *et al.*, 2011). However, most previous reviews could be biased towards restricted geographic locations or 'iconic' species of interest, thus limiting robust generalisations (Wilson *et al.*, 2007).

Over the last two decades, climate change scenarios have been continuously refined. In the meantime, ecological modelling techniques have diversified, and major methodological advances have improved our ability to forecast how species and assemblages could respond to climate change (Guisan & Zimmermann, 2000; Elith *et al.*, 2010). However, previous reviews have rarely focussed on methodological considerations, and how research activities assessing the effects of climate change on freshwater fish have changed in recent decades still remains unanswered. In particular, although theoretical considerations about the causes and consequences of climate-induced effects at different levels of biological organisation have already been reviewed (e.g. Woodward *et al.*, 2010), the compilation of recent evidence of climate-induced effects on freshwater fish remains limited (e.g. Heino *et al.*, 2009; Jeppesen *et al.*, 2010). Moreover, comparisons between observed and predicted effects have never been investigated thoroughly, and we argue here that (i) such comparisons could be a crucial component for supporting the reliability of these projections (Araújo *et al.*, 2005; Maclean & Wilson, 2011) and (ii) our ability to forecast more realistic future effects would greatly benefit from the knowledge of recent climate-induced effects on freshwater fish.

This article sets out to review our knowledge of climate-induced effects on freshwater fish species distribution. By providing a general synthesis of the literature reporting observed and predicted climate-induced changes, we investigate how our perception of climate change effects may have been biased towards specific geographic areas or families and related to the conservation status of species. We then used both qualitative and quantitative meta-analyses to find out whether observed taxonomic patterns of responses to climate change match the predictions for the future. We also explored how methodological considerations have evolved in climate change studies and which methodological advances could strengthen our ability to detect or predict the consequences of climate warming. We conclude by highlighting the areas of research needed to address current gaps and to further our scientific understanding of the effects of climate change on freshwater fish distribution.

LITERATURE REVIEW

We used the ISI Web of Knowledge to search for published articles reporting observed (i.e. empirical evidence recently documented in the field) or predicted (i.e. projections under future climate change scenarios) effects of climate change on freshwater fish distributions. Our search terms included all combinations containing (1) freshwater or 'fresh water*' or stream* or river* or lake*, and (2) 'fish*', and (3) 'climat* change*' or warming (2 December 2011). From this initial search, we selected the articles related to changes in the distribution of fish species. We excluded studies that focussed on individual or population climate-induced stress (e.g. effect on growth, reproduction, feeding and abundance). In addition, reports from the 'grey' literature were obtained, and non-peer-reviewed studies were selected for inclusion only if similar data had not been published elsewhere. A total of 77 studies published between 1980 and 2011 were included in the review, of which 11 and 66 corresponded to effects observed recently or predicted, respectively.

We recorded the realm, biome and ecosystem type where the studies were conducted and assigned each of the freshwater fish species studied to its family. We also assigned all species to IUCN (IUCN, 2011b) threat categories [i.e. critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC) and data deficient (DD)]. In accordance with the IUCN Red List, species assessed as CR, EN or VU were assigned to the threatened species category (IUCN, 2011a).

We also listed all the drivers cited or used as predictors to identify the relative contribution of climate change to both observed and predicted changes. More specifically, for the studies dealing with recent climate-induced effects, we recorded whether statistical analyses were carried out to link climate trends with fish responses or whether the relationship with climate was only discussed or hypothesised. For predictive studies, we categorised the different methodological approaches used (Table 1) and described how the projections had been generated (e.g. the climate scenarios employed, the number of projections) to obtain an overview of the evolution of predictive methods.

Finally, we listed all the metrics used to quantify the potential effects of both recent and future climate change on fish distribution. Metrics that had been given different names, but in fact corresponded to the same effect measurement were pooled. A total of 21 metrics quantifying climate-induced effects were identified and assigned to two classes: habitat suitability (14) and range shift (seven) (Table 2). We collected a total of 88 observed effects for 68 different species belonging to 24 families, and 773 predicted effects for 161 different species belonging to 25 families.

Qualitative assessment of effects

To determine the global trends in how fish are responding to climate change, we first assigned the quantitative values of the measured effects to a 'positive' (e.g. increase in habitat suitability) or 'negative' (e.g. decrease in habitat suitability) effect. Distributional shifts metrics were not included in the analysis if neither positive nor negative effects could unambiguously be assigned to these metrics (e.g. change in altitudinal optimum).

Table 1 Summary of the modelling approaches used in the freshwater fish literature for assessing climate-induced effects on fish distribution

Modelling approach	Aim	Biological input data	Output	References
Physiological (N = 39)	Delineation of suitable habitats from environmental information about known limiting factors	Physiological tolerance limits: Temperature Dissolved oxygen	Suitable habitat for fish species	Meisner (1990b), Fang *et al. (*1999)
Empirical (N = 13)	Mechanistic link between species distribution and environmental variables	Measurements of life history strategies and population dynamics: Life stage abundances Fecundity Growth rate Survival rate	Specific demographic parameters integrated in an overall model to assess species distribution	Mackenzie-Grieve & Post (2006), Williams *et al. (*2009)
Distributional (N = 14)	Correlative relationship between fish distribution and environmental variables	Species distribution: Abundance Presence-absence	Probability of presence Abundance	Buisson *et al. (*2008), Lassalle & Rochard (2009)

N: number of studies published between 1980 and 2012.

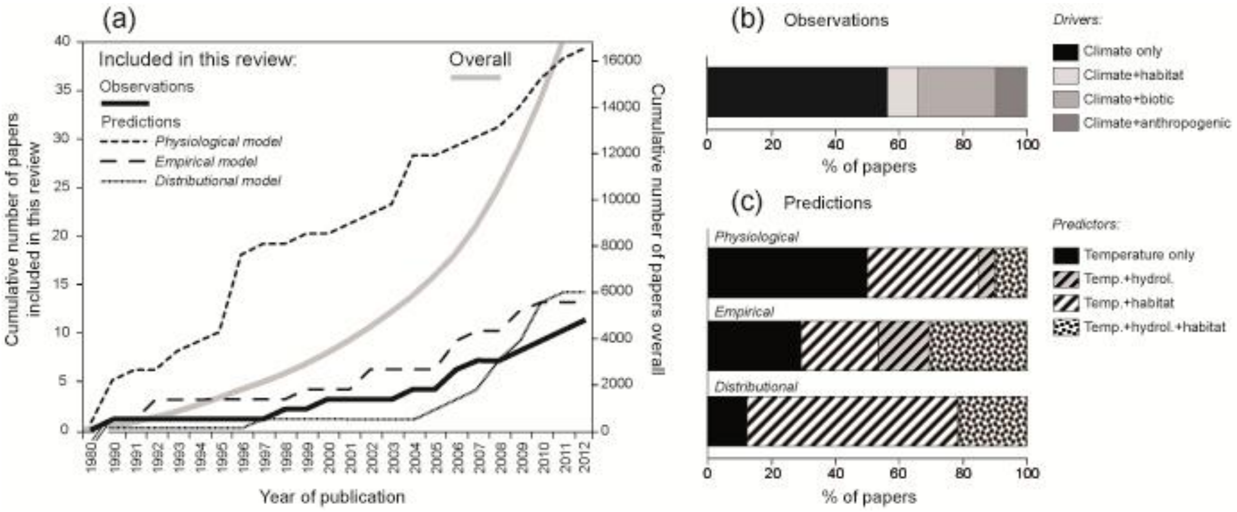

Figure 1 (a) Cumulative number of published articles from 1980 to 2012 (i) included in this review that report climate-induced shifts in freshwater fish distribution (left axis, black lines), and (ii) resulting from a broader search of the ecological literature using species and (‘climat* change*’ or warming) as search terms (right axis, grey line). Articles reporting climate-induced shifts in freshwater fish distribution were divided into observations (continuous black line) and future predictions (dashed black lines). Those assessing potential future changes were classified according to the type of modelling approach used (see Table 1 for details); (b) proportion of published articles according to the categories of drivers presumed to be related to the observed effects. The categories of drivers consisted of climate only (e.g. precipitation, temperature), habitat, for habitat degradation (e.g. pollution, fragmentation, dewatering), biotic, for invasive species and biotic interactions (e.g. parasitism, predation) and anthropogenic, for human activities (e.g. fishing, stocking); (c) proportion of articles using the different kinds of environmental predictors according to the modelling approach performed to predict future effects.

The proportion of positive and negative effects was tested against the random expectation of an equal probability of observing changes in either direction using binomial tests (H_0: $P = 0.5$). Observed and predicted effects were analysed separately to make it possible to compare the different patterns of research activity. Within each family, binomial tests were also used to compare the proportion of each categorical effect (negative or positive) between observed and predicted effects (H_0: $P_{obs} = P_{pred}$).

Quantitative assessment of effects

Focussing on quantitative effects, our goal was to compare observed and predicted rates of climate-induced change. We first combined similar types of metrics that reported quantitative estimates of change over a specified time period or warming scenario. Only effects reported in terms of change per individual species were included. This meta-analysis was restricted to changes related to habitat suitability (Table 2), as the number of effects reported in this class made such a comparison possible, unlike range shift classes, which did not. We defined habitat suitability effects as any change in the distribution previously occupied by species (e.g. stream length, area). These changes were expressed as a percentage change per degree of warming ($\%°C^{-1}$). This required converting each change measured over a time period or under a warming scenario within each study to a rate of change that was assumed to be constant over the time covered by the study. If not explicitly reported in the study, the time span for observed effects was converted to an overall temperature increase according to the estimated rates of global mean temperature increase over the study period (IPCC, 2007). For predicted effects, warming was estimated according to the general circulation models (GCM) and greenhouse gas emission scenario used, as well as to the geographic areas where the study was conducted and the time horizon (IPCC, 2007).

Table 2 Examples of climate-induced effects on fish species distribution in freshwater ecosystems

Climate-induced effects	**Ecosystem type**	**Selected references**
Habitat suitability (*N* = **4**; 57)		
Number of suitable entities		
stations	S	Eaton & Sheller (1996), Nakano *et al.* (1996), Mohseni *et al.* (2003), Buisson *et al.* (2008)
catchments	S	Chu *et al.* (2005), Lassalle & Rochard (2009)
streams	S	Flebbe (1993)
habitat patches	S	Rieman *et al.* (2007), **Isaak *et al.* (2010)**
lakes	L	Stefan *et al.* (2001)
Size of suitable entities		
stream length	S	Keleher & Rahel (1996), Flebbe *et al.* (2006), Kennedy *et al.* (2009), Lyons *et al.* (2010)
habitat volume	L	Mackenzie-Grieve & Post (2006), Elliott & Bell (2011)
distribution area	S	Keleher & Rahel (1996), Rahel *et al.* (1996), Flebbe *et al.* (2006), Buisson *et al.* (2010),
large habitat patches	S	Flebbe *et al.* (2006), Rieman *et al.* (2007)
thermal habitat	S	**Hari *et al.* (2006)**, **Isaak *et al.* (2010), Almódovar *et al.* (2012)**
	L	Magnuson *et al.* (1990), Meisner (1990b), De Stasio *et al.* (1996),
good growth habitat area	S	Stefan & Sinokrot (1993)
	L	Fang *et al.* (1999)
cold-water habitat	S	Preston (2006)
Probability of presence	S	Buisson *et al.* (2008), Steen *et al.* (2010), **Poulet *et al.* (2011)**
Range shift (*N* = **6**; 15)		
Altitudinal range	S	**Hickling *et al.* (2006)**, Matulla *et al.* (2007), Kennedy *et al.* (2009)
Lower altitudinal limit	S	Meisner (1990a), Nakano *et al.* (1996), **Hari *et al.* (2006)**
Northern limit	S-L	Shuter *et al.* (1980), Minns & Moore (1992), **Hickling *et al.* (2006)**
Southern limit	S	Meisner (1990a)
	S-L	McCauley & Beitinger (1992)
Expansion	S	**Gómez *et al.* (2004)**
	S-L	**Babaluk *et al.* (2000)**
	L	**Johnson & Evans (1990)**
Fragmentation	S	Keleher & Rahel (1996), Rahel *et al.* (1996), Flebbe *et al.* (2006)
Harvest / yield capacity	L	Mackenzie-Grieve & Post (2006)
	W	Minns & Moore (1992)
Extinction	L	**Trape (2009)**

S: stream, L: lake, W: watershed

N: number of studies published between 1980 and 2012 reporting observed and predicted effects. Values and references in bold indicate observed effects.

We considered separate results within a single study as independent observations when they involved different species. In contrast, when different effects were reported for the same species in a given location, the mean change across different effects or warming scenarios was computed. In total, 50 observed and 277 predicted effects met the different criteria for the analysis, covering 16 and 22 families, respectively. As many studies did not report measures of variability, we attached the same weight to all effects, irrespective of either sample size or the number of species studied (Gurevitch & Hedges, 1999). Rates of observed change were compared with rates of predicted change using generalised linear mixed effect model (GLMM) with species nested within families specified as a random effect in the model (Sodhi *et al.*, 2008). Indeed, due to their common evolutionary histories, species are not in fact statistically independent units (Paradis & Claude, 2002) and as such, some variation of responses among families might be expected. Negative and positive rates of change were analysed separately, making it possible to compare effects among potential 'winners' and 'losers' of climate change (Rosset & Oertli, 2011). Lastly, to test for consistency between general trends among families, the mean observed and predicted rates of changes were calculated and compared (Spearman's rank correlation test).

All the statistical analyses were conducted using the R environment software v 2.13.0 (R Development Core Team, 2011).

Patterns in publication activity

The number of published studies has accelerated gradually over time, the first article dealing with predicted future climate-induced change in species distributions having been published in 1980 (Fig. 1a; see Table 1 for details). In contrast, the first article focussing on empirical evidence for the influence of climate change was published 10 years later. Given the recent intensity of climate alterations (IPCC, 2007), it is not surprising that studies reporting effects of climate change on freshwater organisms have increased rapidly during the last two decades. However, the number of articles reporting observed effects on freshwater fish hitherto still remains disproportionately low compared to the number of studies devoted to forecasted effects (Fig. 1a). Nevertheless, although the increasing trend in the publication of studies dealing with the influence of climate change on freshwater fish distribution follows the overall trend of increasing publication activity, the number of studies included in this review still corresponds to only 0.5% of the papers in ecology dealing with climate change and biodiversity that have been published during the same period (Fig. 1a).

Assessment of potential geographic bias

Not surprisingly, publication activity appears to be geographically localised, with a strong bias towards the Northern hemisphere for both observed and predicted climate-induced changes (Fig. 2). We found that more than 90% of the studies reviewed were conducted in the Nearctic and Palaearctic realms, whereas only one paper per realm has been published for realms located in the Southern hemisphere (i.e. Australasian, Oriental and Neotropical realms; Fig. 2a). In addition, almost 50% of the studies were conducted in the temperate biome, whereas mountainous, Mediterranean and arid biomes have been poorly studied, even in the Northern hemisphere (Fig. 2b). Interestingly, many of the studies analysing recent climate-induced changes were located in the Palaearctic (45.5%) realm, while three quarters of the

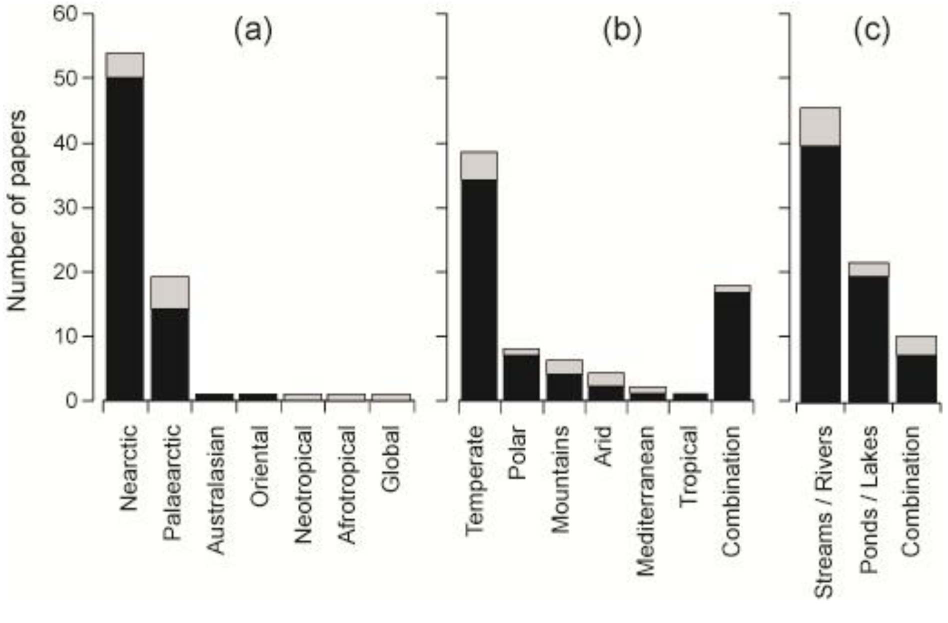

Figure 2 Number of articles published according to (a) the realm, (b) the biome, and (c) the type of ecosystem where climate-induced shifts in freshwater fish were observed (in grey) or predicted (in black).

future predictions were for the Nearctic realm. This stemmed from the availability of historical or long-term surveys in these regions, often derived from fisheries data or interest in species with high commercial value. Lastly, streams and rivers are the most studied ecosystem types (58.4%), while studies focussing on ponds and lakes account for only around one quarter of the articles (Fig. 2c).

Assessment of potential taxonomic bias

Overall, a majority of the studies focussed on one or a small number of fish species, and importantly on a single family. Specifically, articles dealing with observed changes often focussed on at least one salmonid species (54%), while recent trends for 91% of the species studied have been described only once. As a result, empirical evidence of the influence of climate change on freshwater fish distribution is still very patchy. A non-negligible proportion (24.2%) of predictive studies have forecasted the potential effects of climate change on fish thermal guilds (i.e. cold-, cool- or warm-water fish, *sensu* Magnuson *et al.*, 1979) rather than on species.

Taxonomic bias in both observed and predicted climate-induced effects was also apparent when it comes to examining the level of threat to the fish species under investigation (Fig. 3). While most empirical studies reported observed climate-induced effects for species of LC, most of the predictive studies focussed on species of unknown threat levels. In the published articles as a whole, we found that threatened freshwater fish were under-represented compared to their prevalence in the IUCN Red List (Fig. 3c). Indeed, although far from complete, categorisation of freshwater fish into IUCN classes revealed that 37% of the freshwater fish species assessed are threatened with extinction (IUCN, 2009). However, these species have been the topic of < 10% of the studies devoted to climate-induced changes in freshwater fish distribution. Although Red List categories clearly need further refinement to identify the full suite of species at risk from climate change (Foden *et al.*, 2008), one can reasonably hypothesise that current threat status is likely to be related to climate change vulnerability of the species (e.g. with threatened species also being those that are the most vulnerable). The lack of studies reporting climate-induced effects on threatened species could, therefore, have severe implications, as these species may be precisely those that have been the most severely affected by recent climate change and for which conservation efforts could be needed most urgently.

Methods used to assess climate-induced changes

Observed changes

Sources of long-term data are diverse, including catch data derived from fisheries or recreational activities (e.g. Hari *et al.*, 2006), national monitoring surveys (e.g. Poulet *et al.*, 2011), or compilations of all the available information on

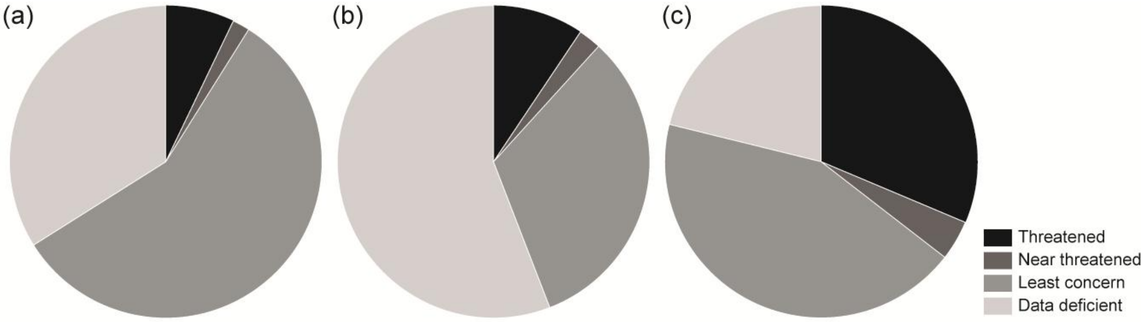

Figure 3 Proportion of species classified according to the IUCN Red List assessment in published articles addressing (a) observed and (b) predicted climate-induced changes in freshwater fish distribution. (c) Proportion of the world's freshwater fish in each Red List category based on 3120 freshwater fish species according to the 2009 IUCN Red List (IUCN, 2009). Species assessed as critically endangered, endangered, or vulnerable are collectively classified here as 'threatened species'.

species distribution over large temporal (e.g. Van Damme *et al.*, 2007) and spatial (e.g. Parrish *et al.*, 1998) scales. The length of the data sets used to study the recent influence of climate change ranged from occasional reports outside of the well-established distribution area of species (e.g. Babaluk *et al.*, 2000) to more than seven centuries for a study using a combination of contemporary, historical and archaeological data (Van Damme *et al.*, 2007). Overall, 50% of studies covered a time span of between 11 to 35 years, with a median value of 21 years. Temperature warming has accelerated and intensified during the last 30 years (IPCC, 2007), and it has been demonstrated that the response of species often lags behind environmental change (Magnuson, 1995; Devictor *et al.*, 2008; Bertrand *et al.*, 2011). As a result, our ability to detect climate-induced range shifts is probably limited due to both the scarcity of available long-term data series and the recent unprecedented magnitude and speed of current climate change (Battarbee, 2010).

The link between observed biological changes and climate trends was tested statistically only occasionally (9%) and merly hypothesised or discussed in more than 60% of the articles. When tested, the effects of climate change were addressed mainly through mean temperature increase, and rarely considered hydrological descriptors or extreme events (but see Trape, 2009). The implications of recent climate change appeared to be difficult to establish, because of the existence of other drivers, as has already been noted for other organisms (Archaux, 2004). Biological effects were attributed to trends in climate alone in 55% of the articles, while interactions with other habitat, biotic and anthropogenic related factors such as damming, species introductions or fishing activities, were also frequently cited (Fig. 1b).

Predicted future changes

When the articles were grouped according to the modelling approach used to project future fish distribution in response to climate change (Table 1), we found that the physiological approach was the one most commonly used (59.1%), followed by the distributional (21.2%) and empirical (19.7%) models. The popularity of the physiological approach lies in its simplicity, as these models are usually restricted to the known thermal tolerance of the species (Fig. 1c). In contrast, distributional models frequently combine temperature and other habitat predictors, while empirical models intended to capture mechanisms are mainly based on complex combinations of predictors, including hydrology (Fig. 1c). It is worth noting that the number of studies using species distribution models has risen sharply since 2005 (Fig. 1a), focussing on large numbers of fish species (on average 15 species per paper, ranging from 1 to 50), probably driven by recent advances in species distribution modelling (Elith *et al.*, 2010). As empirical models require more detailed knowledge about the physiological and ecological constraints on species distribution, they have only been applied to a very limited number of well-studied species.

Although many of the methodological decisions taken during the forecasting process are known to have a major influence on the effects predicted, the inherent uncertainty in those remains rarely assessed (but see Buisson *et al.*, 2010). Overall, potential future shifts in the distribution of freshwater fish species are more often projected using climate scenarios from GCM (67%) rather than using uniform scenarios (e.g. predicted warming of +3°C). However, most studies have projected these shifts using a single GCM and a single greenhouse gas emission scenario, and 49% of the studies rely on a single projection. Finally, only five of the 66 articles have accounted for the variability that results from using different kinds of models or climate scenarios. Thus, the variability between different projections undoubtedly deserves further attention.

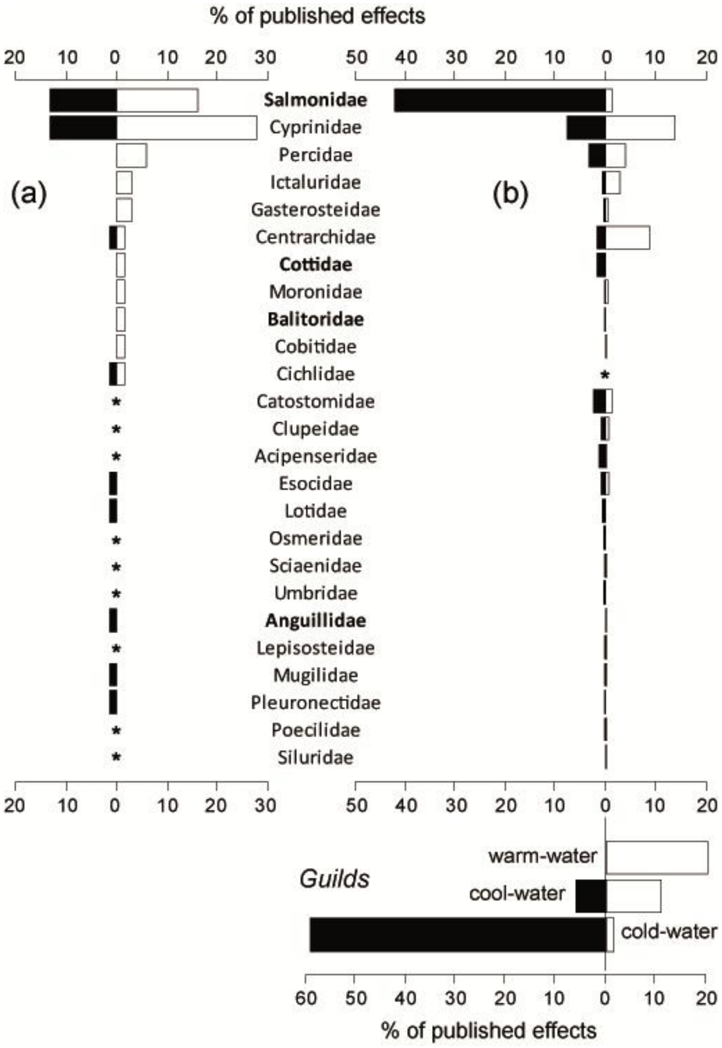

Figure 4 Proportion of negative (black bars) and positive (white bars) effects reported: (a) observed effects and (b) predicted effects according to the level of biological organisation for which predictions have been made (thermal guilds versus species). Asterisks indicate families of which no species has been studied. Bold indicates families for which the proportion of categorical effects differed between the observed and predicted effects, according to binomial tests ($P < 0.05$).

The influence of climate change on fish distribution

Global trends: qualitative assessment of effects

When global trends on how fish are responding to climate change were analysed, we first noted that the responses of the Salmonidae, Cyprinidae, Centrarchidae and Percidae families have been particularly thoroughly investigated. In contrast, there have been only a limited number of published effects for other fish families (Fig. 4). The overall patterns of observed and predicted effects were similar for most families (binomial test, $P > 0.05$), and it is worth noting that the responses of most families were not unidirectional (Fig. 4). Indeed, both positive and negative effects have already been observed or predicted for almost all the families included in our analysis. However, although the observed effects showed a higher proportion of positive effects (66%; binomial test, $P < 0.01$), most predicted influences were negative (65%; binomial test, $P < 0.001$). Observed positive effects were mainly reported for Cyprinidae, Percidae, Ictaluridae and Salmonidae, although negative effects were also reported frequently for this family (Fig. 4a). The higher proportion of predicted negative effects can be explained by the large number of studies focussing on cold-water species (Fig. 4b). Indeed, we found that 59.7% of the effects derived from published studies addressing fish thermal guilds focussed on cold-water fish, and 42.5% of future species-specific effects were devoted to salmonids (Fig. 4b).

Although no overall directional trend is yet apparent for the Salmonidae, it seems likely that cold-water species could be negatively affected by future climate changes. In contrast, warm-water species (e.g. Centrarchidae and Cyprinidae) could benefit from them. The response of cool-water species could be more variable, with 12 and 6% of the total predicted effects being reported as positive and negative, respectively (Fig. 4b).

A quantitative assessment of effects

When quantitative effects on species habitat suitability were estimated (i.e. the rate of change per degree of warming), we found that the magnitude of the observed effects was almost eight times higher than those predicted (GLMM, $P < 0.001$; Fig. 5). Across all studies reporting a decline in habitat suitability, the mean rate of change was -81.00 and -10.66%°C^{-1} for observations and future predictions, respectively. For positive changes, these values were 100.06 and 18.82%°C^{-1}, respectively. The degree of variability in habitat change was also much higher for observations than for predictions (Fig. 5), indicating stronger species-specific responses to climate change than predicted by models.

When changes were quantified for each family (Table 3), there was evidence that directional trends were not independent, thus supporting the proposal that there are some potential 'winners' (e.g. Ictaluridae, Centrarchidae, Cyprinidae) and some potential 'losers' (e.g. Lotidae) of climate change. This finding was also highlighted by the high degree of correlation between observed and predicted trends in family-specific effects ($\rho_{Spearman} = 0.60$; Fig. 6). Most of the families observed to have been positively affected by recent climate change were also predicted as likely to benefit in the future, although the consistency of negative effects was less consistent (e.g. Salmonidae). However, the taxonomic imbalance (i.e. high differences in the number of species per family) may introduce an artificial variability in the direction and magnitude of the effects for families composed of many species sharing different ecological features (e.g. Cyprinidae), thus

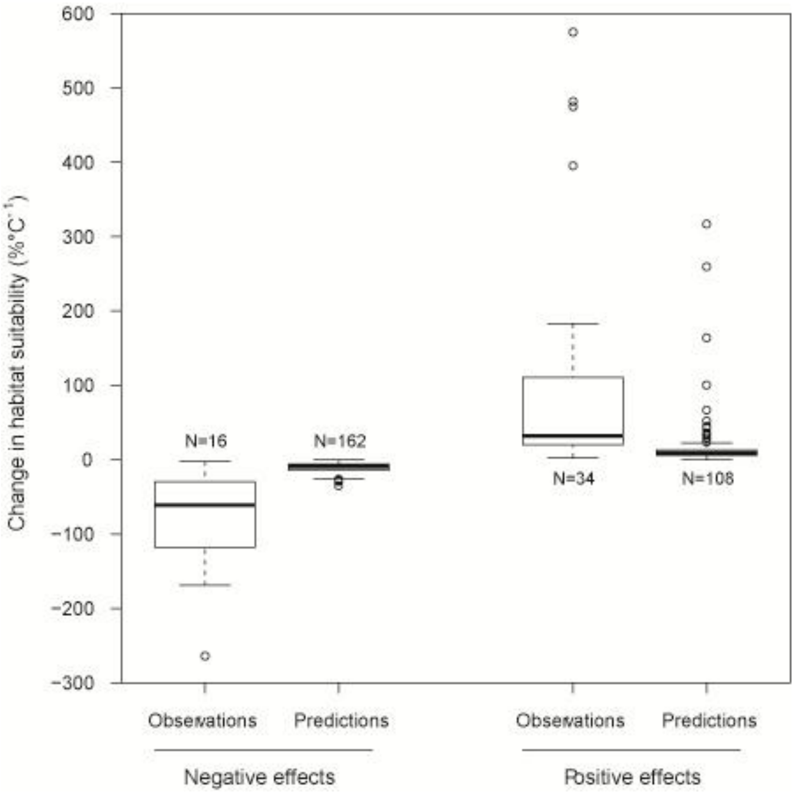

Figure 5 Changes in habitat suitability observed and predicted according to the direction of the effect (i.e. negative or positive). *N* indicates the number of species × location included in the analysis.

leading to more ambiguous trends than for families composed of only few species (e.g. Siluridae). Nevertheless, we confirmed that rates of both positive and negative observed changes exceeded those of the predicted changes within each family. This may in part be triggered by a positive result bias, although previous studies have clearly confirmed that the evident signal of climate-induced biological changes was not driven by publication bias (Menzel *et al.,* 2006). In addition, the fact that species can respond to climate alterations in a nonlinear way (e.g. threshold effect) might lead to under- or over-estimated rates of changes. The influence of other additional drivers of change may also explain these differences, as these factors are usually neglected in predictive models (but see Steen *et al.*, 2010). Therefore, although our results suggested that predictions can be supported by empirical evidence (Maclean & Wilson, 2011), the synergism between climate change and non-climatic stressors could also drive an unpredictable variability in how species respond to climate change (Heino *et al.,* 2009).

Some illustrations

Changes in habitat suitability

Changes in fish habitat suitability in response to climate change have been quite well documented. In particular, many studies have focussed on species of commercial or recreational interest. As a result, because of their ecological, economic and cultural importance, salmonid species have been the focus of numerous studies. In addition, the preference of salmonid species for cold waters makes them a good model for studying climate change effects, especially in the early decades of climate alteration as they might be more prone to respond than other tolerant species.

First, the thermal habitats of several native salmonids have already been reported to have been affected by the recent rise in temperature (Hari *et al.,* 2006; Isaak *et al.*, 2010; Almodóvar *et al.*, 2012). Isaak *et al.* (2010) estimated a potential loss of 11–22% of suitable headwater stream length in central Idaho (USA.) for the bull trout (*Salvelinus confluentus*), and small gains in the number of suitable patches of habitat for the rainbow trout. In addition, estimated changes in the thermal habitat of the brown trout in Switzerland and

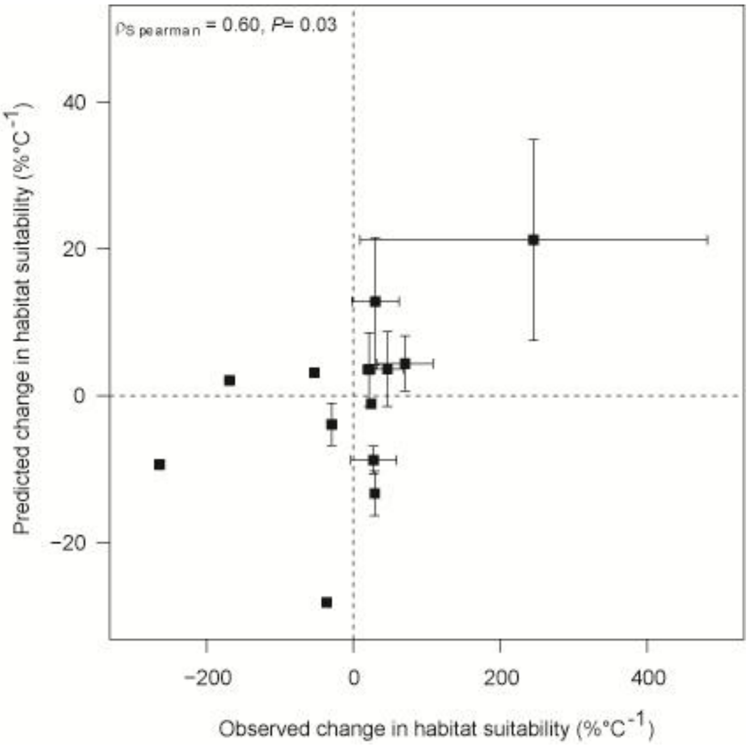

Figure 6 Predicted versus observed changes in habitat suitability per family. Squares represent average values and bars the standard errors.

Spain were consistent with longterm population decreases, thus supporting the evidence of negative climate-induced effects (Hari *et al.*, 2006; Almodóvar *et al.*, 2012). However, differential effects can also occur at smaller spatial scales (e.g. along environmental gradients; Hari *et al.*, 2006), and some other salmonids displayed strong increases in their probability of presence over recent decades (Poulet *et al.*, 2011).

Future local extinctions and distribution contractions are also projected as a result of the decline in the number and size of areas of suitable habitat for most cold-water fish species (e.g. Flebbe, 1993; Keleher & Rahel, 1996; Chu *et al.*, 2005; Rieman *et al.*, 2007). The potential effects of climate change on the habitat of cold-water species have also been widely studied in lakes, where both the number of lakes and habitat area per lake suitable for fish species were predicted to decrease (Stefan *et al.*, 2001; Mackenzie-Grieve & Post, 2006). However, some studies have also argued that in some North American lakes, climate change could result in an increase in suitable thermal habitats for all thermal guilds, including cold-water species (Magnuson *et al.*, 1990; De Stasio *et al.*, 1996; Fang *et al.*, 1999).

In addition, a large discrepancy was found between the negative effects identified by studies that focussed solely on cold-water species (i.e. salmonids), and the more patchy results of those that analysed climate-induced changes in habitat for the entire fish fauna of a region. In particular, the potential responses of cool- and warm-water species to future climate change show greater variation, and often depend on the location and the climate change scenario used. It appears that cool-water species are likely to follow the same general trend as cold-water species (i.e. a decline in the range and amount of suitable habitat, contraction of

Table 3 Observed and predicted changes in habitat suitability among freshwater fish families

	Habitat suitability change (%°C^{-1})			
	N	Observations	*N*	Predictions
Acipenseridae	-	-	6	-5.5 (-16.6;-0.6)
Anguillidae	1	-53.5	2	3.1 (3.0;3.2)
Balitoridae	1	23.9	1	-1.1
Blenniidae	1	-89.6	-	-
Catostomidae	-	-	16	-2.8 (-18.2;52.1)
Centrarchidae	2	29.9 (-2.2;62.0)	37	12.8 (-15.1;316.7)
Clupeidae	-	-	6	-1.2 (-9.0;9.0)
Cobitidae	1	86.8	0	-
Cottidae	1	28.8	5	-13.3 (-20.2;-4.9)
Cyprinidae	23	70.2 (-159.2;575.0)	74	4.4 (-27.0;259.6)
Esocidae	1	-29.7	6	-3.9 (-12.4;3.1)
Gasterosteidae	2	21.2 (13.1;29.2)	3	3.6 (-6.1;10.6)
Ictaluridae	2	245.2 (8.5;481.9)	12	21.2 (-13.4;164.1)
Lepisosteidae	-	-	2	-0.5 (-9.7;8.7)
Lotidae	1	-36.5	1	-28.1
Moronidae	-	-	4	0.5 (-10.8;8.4)
Mugilidae	1	-169.0	1	2.1
Osmeridae	-	-	1	-14.5
Percidae	4	46.2 (9.4;110.9)	23	3.6 (-20.3;100.0)
Pleuronectidae	1	-264.2	1	-9.4
Poecilidae	1	26.3	-	-
Poeciliidae	-	-	2	3.9 (-1.2;9.0)
Salmonidae	7	27.2 (-65.7;155.7)	71	-8.8 (-35.0;66.7)
Sciaenidae	-	-	2	0.8 (-7.4;9.0)
Umbridae	-	-	1	-9.6

N indicates the number of species × location included in the analysis. Numbers in parentheses correspond to the minimum and maximum values of effects. Dashes indicate families for which no quantitative effects were reported.

the distribution) but to a lesser degree (Stefan *et al.*, 2001; Mohseni *et al.*, 2003; Lyons *et al.*, 2010). Nevertheless, some studies have also suggested that some cool-water species could increase their probability of presence in some streams (Buisson *et al.*, 2008; Steen *et al.*, 2010) or could experience an increase in the area of suitable lake habitat (Magnuson *et al.*, 1990; De Stasio *et al.*, 1996).

Lastly, most studies are consistent in finding that warm-water species may stand to benefit from future climate warming. These species, which often constitute the greatest number of species in the fish fauna, could experience an increase in their suitable thermal habitat and their distribution (Stefan *et al.*, 2001; Mohseni *et al.*, 2003; Chu *et al.*, 2005). The observed increase in the probability of presence of 20 of 47 stream fish species in France over the two last decades (Poulet *et al.*, 2011) is consistent with the predicted increase in species richness under climate warming scenarios (Buisson & Grenouillet, 2009).

Changes in distributional range

As a result of changes in habitat suitability, the spatial position or altitudinal and/or latitudinal limits of fish species are expected to change. The most likely response is a shift in fish distribution to higher altitude or latitudes (i.e. northward in the Northern hemisphere), especially for cold-water species.

To date, the work of Hickling *et al.* (2006) remains one of the key studies quantifying recent shifts in the spatial distribution of freshwater fish. Using long-term data covering 25 years in Great Britain for 15 stream fish species, they have documented mean poleward shifts in northern range margin and altitudinal shifts in optimum by up to 51 km and 32.7 m, respectively. This pattern has also been reported for salmonid species in different parts of the northern hemisphere. For instance, population decline in the brown trout (*Salmo trutta*) at the vulnerable southern periphery of its range has recently been related to the loss of its thermal habitat (Almodóvar *et al.*, 2012), whereas Hari *et al.* (2006) have documented an upward habitat shift of about 130 m for this species in Switzerland. They also demonstrated that the contraction at the lower boundary of the distribution was linked not only with climate, but also with the interacting effects of the increase in the incidence of temperature-dependent Proliferative Kidney Disease since the early 1980s. There have also been several recent reports of pacific salmon (*Oncorhynchus* spp.) located outside their previously known distribution area which parallel an observed increase in water temperature (Babaluk *et al.*, 2000). Changes in precipitation regime have also been reported to explain recent population threats. For instance, Trape (2009) showed that the tropical fish populations of Central Sahara have experienced an increased extirpation risk following an unprecedented period of drought.

Future shifts to higher altitudes, or shifts in northern and southern limits have also been predicted for a large number of species. For instance, Matulla *et al.* (2007) predicted a displacement to an upper altitude of 70 m for the entire fish community of a river in Austria. Other studies that have quantified the potential altitudinal shift of several trout species under climate change scenarios found that they could either increase their distributions to upper altitudes (+269 to 286m, Kennedy *et al.*, 2009) or increase the altitude of their lower habitat boundary (Meisner, 1990a: up to 714m; Nakano *et al.*, 1996: up to 640-720m depending on species). Meisner (1990a) also predicted that, in response to a 3.8°C increase in water temperature, brook trout may disappear from the most southern states of its native range in the north-eastern United States.

However, these latitudinal shifts may not be restricted to cold-water fish, as populations of smallmouth bass (*Micropterus dolomieu*), walleye (*Stizostedion vitreum*), northern pike (*Esox lucius*) and channel catfish (*Ictalurus lacustris*) are also predicted to move northwards (Shuter *et al.*, 1980; McCauley & Beitinger, 1992; Minns & Moore, 1992). In fact, expansions beyond the currently known spatial distribution of several fish species have already been reported, potentially promoting the colonisation or establishment of non-native species. Johnson & Evans (1990) suggest that climate warming has permitted an invasive species, the white perch (*Morone americana*), to invade the Great Lakes, thus potentially endangering native populations. Similarly, the spatial distribution of the European bitterling (*Rhodeus amarus*) appears to have recently expanded in Eastern Europe, probably due to a combination of factors including a rise in ambient temperature (Van Damme *et al.*, 2007). Finally, whereas evidence of recent effects of climate change on stream fish has mostly been documented in the Northern hemisphere, Gómez *et al.* (2004) demonstrated that species located in the Southern hemisphere could also be affected. Specifically, they showed that water bodies located in dry areas of the Pampa regions were colonised by 10 fish species after a 30% increase in rainfall over the last half century; this area was previously known as being fishless.

These shifts in spatial distribution may result in an increase in fragmentation, as populations are expected to become restricted to isolated patches at high altitudes or latitudes, and isolated from other appropriate habitat areas (Keleher & Rahel, 1996; Flebbe *et al.*, 2006; Hari *et al.*, 2006). This potential increase in fragmentation has been mainly addressed for salmonid populations in North America, but patterns are congruent across studies. For instance, Rahel *et al.* (1996) have demonstrated that, for cold-water species of the North Platte River Basin in the Rocky Mountains, single large enclaves of suitable habitat could be fragmented into numerous smaller ones and experience a 47-90% decline in size depending on the warming scenario. This could considerably increase the vulnerability of isolated populations to future extinction. However, the lack of observations makes it impossible to support the predicted risk, even though similar assertions have already gained strong empirical support for many other taxa (Maclean & Wilson, 2011).

CONCLUDING REMARKS AND FUTURE RESEARCH

This global overview and meta-analyses of the literature reporting observed and predicted climate-induced effects on freshwater fish distribution confirm that freshwater fish species could be severely affected by contemporary climate change. Observations and predictions are quite correlated, thus supporting the reliability of future projections. Nevertheless, the magnitude and variability of changes actually observed in habitat suitability in response to recent climate warming exceeded those predicted under future climate scenarios, suggesting the influence of other non-climatic stressors. However, this synthesis also highlights the fact that current knowledge is still incomplete, notably because of geographic and taxonomic biases.

The geographic bias towards the Northern hemisphere and the temperate regions of the Nearctic and Palaearctic realms is not surprising, as this pattern largely mirrors the intensity of ecological research (Wilson *et al.*, 2007; Pyšek *et al.*, 2008). This geographic bias could have important implications when scientific findings are translated into conservation measures. Indeed, the ongoing regional and global freshwater assessment programmes are accumulating evidence that threatened or ‘climate-change-susceptible’ species show clear geographic patterns, with high concentrations of species at-risk in the Southern hemisphere (e.g. Foden *et al.*, 2008). As these regions account for a major proportion of freshwater fish endemism (Oberdorff *et al.*, 2011), our overall understanding of climate-induced effects on freshwater fish distribution would greatly benefit from further research in so far poorly studied regions.

By meticulously reporting each targeted fish species and its representative family across all published articles, our study provides the first quantitative evidence of a serious taxonomic bias in studies assessing climate-induced changes in freshwater fish distribution. The list of reported fish species (n=183) represents only a tiny proportion of the global freshwater fish fauna that probably comprises around 13 000 species. More surprisingly, the bias against threatened species and towards a small number of thoroughly studied species persists in regions with high research intensity, reflecting human interest in some particular fish species. Undoubtedly, this taxonomic bias towards salmonids and cold-water species is problematic, as it affects our perception of the influence of climate on freshwater fish overall. Indeed, the general impression emerging from the literature is that freshwater fish may respond negatively to climate change. However, the dramatic effects predicted for most cold-water fish species do not hold for all fish species, and many others have already responded in a more mitigated (or even contrary) manner. In particular, despite their important role in ecosystem processes (Vanni, 2002), fish species with no commercial or recreational interest have been poorly studied. We suggest that broadening the range of studied species is critical in depicting the potential effects of climate change more effectively, thus providing more reliable assessments of freshwater fish vulnerability that will make it possible to identify the appropriate conservation measures.

More importantly, the threats facing freshwater fish are not limited to habitat loss, as species-specific shifts in distributions may result in novel species assemblages displaying changes in competition, predation, or other biotic interactions (e.g. Williams & Jackson, 2007; Stralberg *et al.*, 2009). Because future climate-induced changes in assemblage composition have rarely been addressed for freshwater fish (but see Buisson & Grenouillet, 2009), the consequences of such novel species assemblages remain unexplored and deserve more attention. Empirical studies could also greatly benefit from community ecology, as the analysis of assemblage responses through functional diversity (i.e. the composition of biological traits) provides a promising area for future research (Olden *et al.*, 2010). Taking into account the ecological characteristics of species should be helpful for investigating the functional consequences of climate change, identifying similar responses across contrasting assemblages and thus enhancing our understanding of climate-induced changes across a broad level of organisation.

From a methodological point of view, the empirical evidence of climate-induced changes in freshwater fish distribution need to be related statistically to trends in climate using appropriate approaches (reviewed in Brown *et al.*, 2011), as sufficiently robust approaches have rarely been used so far. One of the critical challenges facing long-term analyses is to enhance our ability to disentangle the relative effects of climate change and those of other stressors that affect freshwater fish distribution, especially as they may interact with one another (Olden *et al.*, 2010). In the case of predictive studies, a number of criticisms about distributional models have called their validity into question (reviewed in Pearson & Dawson, 2003; Elith & Leathwick, 2009). Although these acknowledged drawbacks fall outside the scope of this review, we claim that accounting for most of the recent advances in predictive modelling will reinforce our ability to refine projections of future freshwater fish distribution. Among these ongoing and future improvements, we suggest that particular attention should be paid to the inherent uncertainty in projections, the need to include the biological characteristics (i.e. dispersal abilities) of the species, and the promising combination of both distributional and empirical approaches (Kearney & Porter, 2009; Dormann *et al.*, 2012) to provide more robust and detailed projections. Given that predictions of future effects limited to changes in climate appear to be underestimated relative to recently measured changes, including other non-climatic stressors (e.g. change in land-use, invasive species, habitat destruction) would also enhance our ability to assess the potential influence of global change in the future.

Finally, our study has revealed that further empirical evidence of recent climate-induced changes in freshwater fish distribution is needed to allow a comprehensive comparison with predicted changes under climate change scenarios. Our encouraging results comparing observed and predicted changes in habitat suitability for a limited subset of freshwater fish families lead us to believe that this research topic deserves further attention. As national monitoring programmes are growing in number in response to the environmental policies being implemented in several countries for protecting and managing water bodies over the last decade (e.g. the Water Framework Directive in Europe), it is likely that long-term data will accumulate in the coming years. These data will provide a baseline guide allowing future methodological advances and better anticipation of future changes to be achieved. Observed and predicted trends would then provide more comprehensive knowledge to enhance the reliability of projections, thus reinforcing our ability to assess climate-induced effects on freshwater fish.

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ARTICLE II (P_{II})

Comte L & Grenouillet G (2013**)** Species distribution modelling and imperfect detection: comparing occupancy versus consensus methods. ***Diversity and Distributions*** 19: 996–1007.

Species distribution modelling and imperfect detection: comparing occupancy versus consensus methods

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ABSTRACT

Aim We assessed the influence of species non-detection in modelling species distributions with an ensemble consensus approach that did not account for imperfect detection, compared with an occupancy model that did.

Location The hydrographic network of France.

Methods We compared range maps of 35 stream fish species with differing degrees of detectability predicted using a consensus approach combining eight species distribution models (SDMs) to maps produced using an occupancy model. Using a spatially and temporally extensive monitoring database of fish populations (France), we modelled the occurrence of species as a function of several climatic and habitat variables and projected species distributions across the whole of the French hydrographic network. The benefits of occupancy models were then assessed from the differences in both predictive performance and species distribution.

Results We found that although the occupancy models enhanced the performance for difficult to detect species, consensus models outperformed occupancy models for highly detectable species. In contrast to the minor differences observed in performance measures, estimates of species distributions were severely affected by whether or not imperfect detection was accounted for and varied linearly according to species detectability.

Main conclusions This study demonstrated that false absences could have major consequences in estimating species distribution ranges. However, accounting for imperfect detection may not be enough to improve conventional SDMs. These findings could have important implications for conservation, notably in developing large-scale distribution models and documenting species range shifts in the context of recent climate change.

Keywords: consensus method; false absence; global change; occupancy model; species distribution model

INTRODUCTION

Quantifying the spatial distribution of species is of crucial concern in most conservation studies and biodiversity monitoring programmes (Holt & Keitt, 2005; Gaston & Fuller, 2009). Conservation decisions are often made at large scales (Guisan & Thuiller, 2005), and so accurate mapping of species distributions is of utmost importance, for both fundamental and applied purposes (Hanspach *et al.,* 2011; Rocchini *et al.,* 2011). Describing species distributions at different spatial and temporal scales has a long history in ecology and biogeography. Increasing interest in how species respond to climate change makes it essential to be able to determine species distribution ranges accurately. Indeed, changes in species prevalence or the areas occupied have been used as key components in assessing responses to environmental change as they could reflect range contraction or expansion (Fagan *et al.,* 2005; Isaak *et al.,* 2010). Distribution optima along environmental gradients have also been recognized as being especially relevant indicators of climate-induced range shifts (Archaux, 2004; Shoo *et al.,* 2006; Matulla *et al.,* 2007; Lenoir *et al.,* 2008). Species distribution models (SDMs) have become a useful approach for modelling species distributions, based on the relationships between recorded presences of the species and environmental variables. Sampling records often have limited coverage, and so predictive approaches make it possible to model the spatial distribution of species over wide geographical areas (Guisan & Zimmermann, 2000) and to compare species ranges based on occurrence data from unpaired sites (Crimmins *et al.,* 2011; Maggini *et al.,* 2011).

The increased use of distribution maps to depict the geographical distribution of biodiversity makes assessing sources of error and uncertainty a key issue in species distribution modelling (Hanspach *et al.,* 2011; Rocchini *et al.,* 2011). The reliability of predictions is acknowledged to depend on various uncertainty components, such as data quality (e.g. Graham *et al.,* 2008), methodological choices (e.g. Buisson *et al.,* 2010; Nenzén & Araùjo, 2011) and species traits (e.g. Luoto *et al.,* 2005). In particular, the statistical method chosen is known to be an important source of variability (Thuiller, 2003; 2004). In recent years, consensus methods have demonstrated their ability to cope with prediction variability by combining an ensemble of SDM predictions (Lawler *et al.,* 2006; Marmion *et al.,* 2009; Grenouillet *et al.,* 2011). They are increasingly being used for conservation purposes and are routinely applied (e.g. BIOMOD, Thuiller, 2003). They combine several predictions from different modelling methods to yield a final occurrence probability reflecting the majority trend, which usually provides more accurate predictions (Marmion *et al.,* 2009).

Although they are often ignored, false absences resulting from imperfect detection have also been highlighted as a fundamental potential source of uncertainty (Wintle *et al.,* 2004; Rocchini *et al.,* 2011; Kéry, 2012). False absences occur when species that have not been detected are recorded as absent although they are in fact present, and the detectability of species (p) (i.e. the probability of detecting a species that in fact occurs at a site), is generally < 1 (MacKenzie *et al.,* 2002; Kéry & Plattner, 2007; Gibson, 2011; Meyer *et al.,* 2011). False absences reduce the predictive accuracy of conventional SDMs that do not account for detection bias (Lobo *et al.,* 2010; Rota *et al.,* 2011) and introduce bias into the relationships between a species and its environment (Tyre *et al.,* 2003; Gu & Swihart, 2004; Gibson, 2011). However, changes in biodiversity due to global change are mainly inferred from models that confound the occurrence (Ψ) and detectability (p) of species, and species range maps are generally inferred from static occurrence data, assuming that $p = 1$. As a result, the evaluation of the effects of global change on biodiversity may be biased (Kéry & Plattner, 2007; Tingley & Beissinger, 2009), reducing our capacity to initiate effective conservation management strategies.

Occupancy models explicitly account for species detectability, thus improving prediction reliability (MacKenzie *et al.,* 2002; Tyre *et al.,* 2003) and produce more accurate species range estimates (Kéry *et al.,* 2010). Based on the replication of observations, these models consist essentially of two nested binomial logistic regressions; the first models the occurrence of species (i.e. their true presence or absence), while the second models species detection (i.e. their detection or non-detection), conditional on a species being present (Wintle *et al.,* 2004; Kéry, 2012). In recent years, they have been shown to be useful in attempting to model *true* rather than apparent species distributions (Karanth *et al.,* 2009; Kéry *et al.,* 2010; Gibson, 2011), as well as for assessing the effects of anthropogenic changes (Altwegg *et al.*, 2008; Moritz *et al.*, 2008; Tingley *et al.,* 2009). Although the considerable potential of site-occupancy models has been impaired by the difficulty of obtaining the data required, many biodiversity monitoring programmes involve replicate observations, which makes many datasets amenable to this approach, even though the data collection protocol was not initially designed with this in mind (Kéry *et al.,* 2010; Gibson, 2011).

So far the effects of false absences on species distributions as predicted by conventional SDMs have rarely been investigated (but see Kéry *et al.,* 2010; Lobo *et al.,* 2010) and never been investigated using a consensus approach. Attempts are now being made to assess the benefits of using site-occupancy models for modelling species distributions instead of the models that are routinely used and that do not account for imperfect detection. To explore the influence of false absences on the predicted spatial distribution of species with differing degrees of detectability, we compared range maps of 35 stream fish species predicted using a consensus approach combining eight SDMs that assume $p = 1$, to maps based on an occupancy model. We modelled the occurrence of species as a function of several climatic and habitat variables and projected species presence-absence distributions over the entire French hydrographic network. We then produced maps of species distribution providing information about the variability associated with data quality and methodological choices (e.g. Puschendorf *et al.,* 2009; Grenouillet *et al.,* 2011). Our aim was to compare approaches that do not account for detection bias to those that do explicitly account for imperfect detection, to (1) determine how much the reliability of predictions was improved when imperfect detection is accounted for and (2) quantify the potential impacts of species detectability on the predicted species distributions.

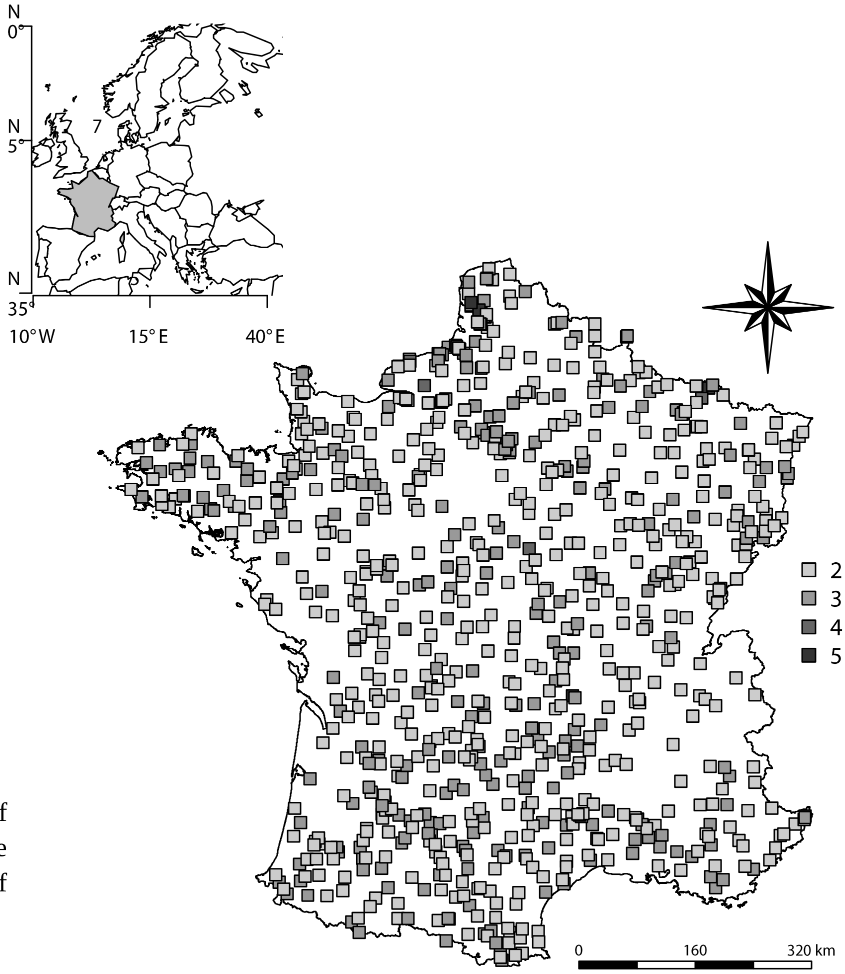

Figure 1 Spatial distribution of the sites with a grey scale indicating the number of sampling occasions.

METHODS

Study area and sampling design

Our analyses drew on the electrofishing database of the French National Agency for Water and Aquatic Environment (Onema), representing a spatially and temporally extensive surveys of freshwater fish at the national scale. Since 1995, surveys coordinated throughout the entire French river network have monitored all fish assemblages representative of the wide diversity of environmental conditions found in rivers and streams across the different hydrographic units (Poulet *et al.,* 2011). Sampling sites corresponded to stream reaches (mean sampling area = 832 m² ± 395 SD) and included several pool and riffle sequences. At each site, a standardized electrofishing protocol during low-flow periods (mainly May–October) was carried out, and a removal method was used to sample stream fish in one to three successive passes. Several procedures were used depending on river width and depth. Small streams were sampled by wading, by single- or multiple- (i.e. two or three) pass removal, and large rivers by boat or combined prospection methods (i.e. boat plus wading), usually by single-pass removal. Sampling strategies involved either a complete prospection of the stream reach, with partial sampling of the different types of mesohabitat, or of the river margins and delimited areas of habitat (Belliard *et al.,* 2008).

Because repeated surveys across large temporal and spatial scales provide more opportunities to obtain an accurate description of species range structure and geographical extent (Fortin *et al.,* 2005; Mackenzie & Royle, 2005; Feeley, 2011), we initially limited our analyses to sites that had been sampled at least twice over a 3-year period (i.e. from 2007 to 2009). This resulted in 839 sites, which were sampled on a total of 1984 occasions, ranging from two to five samples per site (mean 2.4 ± 0.5 SD) (Fig. 1).

Study species

For statistical reasons, we selected only the species that would provide enough data for developing SDMs, and only retained those detected in at least 5% of the sites during the study period, that is a total of 35 species (Table 1). Estimates of mean detectability were calculated from the probabilities of detections predicted by the occupancy models (see below) and ranged from 0.18 to 0.87 (Table 1).

Table 1 Mean detection probabilities and species prevalence

Species	Detection probability	Prevalence
Abramis brama	0.32	0.22
Alburnoides bipunctatus	0.80	0.20
Alburnus alburnus	0.72	0.42
Ameiurus melas	0.48	0.12
Anguilla anguilla	0.87	0.57
Barbatula barbatula	0.84	0.66
Barbus barbus	0.79	0.38
Blicca bjoerkna	0.40	0.21
Carassius carassius	0.31	0.11
Chondrostoma nasus	0.66	0.15
Cobitis taenia	0.57	0.05
Cottus gobio	0.87	0.50
Cyprinus carpio	0.30	0.17
Esox lucius	0.54	0.31
Gasterosteus aculeatus	0.60	0.12
Gobio gobio	0.87	0.72
Gymnocephalus cernua	0.36	0.17
Lepomis gibbosus	0.58	0.34
Leuciscus leuciscus	0.68	0.36
Micropterus salmoides	0.18	0.05
Parachondrostoma toxostoma	0.55	0.07
Perca fluviatilis	0.70	0.46
Phoxinus phoxinus	0.84	0.61
Pseudorasbora parva	0.38	0.10
Pungitius pungitius	0.53	0.11
Rhodeus amarus	0.63	0.20
Rutilus rutilus	0.80	0.60
Salmo salar	0.56	0.09
Salmo trutta	0.70	0.54
Sander lucioperca	0.28	0.11
Scardinius erythrophthalmus	0.42	0.23
Silurus glanis	0.43	0.17
Squalius cephalus	0.86	0.68
Telestes souffia	0.80	0.07
Tinca tinca	0.43	0.25

Occurrence and detection covariates

We modelled the occurrence of each species as a function of several habitat and climatic variables strongly related to fish spatial distribution (Buisson *et al.,* 2008). All variables were derived from the Geographic Information System (GIS), based on the geographical coordinates of the sampling sites. Elevation (*m*) was extracted from a 50-m resolution digital map, and slope (SLO, ‰) from a RHT hydrological layer (Pella *et al.*, 2012). We derived catchment variables from Catchment Characterisation and Modelling River and Catchment database for Europe (CCM2) layers (Vogt *et al.*, 2007): the full area drained by the upstream area (km²) and the cumulated length of the upstream flow network (*m*). We then used a principal component analysis (PCA) of these two catchment variables to obtain a synthetic variable representative of the upstream-downstream gradient (*G*) accounting for 97.80% of the total variability. Climatic variables were extracted from 30 arc-s resolution WorldClim layers for the period 1961-1990 (Hijmans *et al.*, 2005): mean temperature of the coldest quarter (°C), mean temperature of the warmest quarter (°C), temperature seasonality (SD × 100), precipitation of the wettest quarter (mm), precipitation of the driest quarter (mm) and precipitation seasonality (CV).

We modelled detection probability as a function of several variables related to the characteristics of the surveys (i.e. sampling-level covariates) and of the sampling sites (i.e. site-level covariates). For all the species, sampling-level covariates included in the model were as follows: the Julian date of the survey, the year of the survey, the surface area prospected, the number of removal passes, the prospection method (i.e. wading, boat, or combined) and the sampling strategy (i.e. complete or partial). As electrofishing efficiency is influenced by many environmental factors (e.g. water depth, discharge) that vary along the upstream-downstream gradient (Meador, 2005), we included *G* as the single site-level covariate. Linear and quadratic effects of the Julian date of survey and of *G* were also considered in the models. To improve the model convergence of occupancy models, all non-categorical variables were normalized (Fiske & Chandler, 2011).

CONS - Consensus models

An ensemble consensus approach consists in the combination of an ensemble of predictions generated by a number of different modelling methods with different predictive abilities, using a consensus algorithm. To account for the variability introduced by the modelling methods, we followed the procedure applied in Marmion *et al.* (2009) by simply averaging the probabilities of occurrence predicted by eight SDMs: Generalized Linear Models (GLM), Generalised Additive Models (GAM), Multivariate Adaptive Regression Splines (MARS), Mixture Discriminant Analyses (MDA), Classification and Regression Trees (CART), Random Forest (RF), Generalized Boosted Trees (GBT) and Artificial Neural Networks (ANN). Details are presented in Appendix S1 in Supporting Information.

OCCU - Occupancy models

We used a single-season occupancy modelling approach (MacKenzie *et al.*, 2002; Tyre *et al.*, 2003), which allowed us to model two nested processes: the species occurrence state at the site (i.e. occupied/not occupied) and the success of observation (i.e. detected/not detected). The occurrence state at each site, z_i, is a binary variable (presence, $z_i = 1$; absence, $z_i = 0$) that can be modelled as a Bernoulli random variable:

$$z_i \sim \text{Bernoulli}(\Psi)$$

Where Ψ is the probability of the occurrence (or site occupancy) of the species at site *i*. Unlike conventional SDMs, which confound the probability of occurrence at site *i* (represented by Ψ) and the detection process during the survey *j* (represented by the detection probability *p*), occupancy models include an additional observation model to account for imperfect detection. The actual observations at site *i* during survey *j*, y_{ij}, is also a binary variable conditioned by the presence of the species (detection, $y_{ij} = 1$; non detection, $y_{ij} = 0$), that can be modelled as a Bernoulli random variable:

$$y_{ij} | z_i \sim \text{Bernoulli}(z_i \times p_{ij})$$

Therefore, the likelihood of observing a detection history for a site (a combination of detection and non-detection events) is a function of the occurrence probability (occupancy, Ψ) and detection probability (detectability, *p*), and maximum likelihood methods can be used to estimate the detection and occupancy parameters.

We also modelled Ψ_i and p_{ij} as linear functions of the above-mentioned covariates using the logit link function (MacKenzie *et al.*, 2002; Tyre *et al.*, 2003). We used the Akaike information criterion (AIC) to rank competing models and select the most parsimonious model

(Burnham & Anderson, 2004). Initially, we fitted models while keeping the occurrence component constant [Ψ (.)], and optimized the component for detection probability with a suite of competing models with all additive combinations of variables. The model most supported according to AIC determined the form of the detection function to be used to model the occurrence probability. In this second set of competing models, the component for detection probability was kept constant, allowing Ψ to vary with all additive combinations of variables to find the best set of variables explaining site occupancy adjusted for imperfect detection for each stream fish species.

Occupancy models were developed using the package *unmarked* (Fiske & Chandler, 2011) in R environment software v 2.13.0 (R Development Core Team, 2011). Results for the variable selection of the model's component for detection probability are given in Appendix S2 (Supporting Information).

Modelling process

To compare distribution maps modelled using consensus and occupancy models, we ran independent models on the same pool of sites for both modelling approaches. The models were calibrated on 70% of the sites, while the remaining 30% were used for evaluation and threshold selection. To construct the consensus models, we randomly selected one detection/non-detection event at each site to avoid pseudo-replication. In contrast, all detection histories were used to calibrate the occupancy models. Evaluation and threshold selection were based on the same data set for both modelling approaches, composed of one detection/non detection event randomly chosen for each of the testing sites. Following Hijmans (2012), the testing sites were selected after subsampling the remaining 30% sites using pairwise distance sampling to remove spatial sorting bias from the testing data set (i.e. the difference between the geographic distance from testing-presence to training-presence sites and the geographic distance from testing-absence to training-presence sites). Finally, the different steps of the modelling process were repeated 100 times (hereafter referred to as 'iterations').

Comparing predictive performance

For conventional single-SDMs and consensus methods, we predicted probabilities of occurrence at the testing sites and compared them with observations. However, for the occupancy models, we adjusted the probabilities of occurrence at the testing sites for imperfect detection by multiplying the predicted probabilities of occurrence by the predicted probability of detection (Rota *et al.*, 2011). We then compared the adjusted predictions of detection or non-detection to the observed data using several performance measures.

The predictive performance of all models was first evaluated using a threshold-independent measure, the calibrated area under the receiver operating curve (cAUC), which controlled for the effect of any remaining spatial sorting bias (Hijmans, 2012). The cAUC allows the AUC value of each model to be adjusted using a geographic null model based solely on the spatial pattern of the model calibration sites. The null model did not use any environmental data but was computed using the inverse geographical distance to the nearest model presence calibration site. The null model was then evaluated with the same testing data set to provide a null model AUC (nAUC), and the cAUC computed as follows:

$$\text{cAUC} = \text{AUC} + 0.5 - \max(0.5, \text{nAUC})$$

This procedure establishes how easy it is to predict presence/absence in the testing data from the geographic position of the calibration data alone and allows for the comparison of cross-validation results for different species and/or calibration datasets.

For many applications in conservation planning, presence-absence maps are generally preferred to continuous maps of probability of occurrence (Wilson *et al.,* 2005), which entails selecting a threshold for converting probabilities of occurrence into binary data (Manel *et al.,* 2001; Liu *et al.,* 2005; Freeman & Moisen, 2008). To convert predicted occurrence probabilities into binary data (i.e. presence or absence), we thus used threshold values that maximized the sum of sensitivity and specificity, as this selection method is not affected by pseudo-absences in the testing data set (Liu *et al.*, 2013). The binary maps obtained allowed us to depict the modelled spatial distribution of the species and to provide other estimates of model accuracy based on comparing observed versus predicted presences and absences (Hanspach *et al.*, 2011).

Specifically, we used criteria derived from the confusion matrix, the probabilities of presence (i.e. sensitivity) correctly predicted and the true skill statistic (TSS, Allouche *et al.*, 2006).

To determine whether the occupancy models provided better predictive performances than conventional single-SDMs and the consensus method, we used paired *t*-tests corrected for multiple comparisons using the Benjamini-Hochberg method (Benjamini & Hochberg, 1995).

To compare the modelling approaches with regards to species detectability, we first calculated the differences in predictive performances between the consensus and occupancy models (i.e. CONS - OCCU) for each combination (species × iteration), revealing only the differences introduced by correcting for imperfect detections. We then used linear regressions between the differences in model performance and species detectability using a Gaussian error distribution.

Mapping species distributions

Finally, we predicted the probabilities of occurrence of the 35 species on the French hydrographic network based on the reaches extracted from the CCM2 database (Vogt *et al.*, 2007), for which environmental conditions did not differ from those of the calibration data sets. Probabilities were then transformed into presence-absence using the previously calculated thresholds. We thus obtained 100 final predictions per species for each modelling approach.

For both the consensus and occupancy modelling approaches, we mapped the sum of the presence-absence outputs across the 100 predictions for each reach of the French hydrographic network and for each species. This enabled us to visualize geographical areas of agreement for both absence (i.e. sum equals 0) and presence (i.e. sum equals 100), and areas of high disagreement (i.e. intermediate sum values) among the predictions (e.g. Lawler *et al.*, 2006; Grenouillet *et al.*, 2011). We also mapped the differences between the sum of the predicted presences and absences between the consensus and occupancy predictions (i.e. CONS - OCCU), thus highlighting geographical areas of agreement (i.e. difference equals 0), and areas of high disagreement (e.g. -100 indicated 100 presences predicted only by the occupancy model).

Comparing species distributions

Similarity among predictions

To compare the species distributions between methods, we calculated the similarity between spatial distributions predicted by the consensus and occupancy models, for each species and each iteration using the Jaccard index (Gower & Legendre, 1986).

Species distribution range

To find out whether incorporating false absences affected the species ranges predicted by conventional SDMs compared to those predicted by occupancy models, we calculated the differences in several range descriptors between predictions (i.e. CONS - OCCU), for each species and iteration. We first considered the spatial extent of the species defined as the length of the hydrographic network occupied by the species (e.g. Fagan *et al.*, 2002), expressed as a percentage of the total network length. We also defined the centre of the species' distribution (hereafter referred to as the 'range centre') along the distance-from-source gradient in terms of the median values of the stream reaches where the species was predicted to be present (e.g. Zuckerberg *et al.*, 2009). For both similarity and distribution ranges, linear regressions including species detectability were used, assuming a Gaussian error distribution.

RESULTS

Comparing predictive performance

All model performances are shown in Appendix S3 (Supporting Information). As expected, consensus models displayed better predictive performances than conventional single-SDMs (i.e. cAUC, TSS, sensitivity; paired *t*-test, $P < 0.001$), except compared to RF (TSS; $P > 0.05$). Occupancy models provided a better ability than single-SDMs to predict where species would be detected ($P < 0.001$), except compared to RF (cAUC, TSS; $P > 0.05$). Surprisingly, occupancy models did not show better predictive accuracy than consensus models ($P > 0.05$).

Differences in predictive performance between the consensus and occupancy models varied as a function of species detectability, particularly for cAUC and TSS values (Fig. 2). Although not significant, the relationship between sensitivity values and species detectabilities displayed the same trend. Overall, occupancy models tended to have better performance measures than consensus models for species with low detectability and poorer performance measures for species with high detectability. However, mean differences in performance measures between the modelling approaches were minor and ranged from -0.04 to 0.07, -0.05 to 0.11, and -0.10 to 0.10 for the cAUC, sensitivity and TSS measures, respectively.

Comparing species distributions

The similarity between consensus and occupancy model predictions appeared to be linearly affected by species detectability (Fig. 3). For poorly detectable species (e.g. *Cyprinus carpio*), marked differences were observed in modelled spatial distributions, but the mean similarities observed for highly detectable species (e.g. *Cottus gobio*) also indicated an effect of species non-detection.

Overall, the modelled spatial distributions were considerably affected by the false absences, as reflected by the marked differences between the descriptors of spatial distribution estimated using the consensus and the occupancy models (Fig. 4). Differences were higher for poorly detectable species, but also appeared for highly detectable species. Failing to account for imperfect detection reduced species spatial extent (Fig. 4a) and the range centre was located further downstream (Fig. 4b). Conventional models almost always resulted in a narrower species spatial extent than models that incorporated imperfect detection (Fig. 4c), regardless of the species and/or the calibration dataset involved. Similarly, the choice of conventional models most often triggered downstream expansion of the distribution, although smaller upstream expansions were also observed (Fig. 4d). As a result, the percentage of the reach occupied fell on average by about 14%, and the range centre shifted along the distance-from-source gradient by about 18 km downstream.

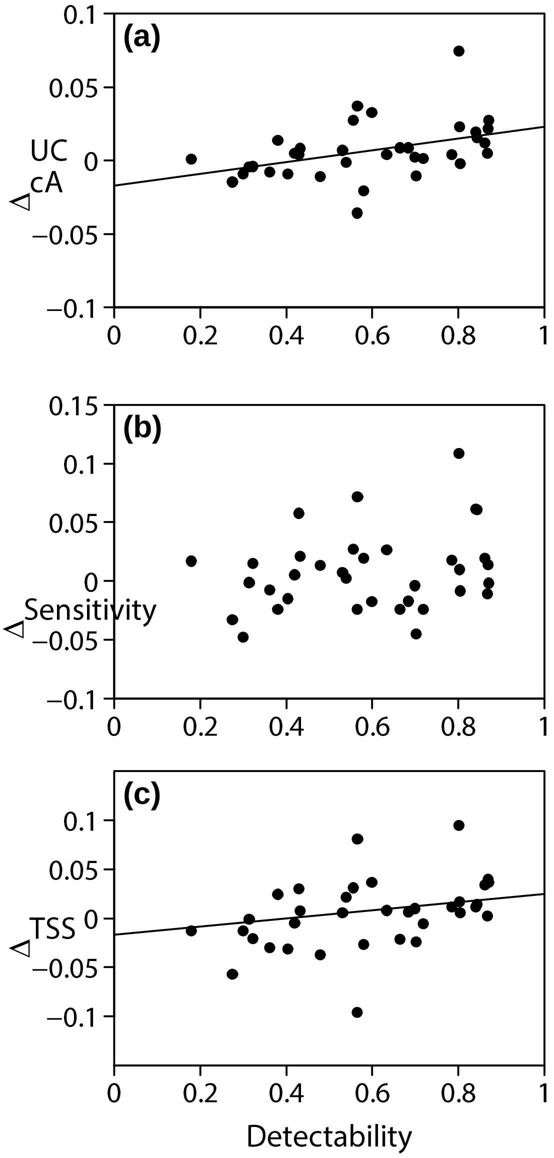

Figure 2 Effect of species detectability on the differences in predictive performances of the consensus and occupancy models (i.e. CONS - OCCU) for (a) calibrated area under the receiver operating curve, (b) Sensitivity and (c) true skill statistic. Lines indicate significant linear relationships ($P < 0.05$).

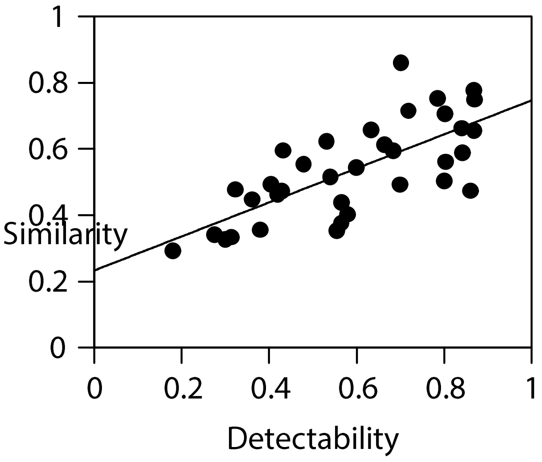

Figure 3 Effect of species detectability on the similarity between the consensus and occupancy model predictions. Line indicates significant linear relationship ($P < 0.05$).

To illustrate the geographical areas of agreement and disagreement between consensus and occupancy predictions, we produced maps summing the predicted presence-absence under both models, for two species with differences in detectability (Fig. 5). For the highly detectable species (*Cottus gobio*), areas of disagreement appeared to be spatially structured, with the most noticeable differences occurring at the edge of the modelled spatial distribution (blue or red, Fig. 5). Indeed, although maps resulting from the two models appeared to be similar, the differences between them revealed a systematic loss in predicted occurrences for the downstream reaches, when modelled with consensus methods (shown in blue). This caused a decrease in the spatial distribution for consensus models of 7% of the total network length, although the resulting difference in range centre along the distance-from-source gradient appeared to be relatively small (about 1.2 km upstream). Differences in spatial

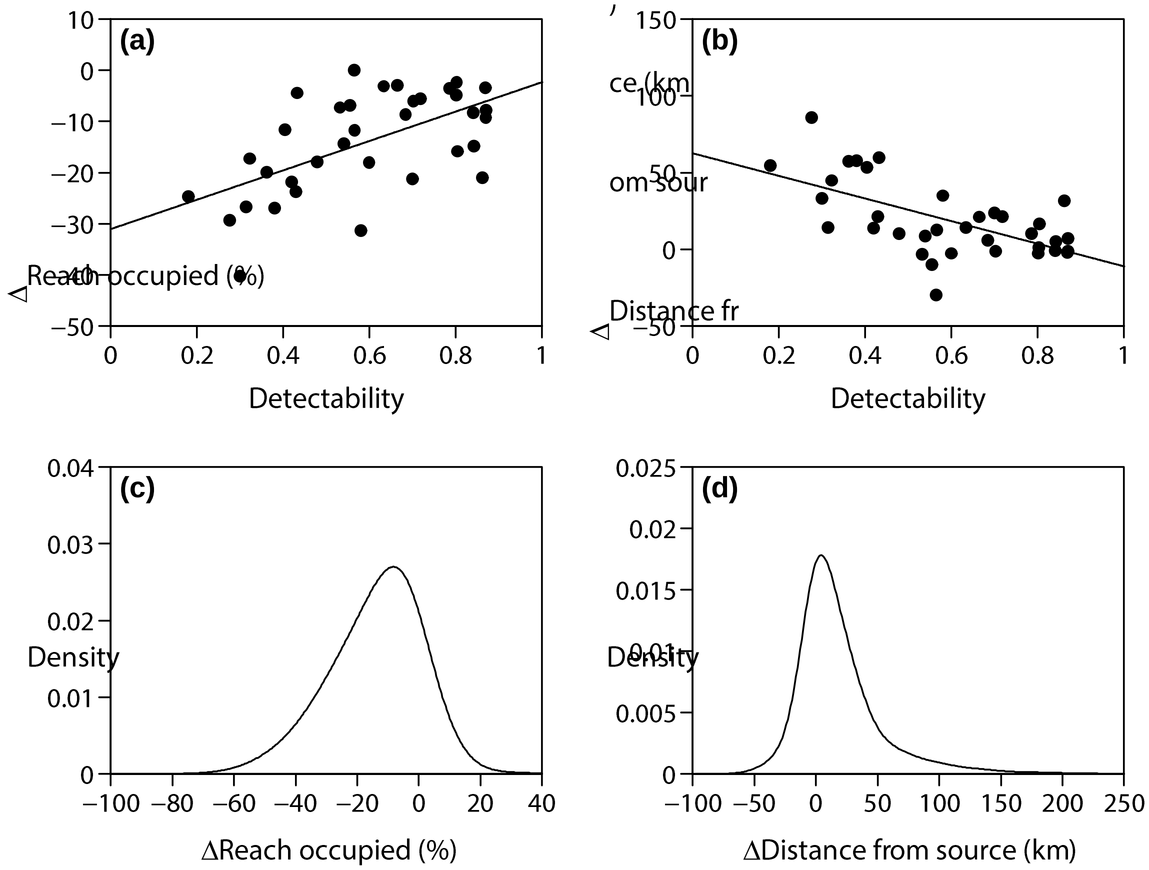

Figure 4 Effect of species detectability on the differences in the predictions of (a) the length of reach occupied (%) and (b) the location of the species range centre along the distance-from-source gradient between consensus and occupancy models (i.e. CONS - OCCU). Lines indicate significant linear relationships ($P < 0.05$). Probability density functions for the differences in (c) the length of the reach occupied, and (d) the location of the range centre along the distance-from-source gradient, across all species and all iterations.

distribution did not only result in a loss of suitable habitat when based on consensus models, but also in stream reaches predicted as being unsuitable by occupancy models but as being suitable by consensus models (in red). For the poorly detectable species (*Cyprinus carpio*), major differences were observed between the consensus and occupancy prediction maps across the entire distribution (blue, Fig. 5). Failing to account for imperfect detection caused a reduction in the spatial distribution of the species by about 40% of the total network length and a difference in the range centre along the distance-from-source gradient by 27 km downstream.

DISCUSSION

While overcoming model prediction errors and uncertainty has become an integral part of research in species distribution modelling (Hanspach *et al.,* 2011; Rocchini *et al.,* 2011), the problems raised by variable species detectability has not so far been widely recognized in the field (Kéry, 2012). In this study, our main objective was to compare range maps modelled using occupancy models that account for imperfect detection to consensus models routinely used in conservation studies.

Occupancy models did not always demonstrate the better predictive performances than models that did not account for imperfect detection, except for poorly detectable species. Indeed, occupancy modelling methods did not always lead to better predictions of where species would be detected than consensus models, and decreases in predictive performances were observed for highly detectable species. However, absolute differences in predictive performances were relatively small, irrespective of the performance

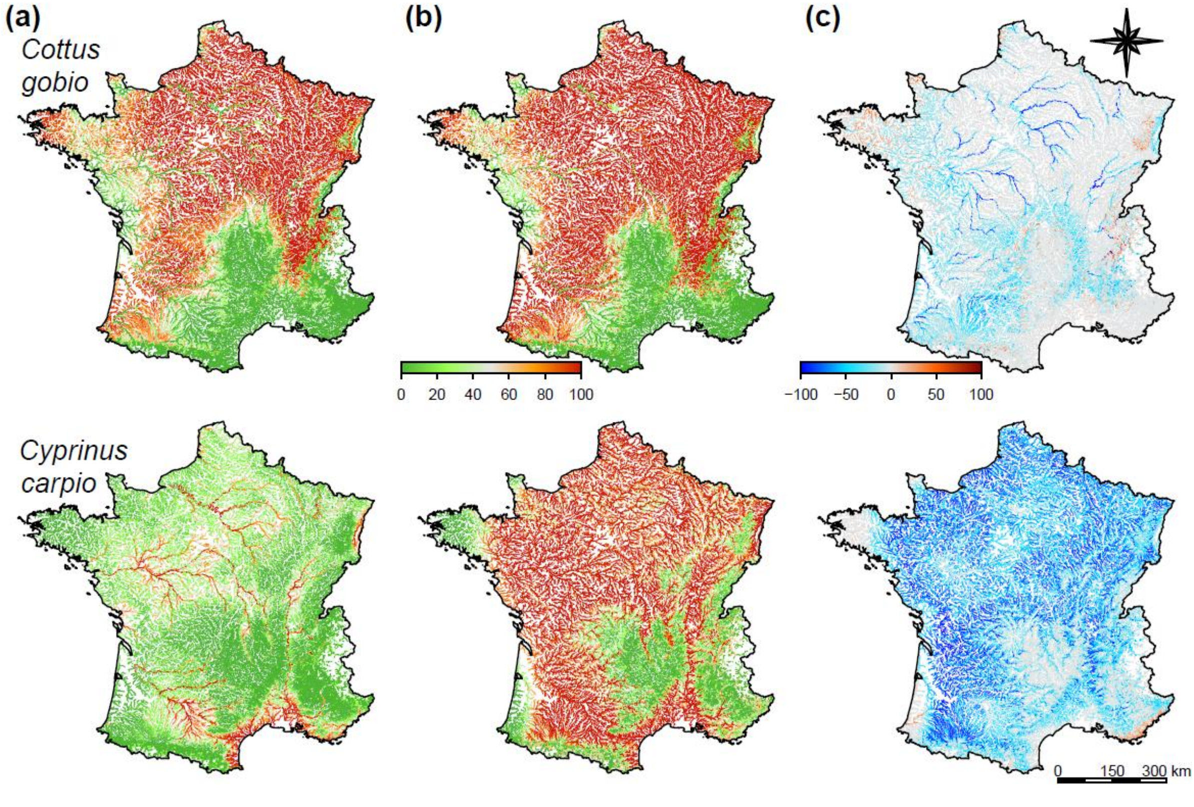

Figure 5 Maps showing examples of the influence of species detectability on the predicted spatial distributions of a highly detectable species *Cottus gobio* and a poorly detectable species *Cyprinus carpio*. The agreement between presence-absence predictions was measured by summing the 100 predictions (iterations) for each reach of the French hydrographic network for (a) the consensus models, and (b) the occupancy models, with a colour scale ranging from green (no predicted presence) to red (100 predicted presences); (c) the differences between the sum of the 100 predictions based on the consensus models and the occupancy models (i.e. CONS - OCCU), with a colour scale ranging from blue (100 presences predicted only by occupancy models) to red (100 presences predicted only by the consensus models).

measures chosen (threshold-independent or threshold-dependent measure). In contrast, the spatial patterns of predicted species distributions were markedly affected by taking imperfect detection into account, particularly for poorly detectable species. As the prevalence of the species was underestimated as a result of non-detection, it seems likely that species distributions estimated using models that confound occupancy and detection probabilities would be consistently underestimated. In this study, differences in species range descriptors inferred from both consensus and occupancy models were linearly affected by the species detectability.

The apparent discrepancy between the differences in performance measures and those in modelled spatial distributions may raise questions about the information provided by synthetic discrimination measures, such as AUC. Recently, several authors have pointed out that AUC values must be interpreted with caution, as they can produce misleading comparisons (Lobo *et al.*, 2008; Lobo *et al.*, 2010). Nevertheless, comparisons of cAUC values, allowing comparison of results for different species and different calibration data sets after removal of spatial sorting bias (Hijmans, 2012), led to the same conclusions: occupancy models only slightly improved predictive performances for poorly detectable species and performed consistently worse for highly detectable species. One possible reason for this might have been the selection of factors that were not relevant to detection probabilities. False absences in the evaluation datasets may also have distorted performance measures by increasing false positive rates. Indeed, despite the potential for misleading evaluation, the imperfect detection of species is still a challenge in determining model accuracy (but see Mackenzie *et al.*, 2004; Zipkin *et al.*, 2012). Although the use of a cross-validation procedure attempting to remove spatial sorting bias improved the way in which model performance was estimated, it did not solve all problems (Hijmans, 2012). Model evaluation is inherently problematic, even when model results are adjusted, as it primarily depends on the quality of the testing data set, and essentially on reliable absences (Lobo *et al.*, 2010). Clearly more work is thus needed to explicitly quantify the uncertainty in the quality of model predictions while accounting for species imperfect detection, as this can lead to crucial insights into changes in species distributions in response to human-induced environmental changes (Zipkin *et al.*, 2012).

However, we found that occupancy models provided better accuracy than individual SDMs, which do not account for detection bias (Rota *et al.*, 2011). In particular, we found that occupancy models outperformed GLMs, demonstrating that accounting for imperfect detection improved species distributions estimated using individual models. In this study, we used a consensus approach integrating a wide range of model specifications that is more likely to provide an accurate description of species-habitat relationships than individual SDMs (Thuiller, 2003; Marmion *et al.*, 2009). Information gaps in the data resulting from imperfect detection (Gu & Swihart, 2004) may be partially compensated for by using a model output that combines the different possible states of the real distribution as estimated by the individual models (Marmion *et al.*, 2009). As a result, some sites may be correctly classified as being occupied or unoccupied by the consensus model and misclassified by the occupancy model, or *vice versa*, even though both methods have similar accuracy. The *true* species distribution could be somewhere between occupancy and consensus predictions, at least for highly detectable species.

To conclude, our results demonstrate that although occupancy modelling is an attractive way to predict the distribution of poorly detectable species, it does not always lead to a substantial improvement over conventional model predictions. Given that the variability in range estimates resulting from false absences could be comparable with the magnitudes reported for contemporary climate-induced range shifts (e.g. Lenoir *et al.*, 2008; Moritz *et al.*, 2008; Crimmins *et al.*, 2011), we strongly recommend caution in reporting distributional shifts if species detectability has concomitantly changed through time. It would be interesting to compare species range shifts assessed using conventional methods and methods that account for imperfect detection to evaluate the impact of this source of uncertainty, thus enhancing our understanding of documented range shifts and our ability to design effective conservation strategies.

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SUPPORTING INFORMATION

APPENDIX S1 Description and implementation of the models

In this study, the eight SDMs were implemented to a great extent part as described in the *BIOMOD* package (BIOdiversity MODelling, Thuiller, 2003), except for some specific model implementations. BIOMOD is an ensemble-modelling platform that can be used to apply a wide range of SDMs using the R (CRAN) software. The descriptions and implementations of the models are given below (explanations adapted from Thuiller *et al.*, 2009 (BIOMOD version 2.13)).

Description and implementation of models

Eight techniques were used in modelling analyses: GLM, GAM, MARS (regression methods), ANN, GBM, RF (machine learning methods), CTA, and MDA (classification methods). Model outputs were then averaged across the eight methods, without weighting, to give a single prediction of the probability of occurrence for each site and/or network reach (Mean(All) sensu Marmion *et al.*, 2009).

GLM - Generalised Linear Models (library *MASS*)
GLM is a flexible generalisation of classical linear regression that provides error distributions for the dependant variable other than normal and non-constant variance functions (McCullagh & Nelder, 1989).

GLMs were fitted using a binomial error distribution. To allow linear or quadratic responses with the predictor variables, a full model was implemented including a linear or quadratic term for each predictor variable. Then, to select the most parsimonious model, stepwise model selection was carried out using the function *stepAIC* (library *MASS*). The statistical criterion used to select models of increasing fit was the Akaike Information Criteria (AIC).

GAM - Generalised Additive Models (library *gam*)
GAMs use a class of equations known as ‘smoothers’ that attempt to generalise data into smooth curves by local fitting to subsections of the data (Hastie & Tibshirani, 1990).

GAMs were fitted using a binomial error distribution and a quadratic spline smoother, which is a collection of polynomials of degree less than or equal to 2 (i.e. quadratic or linear form of the predictor variables), defined on subintervals. As for the GLMs, we used an automated stepwise process to select the most significant variables using the *step.gam* function (library *gam*).

MARS - Multivariate Adaptive Regression Splines (library *mda*)
MARS is a non-parametric regression technique that can be seen as an extension of a linear regression which automatically identifies and estimates the amount of smoothing required for each predictor as well as the interaction order of the predictors (Friedman, 1991; Elith *et al.*, 2006).

We used the functions developed by Elith & Leathwick (2007) to run the models (‘mars.public.functions.3.1.R’). MARS models were implemented using a binomial error distribution. Taking a conservative approach, we allowed only one-level of interaction between predictor variables (i.e. an additive model).

ANN - Artificial Neural Networks (library *nnet*)
Feed forward neural networks provide a flexible way of generalising linear regression functions (Ripley, 1996). They are non-linear regression models, but with so many parameters that they are extremely flexible to approximate any smooth function. The accuracy of ANN is mainly controlled by two parameters: the amount of weight decay and the number of hidden units.

As different runs can provide different results, the best amount of weight decay and the number of units in the hidden layer are selected by using 3-fold cross-validation. The selection of parameter values was done using the function *tune.nnet* (library *nnet*) across a choice of the number of hidden units ranging from 2 to 20 (i.e. 2, 4, 6, 8, 10, 12, 14, 16, 18, or 20), and an amount of decay ranging from 0.001 to 0.1 (i.e. 0.001, 0.01, 0.05 or 0.1). The maximum number of iterations was fixed at 3000.

GBM - Generalised Boosting Models (library *gbm*)
GBMs use a large number of relatively simple models (i.e. classification trees), the predictions of which are then combined to give more robust estimates of the response. GBMs use a recursive partitioning algorithm for developing a final model by progressively adding trees to the model, while re-weighting the data to highlight the cases that are poorly predicted by the previous trees (Ridgeway, 1999; Friedman, 2001).

We selected a Bernoulli distribution for presence absence outcomes. The maximum number of trees to be added was set to 5000, and the interaction depth to 1 (i.e. additive model). We used the function *gbm.perf* (library *gbm*) to choose the optimal number of trees using a 5-fold cross validation. Other parameters were selected by default.

RF - Random Forest (library *randomForest*)
RFs grow many classification trees (Breiman, 2001). Each tree gives a classification, and the forest chooses the classification that has the most votes (out of all the trees in the forest).
Each tree is grown as follows:
If the number of cases in the training set is N, sample N cases at random - but with replacement, from the original data. This sample will constitute the training set for growing the tree. If there are M input variables, a number m << M is specified such that at each node, m variables are selected at random out of the M variables, and the best split of these m is used to split the node. The value of m is kept constant while growing the forest. Each tree is grown to the largest extent possible. There is no pruning.

RFs were implemented based on 750 trees. The number of m variables to be selected at each node was chosen with respect to the Out-of-Bag (OOB) error estimate using the *tuneRF* function (library *randomForest*), from 1 to the total number of predictor variables using a step factor of 2 (relative improvement in OOB error of 0.001).

CTA - Classification Tree Analysis (library *rpart*)
This method consists of recursive partitions of the dimensional space defined by the predictors into groups that are as homogeneous as possible in terms of their response (Breiman *et al.,* 1984). The tree is built by repeatedly splitting the data, defined by a simple rule based on a single explanatory variable. At each split, the data are partitioned into two exclusive groups, each of which is as homogeneous as possible. The algorithm seeks to decrease the variance within the subset as far as possible.

To control the length of the tree, we used a procedure running 10-fold cross-validations (per default) to select the best trade-off between the number of leaves on the tree and the explained deviance.

MDA - Mixture Discriminant Analysis (library *mda*)
MDA is a method for classification (supervised) based on mixture models (Hastie *et al.*, 1994; 1995). It is a flexible extension of the well-known linear discriminant analysis.

We used *'mars'* as the regression method in optimal scaling.

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APPENDIX S2 Detection probability of occupancy models

Table S1: Best models for predicting species detectability for each species. The importance of each covariate is given as the percentage of times this variable was selected across the 100 iterations.

Species names	**G**	**G^2**	**year**	**Julian date**	**Julian $date^2$**	**sampling strategy**	**number of passes**	**prospection method**	**sampling surface**
Abramis brama	93	77	37	79	23	15	3	93	67
Alburnoides bipunctatus	100	99	12	11	7	81	72	98	15
Alburnus alburnus	100	100	96	79	25	67	38	66	94
Ameiurus melas	71	66	99	97	48	44	61	58	13
Anguilla anguilla	42	14	10	48	1	22	90	65	16
Barbatula barbatula	94	24	96	66	9	16	50	60	87
Barbus barbus	100	100	90	63	16	18	8	100	23
Blicca bjoerkna	61	19	22	74	12	29	100	84	99
Carassius carassius	98	19	16	11	2	9	84	20	52
Chondrostoma nasus	100	100	16	9	7	99	99	13	75
Cobitis taenia	83	48	8	17	3	7	42	47	28
Cottus gobio	98	4	61	66	0	2	8	9	14
Cyprinus carpio	100	6	2	20	0	7	8	100	18
Esox lucius	100	100	2	31	24	86	85	100	100
Gasterosteus aculeatus	19	6	38	28	1	9	26	5	8
Gobio gobio	85	83	3	25	13	83	61	98	99
Gymnocephalus cernua	100	100	23	78	2	10	18	100	100
Lepomis gibbosus	100	99	100	100	98	100	94	100	45
Leuciscus leuciscus	100	100	48	94	83	89	88	20	53
Micropterus salmoides	89	88	98	6	0	45	12	89	6
Parachondrostoma toxostoma	85	83	1	34	20	20	64	39	59
Perca fluviatilis	89	87	44	17	10	64	36	89	62
Phoxinus phoxinus	98	98	2	10	6	30	32	98	100
Pseudorasbora parva	100	28	44	35	3	42	100	15	36
Pungitius pungitius	94	42	100	47	1	42	59	28	30
Rhodeus amarus	100	100	78	86	45	100	95	68	60
Rutilus rutilus	100	100	84	15	9	100	35	100	69
Salmo salar	28	24	18	23	3	11	97	95	92
Salmo trutta	100	13	16	73	3	4	6	36	36
Sander lucioperca	89	16	0	37	2	12	51	28	86
Scardinius erythrophthalmus	58	58	1	39	2	58	97	100	36
Silurus glanis	100	92	6	38	17	90	96	100	62
Squalius cephalus	100	100	1	100	39	98	13	99	97
Telestes souffia	70	34	4	26	6	10	21	31	14
Tinca tinca	100	100	24	51	50	100	97	100	21

APPENDIX S3 Performances of the models

When the methods were ranked according to their cAUC values, we found that RF and occupancy methods most frequently gave the best model performances, followed by the average consensus method, while CART and ANN more frequently performed the worst. Nevertheless, it is noteworthy that the average consensus method is the only method which almost never yielded the worst performances (i.e. relative ranking comprised between 3 and 10).

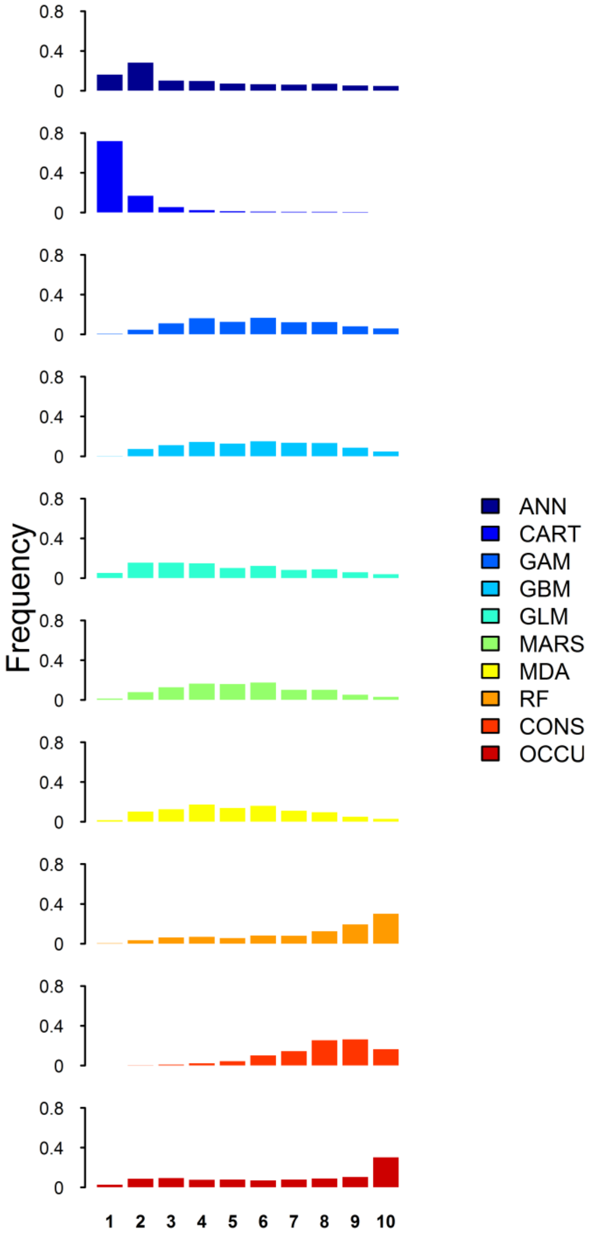

Figure S1 Relative ranking of the eight-single SDMs compared to the average consensus (CONS) and the occupancy (OCCU) models, according to cAUC values across all iterations and all species. Rank 10 corresponds to the best ranking.

Table S2: Mean performance measures across all species and iterations of the eight-single SDMs, the average consensus (CONS) and the occupancy (OCCU) models. Numbers in brackets are standard deviations.

	cAUC	**Sensitivity**	**TSS**
ANN	0.77 (0.09)	0.69 (0.18)	0.47 (0.15)
CART	0.71 (0.09)	0.64 (0.22)	0.41 (0.15)
GAM	0.80 (0.07)	0.78 (0.12)	0.52 (0.13)
GBM	0.80 (0.07)	0.77 (0.12)	0.52 (0.13)
GLM	0.79 (0.08)	0.78 (0.13)	0.51 (0.13)
MARS	0.79 (0.08)	0.77 (0.13)	0.52 (0.13)
MDA	0.79 (0.08)	0.76 (0.14)	0.51 (0.13)
RF	0.82 (0.07)	0.79 (0.11)	0.55 (0.13)
CONS	0.82 (0.07)	0.80 (0.12)	0.55 (0.13)
OCCU	0.81 (0.07)	0.79 (0.12)	0.54 (0.13)

Sub-sampling of the testing dataset and geographic null models were performed using the *dismo* package (Hijmans *et al.,* 2012) in R environment software v 2.13.0 (R Development Core Team, 2011).

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ARTICLE III (P_{III})

Comte L & Grenouillet G (2013**)** Do stream fish track climate change? Assessing distribution shifts in recent decades. ***Ecography*** 36: 1236–1246.

Do stream fish track climate change? Assessing distribution shifts in recent decades

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ABSTRACT

Understanding the ability of species to shift their distribution ranges in response to climate change is crucial for conservation biologists and resources managers. Although freshwater ecosystems include some of the most imperilled fauna worldwide, such range shifts have been poorly documented in streams and rivers and have never been compared to the current velocity of climate change. Based on national monitoring data, we examined the distributional changes of 32 stream fish species in France and quantified potential time lags in species responses, providing a unique opportunity to analyze range shifts over recent decades of warming in freshwater environments. A multi-facetted approach, based on several range measures along spatial gradients, allowed us to quantify range shifts of numerous species across the whole hydrographic network between an initial period (1980-1992) and a contemporary one (2003-2009), and to contrast them to the rates of isotherm shift in elevation and stream distance. Our results highlight systematic species shifts towards higher elevation and upstream, with mean shifts in range centre of 13.7 m.decade^{-1} and 0.6 km.decade^{-1}, respectively. Fish species displayed dispersal-driven expansions along the altitudinal gradient at their upper range limit (61.5 m.decade^{-1}), while substantial range contractions at the lower limit (6.3 km.decade^{-1}) were documented for most species along the upstream-downstream gradient. Despite being consistent with the geographic variation in climate change velocities, these patterns reveal that the majority of stream fish have not shifted at a pace sufficient to track changing climate, in particular at their range centre where range shifts lag far behind expectation. Our study provides evidence that stream fish are currently responding to recent climate warming at a greater rate than many terrestrial organisms, although not as much as needed to cope with future climate modifications.

Keywords: freshwater fish, climate change velocity, range limit

INTRODUCTION

One of the main challenges for biodiversity conservation lies in understanding how species are responding to contemporary climate change, which is essential if we are to improve our ability to forecast changes and initiate management strategies (Dawson *et al.*, 2011). Earth may face its sixth mass extinction if the current dramatic loss of species continues (Barnosky *et al.*, 2011), and evidence is accumulating that many species are responding to recent climate change in a consistent way across ecosystems and regions (Parmesan, 2006; Daufresne *et al.*, 2009; Thomas, 2010). One such response consists of distribution shifts poleward and upward in elevation (Hill *et al.*, 1999; Parmesan & Yohe, 2003; Hickling *et al.*, 2006; Chen *et al.*, 2011), as species attempt to track their favourable climate niche across space (Tingley *et al.*, 2009; Crimmins *et al.*, 2011). However, species have exhibited a wide diversity of range shifts, and recent evidence has suggested that many distributional shifts may not be enough to cope with the acceleration of climate change that has occurred in recent years (Devictor *et al.*, 2008; Bertrand *et al.*, 2011; La Sorte & Jetz, 2012). As recently advocated, one approach to characterizing species vulnerability to climate change is to compare the spread of distribution shifts with the rate which is required to keep pace with isotherm shifts (i.e. climate change velocity, Loarie *et al.*, 2009; Isaak & Rieman, 2013). Several studies have yet examined the rate of climate velocity both historically (Burrows *et al.*, 2011; Dobrowski *et al.*, 2013) and for the future (Loarie *et al.*, 2009), but much less work has been devoted to quantifying time lag in species responses (but see Zhu *et al.*, 2012).

To date, more climate-induced range expansions have been documented than range contractions (Parmesan *et al.*, 1999; Moritz *et al.*, 2008). However, individual species are likely to respond differently to climate change depending on their distribution ranges (Hill *et al.*, 1999; Moritz *et al.*, 2008). Indeed, low-elevation species may be able to expand their ranges, while physical barriers may affect the colonization of high-elevation species, leading them to decline (Hill *et al.*, 2002; Chen *et al.*, 2010). In addition, the determinants of species distribution could differ along environmental gradients, leading to asymmetric species responses (Hampe & Petit, 2005). For instance, warm limits may be determined by complex temperature-mediated biotic interactions, whereas physiological climatic constraints are more likely to be limiting at cold limits (Brown *et al.*, 1996; Normand *et al.*, 2009). Compensatory changes in demographic rates may also temporally buffer the extinction of local populations at the warm limit of their bioclimatic distribution (Doak & Morris, 2010). Alternatively, physiological stress due to climate change may occur not only at range limits, but also among populations experiencing the greatest magnitudes of climate change even within the range of the species (Lenoir *et al.*, 2008). Despite the relevance of using several descriptors to find out whether species are shifting across their entire distribution range, most of the studies available offer only a limited view of ecological responses to climate change, either geographically or with regards to the range parameters analyzed (Hampe & Petit, 2005; Parmesan, 2006).

Globally, rivers and streams are among the most threatened ecosystems, suffering from declines in biodiversity that are far greater than those in even the most severely affected terrestrial ecosystems (Dudgeon *et al.*, 2006). In particular, climate change could be one of the main threats faced by aquatic ecosystems and freshwater biodiversity (Sala *et al.*, 2000; Heino *et al.*, 2009). Like many terrestrial species, the distribution of aquatic organisms could be significantly modified by climate change, as temperature has critical effects on ectotherms through its combined impacts on dissolved oxygen levels and metabolism (Pörtner & Knust, 2007). Changes in stream flows due to increase in temperature can also be expected to further reduce the suitable habitat available for stream fish, even if total precipitation goes unchanged (Carpenter *et al.*, 1992; Leith & Whitfield, 1998). Recent findings have confirmed that changes in water temperatures could have significant effects, leading to alterations of fish growth and recruitment success (Schindler *et al.*, 2005; Daufresne *et al.*, 2009; Clews *et al.*, 2010; Nunn *et al.*, 2010). Furthermore, in contrast to their terrestrial counterparts, stream fish distributions are determined by biotic and abiotic factors that vary along the upstream-downstream gradient (i.e. downstream distance, stream order) (Matthews, 1998; Buisson *et al.*, 2008). Their ability to move in response to environmental change is thus constrained by the dendritic structure of drainage basins (Fausch *et al.*, 2002; Brown & Swan, 2010), although most of the previous studies exploring climate change impacts on freshwater fish have not explicitly considered the spatial structure of dispersal networks. Surprisingly, except for a documented general poleward and upward shift of British fish between 1965-1975 and 1990-2000 (Hickling *et al.*, 2006), range shifts for stream fish have been poorly documented, and in most cases involve salmonids (e.g. Hari *et al.*, 2006; Almodóvar *et al.*, 2012). Therefore, for assessing species vulnerability to climate change in aquatic environments, the question of how fast stream fish are shifting compared to the speed required to keep pace with changing climate has yet to be resolved.

Here, we documented range shifts of stream fish in France, based on comparatively diverse regions and species data, providing a unique opportunity to analyze range shifts over recent decades in freshwater ecosystems. Our description of range shifts considered changes that have occurred at the limits (i.e. range boundaries), as well as at the centre of the species' distributions. These measurements have made it possible to characterize the patterns of range shift in two distinct survey periods along altitudinal and upstream-downstream (i.e. distance from source) gradients, both of which are strongly related to species distribution and climatic gradients (Cassie, 2006). Moreover, we assessed whether range shifts along environmental gradients were related to climate tracking through the potential time lags between climate velocity and biological responses, expecting species to have responded to climate change by modifying their ranges to remain within their preexisting climatic niche (Tingley *et al.*, 2009).

The specific aims of the study were to 1) characterize patterns of range shifts along altitudinal and upstream-downstream gradients for 32 fish species inhabiting French streams between an initial survey period (1980-1992) and a more recent 'contemporary' one (2003-2009), 2) compare these responses according to the distribution preferences of species along environmental gradients, and 3) find out whether changes in distribution were related to climate tracking by comparing species range shifts to the velocity of climate change.

METHODS

Study area and species

The French monitoring programme of freshwater fish populations is ensured by the French National Agency for Water and Aquatic Environments (Onema), which aims to preserve water quality and good ecological status of aquatic systems. The electrofishing database of the Onema provides a spatially and temporally extensive survey of freshwater fish at the national scale, with the potential to assess long-term trends in fish populations (Poulet *et al.*, 2011). From this database, we initially refined our selection to stream sites with reliable GIS data. We then extracted two well-balanced pools of sites sampled during 'cold' and 'warm' temperature regime periods relative to the average conditions between 1965 to 2008 (Fig. A1 in Supporting Information Appendix 1). The first period included 3549 sites sampled from 1980 to 1992 (hereafter referred to as initial surveys). The second period included 3543 sites sampled from 2003 to 2009 (hereafter referred to as contemporary surveys). For both time periods, the sampling sites were distributed throughout France (Fig. 1A, B). Although only 7.5% of sites were common to both time periods, surveys were conducted in all the major hydrographic basins of France and covered the entire range of environmental conditions. Data on the presence-absence of fish species were recorded at each site from 1 to 19 times during the initial period, and from 1 to 14 times during the contemporary period, resulting in 4533 and 7548 sampling records, respectively. After correcting for taxonomic revisions that had occurred during the entire study period (i.e. pooling together existing species in the initial period that have been divided into two or more species in the contemporary period), we considered only species present on at least 75 sites in both periods, for a total of 32 species (Table 1).

Sampling strategies and sampling success

Both surveys were conducted according to standard electrofishing procedures defined on the basis of river width and depth. Small streams were sampled by wading, mostly by two-pass removal, and large rivers by fractional sampling strategies of the different types of mesohabitat, or by partial sampling strategies in the river margins and delimited areas of habitat (Poulet *et al.*, 2011). However, several different

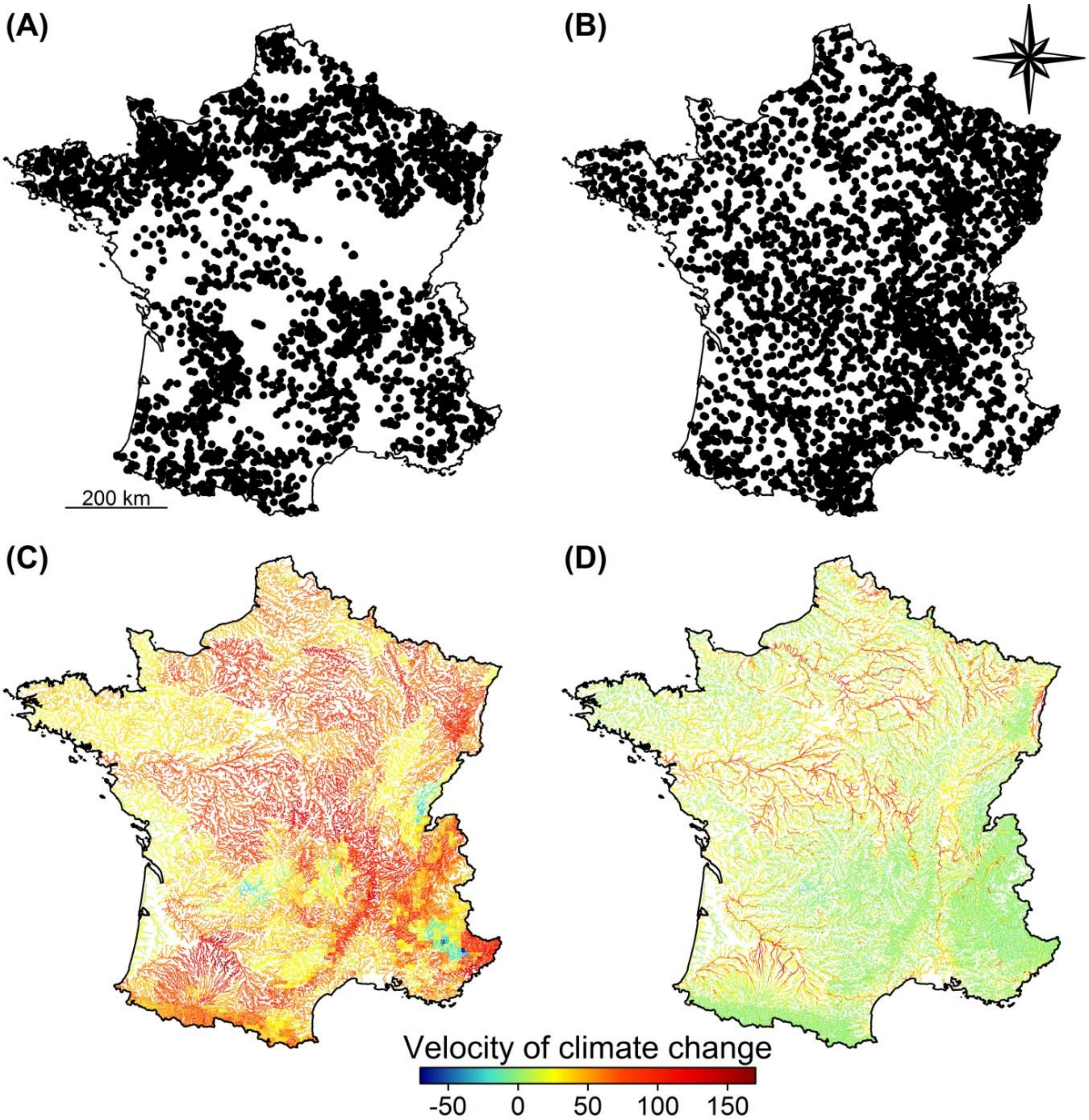

Figure 1 Study area showing the spatial position of (A) initial and (B) contemporary surveys. Velocity of climate change along the reaches of the hydrographic network expressed in (C) altitudinal distance (m.decade^{-1}) and (D) upstream-downstream distance (km.decade^{-1}). Positive velocities means isotherms shifts towards higher elevation or upstream, while negative means isotherms shifts towards lower elevation or downstream.

methods were used successively until the introduction of a unified surveillance monitoring protocol in 1995.

One difficulty that persists in documenting range shifts is reconciling differences between the sampling protocols used in historical and recent surveys (Patton *et al.*, 1998; Shaffer *et al.*, 1998; Shoo *et al.*, 2006; Tingley & Beissinger, 2009). Many factors can have an impact on the probability of detecting a species, and the degree of this impact can differ on temporal, geographic and taxonomic scales (Kéry & Schmid, 2006; Kéry & Plattner, 2007). As a result, real distribution changes may be confounded by changes in detectability, particularly if only two time periods are considered. To tackle this issue, we conducted separated analyses on a restricted dataset in order to assess whether potential variation in the sampling success had in fact impaired our ability to detect range shifts. Following the general approach developed by Kéry & Plattner (2007), we evaluated if the mean proportion of species detected and the species-specific detectability had varied over the temporal scale of our study (details in Supporting Information Appendix 2).

We found that the mean proportion of species detected differed between the initial and contemporary surveys, depending on the sampling prospection method employed (Supporting Information Appendix 2, Table A2). In particular, samplings conducted by boat seemed to be more successful in the contemporary surveys. As a result, the mean proportion of species detected at low to mid upstream-downstream locations (i.e. > 200 km from the source) was higher in the contemporary surveys, whereas no differences were observed either for upstream locations or along the altitudinal gradient (Supporting Information Appendix 2, Fig. A2). In addition, the species-specific estimates of detectability were found to slightly differ in the contemporary and initial surveys, with a mean difference in detectability of 0.05 (Table 1; see Supporting Information Appendix 2, Table A3 and A4 for details on model's results). Nevertheless, there was no link between variation in species detectability and distribution changes (see below) between time periods ($P > 0.05$).

Environmental data

Several variables, all of them strongly related to the spatial distribution of stream fish (Buisson *et al.*, 2008), were used to describe climatic and

Table 1 Spatial distribution preferences of fish species along elevation and upstream-downstream gradients in the initial surveys defined following a hierarchical clustering based on the Ward's method with the Euclidean distance, and species-specific estimates of detectability in the initial (I) and contemporary (C) surveys based on GLMM analysis (see Supplementary information Appendix 2). Detectability could not be estimated in the initial surveys for *Parachondrostoma toxostoma* due to the limited set of capture history data available.

Species names	Code	Altitudinal	Upstream-downstream	Initial detectability (SD)	Contemporary detectability (SD)
Abramis brama	*Abb*	Low	Low	0.58 (0.11)	0.47 (0.11)
Alburnoides bipunctatus	*Alb*	Low	High	0.44 (0.12)	0.79 (0.07)
Alburnus alburnus	*Ala*	Low	Low	0.67 (0.11)	0.79 (0.08)
Ameiurus melas	*Amm*	Low	Low	0.38 (0.12)	0.5 (0.09)
Anguilla anguilla	*Ana*	Low	Mid	0.88 (0.06)	0.81 (0.07)
Barbatula barbatula	*Bba*	High	High	0.77 (0.09)	0.85 (0.06)
Barbus barbus	*Bab*	Mid	Mid	0.67 (0.11)	0.82 (0.06)
Barbus meridionalis	*Bam*	Mid	High	0.81 (0.06)	0.81 (0.12)
Blicca bjoerkna	*Blb*	Low	Low	0.5 (0.12)	0.61 (0.1)
Chondrostoma nasus	*Chn*	Mid	Low	0.54 (0.13)	0.67 (0.1)
Cottus gobio	*Cog*	High	High	0.85 (0.06)	0.84 (0.06)
Cyprinus carpio	*Cyc*	Low	Low	0.33 (0.11)	0.4 (0.11)
Esox lucius	*Esl*	Low	Mid	0.58 (0.11)	0.6 (0.1)
Gasterosteus aculeatus	*Gaa*	Low	High	0.44 (0.12)	0.53 (0.1)
Gobio gobio	*Gog*	Mid	High	0.78 (0.09)	0.89 (0.05)
Gymnocephalus cernua	*Gyc*	Low	Mid	0.44 (0.13)	0.55 (0.11)
Lepomis gibbosus	*Leg*	Low	Mid	0.46 (0.11)	0.68 (0.1)
Leuciscus leuciscus	*Lel*	Low	High	0.65 (0.12)	0.66 (0.1)
Lota lota	*Lol*	Low	Mid	0.5 (0.14)	0.51 (0.11)
Parachondrostoma toxostoma	*Pat*	Mid	High	-	0.57 (0.1)
Perca fluviatilis	*Pef*	Low	Mid	0.82 (0.07)	0.72 (0.09)
Phoxinus phoxinus	*Php*	High	High	0.83 (0.06)	0.85 (0.06)
Pungitius pungitius	*Pup*	Low	High	0.53 (0.11)	0.52 (0.1)
Rutilus rutilus	*Rur*	Low	Mid	0.86 (0.06)	0.83 (0.06)
Salmo salar	*Sas*	Low	High	0.81 (0.06)	0.77 (0.08)
Salmo trutta	*Sat*	High	High	0.88 (0.05)	0.85 (0.06)
Sander lucioperca	*Sal*	Low	Low	0.34 (0.09)	0.37 (0.11)
Scardinius erythrophthalmus	*Sce*	Low	Low	0.51 (0.11)	0.47 (0.1)
Squalius cephalus	*Sqc*	Mid	Mid	0.88 (0.06)	0.91 (0.04)
Telestes souffia	*Tes*	High	High	0.76 (0.1)	0.81 (0.08)
Thymallus thymallus	*Tht*	Mid	High	0.58 (0.07)	0.55 (0.11)
Tinca tinca	*Tit*	Low	Mid	0.48 (0.12)	0.53 (0.11)

habitat conditions over the French hydrographic network and subsequently used to model species distribution (see Supporting Information Appendix 1, Table A1 for details). Habitat characteristics consisted of elevation (ELE, *m*), slope (SLO, ‰), the entire area drained by the upstream area (km²) and the cumulated length of the upstream flow network (*m*) (CCM2; Vogt *et al.*, 2007). To eliminate the colinearity between the last two variables which both reflect the upstream-downstream position, we used a principal component analysis (PCA) and the first axis of the PCA was kept as a synthetic variable describing the upstream-downstream gradient (*G*). High *G* values corresponded to the most downstream sites and low *G* values to the most upstream sites. Bioclimatic variables were derived from the high resolution (8 km grid-data) SAFRAN atmospheric reanalysis over France (Le Moigne, 2002): mean temperature of the coldest quarter (°C), mean temperature of the warmest quarter (°C), temperature seasonality (SD × 100), cumulated precipitation of the wettest quarter (mm), cumulated precipitation of the driest quarter (mm) and precipitation seasonality (CV). For both period, we obtained mean climatic conditions by averaging the climatic variables within each period plus the three preceding years, which correspond to the mean duration of the species life cycle.

Climate change velocity

Long-term temperature and precipitation trends were estimated using linear regressions on mean annual temperature and precipitation for each stream reach over the 1968-2008 period using the SAFRAN climate database. Air temperature was used as a surrogate of water temperature after applying a scaling factor of 0.8°C. To determine the rate of isotherm shifts in space (Loarie *et al.*, 2009), we calculated the velocity of climate change along both the altitudinal and upstream-downstream gradients. Following Isaak & Rieman (2013), we first calculated climate velocity using spatial temperature gradient expressed in elevation distance ($m.decade^{-1}$) as the ratio of long-term temperature trends ($°C.decade^{-1}$) to the stream lapse rates ($°C.m^{-1}$). The stream lapse rates were estimated using linear regression between temperature and elevation within each of the 54 hydrographic units of the stream network. We then calculated climate velocity expressed in stream (i.e. longitudinal) distance ($km.decade^{-1}$) as the ratio of the altitudinal velocities to stream slopes (SLO, °).

Modelling species spatial distribution

To account for uncertainty in comparing observed range limits over time based on data sets not originally collected with the explicit purpose of detecting range shifts (Shoo *et al.*, 2006; Tingley & Beissinger, 2009), we modelled the spatial distribution of each species across the French hydrographic network as a function of several climatic and environmental variables using an ensemble modelling framework (Marmion *et al.*, 2009). Modelling response curves of species along an environmental gradient is considered to be an effective way of carrying out ecological gradient analysis (Lenoir *et al.*, 2008; Crimmins *et al.*, 2011; Maggini *et al.*, 2011), that is insensitive to irregularly-spaced sampling (Oksanen *et al.*, 2001). Although Gaussian functions have usually been applied, combinative algorithms are known to increase the accuracy of an ensemble of model outputs (Marmion *et al.*, 2009; Grenouillet *et al.*, 2011). In addition, although a single gradient may act as suitable surrogate to model the spatial distribution of some animals (e.g. Maggini *et al.*, 2011), species ranges are clearly influenced by multiple habitat and climatic factors, particularly in aquatic systems where environmental conditions vary along the dendritic network (Matthews, 1998). Therefore, modelling fish species distribution by incorporating additional variables should provide more accurate estimates than single-gradient models (Oksanen *et al.*, 2001).

The occurrence of each species was modelled independently for both time periods as a function of the habitat and climatic data extracted at all survey sites to avoid potential bias due to variation in the distribution of the sites over time. To take into account the variability introduced by the modelling method, we followed the procedure applied in Marmion *et al.* (2009) by averaging the probabilities of occurrence predicted by eight single-SDMs: generalized linear models, generalized additive models, multivariate adaptive regression splines, mixture discriminant analyses, classification and regression trees, random forest, generalized boosted trees and artificial neural networks. Datasets for each period were composed of one sampling record randomly chosen for each site, to avoid pseudoreplication.

Models were calibrated on 70% of the sampling records, while the remaining 30% were used for evaluation and threshold optimisation. To take into account the variability induced by the threshold setting-method, three of the most common methods were applied to convert predicted occurrence probabilities into binary data (i.e. presence or absence, Liu *et al.*, 2005). Specifically, we used threshold values maximizing the sum of sensitivity and specificity, sensitivity equalling specificity and maximizing Kappa. Finally, the different steps of the modelling process were repeated 30 times with 30 different sampling record datasets to take into account the variability due to the quality of the calibration dataset.

We then predicted the probabilities of occurrence of the species on the reaches of the French hydrographic network for which environmental conditions did not differ from those of the calibration datasets. These probabilities were then transformed into binary predictions of presence and absence using the previously calculated thresholds. We thus obtained 90 final modelled species distributions for each period and species, resulting from 30 iterations and 3 thresholds.

Details on model performances are given in Supporting Information Appendix 3.

Estimating range descriptors

The thermal regime of a stream depends mainly on its altitudinal and upstream-downstream position within a river basin (Cassie, 2006). Therefore, to test for a potential modification in the distribution of stream fish in response to climate change, shifts along the upstream-downstream gradient were assessed using the distance from source (km), and shifts along the altitudinal gradient using ELE, as these two gradients were uncorrelated when considering the whole French hydrographic network (r_p = -0.21). We defined the centre of species' distributions (hereafter referred to as 'range centre') along both the altitudinal and the upstream-downstream gradients in terms of the median values of the stream reaches where the species were predicted to be present (e.g. Zuckerberg *et al.*, 2009). We also considered the lower and upper range limits as 2.5 and 97.5%, respectively, of the altitudinal and upstream-downstream values of all predicted presences in order to reduce the influence of outliers (Quinn *et al.*, 1996). The overall extent was then defined as the absolute value of the

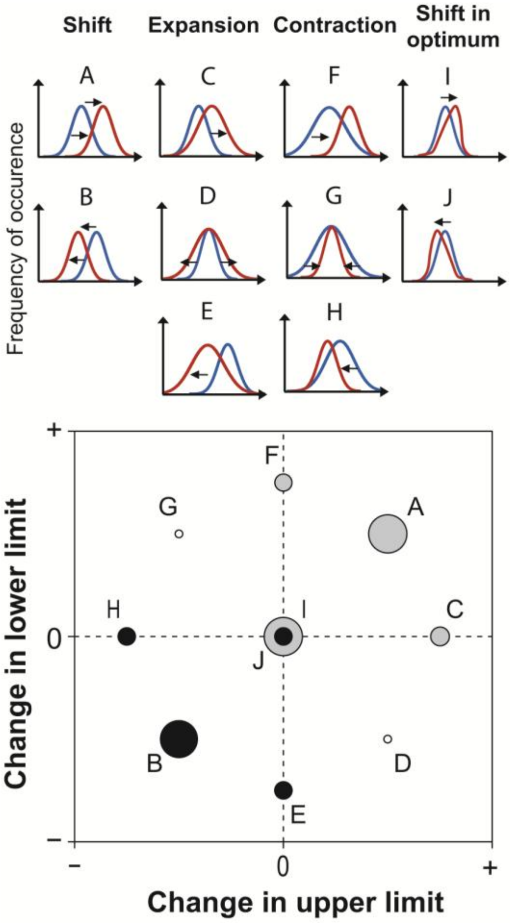

Figure 2 Theoretical plot and associated response curves depicting potential shift patterns (A-J) along an environmental (i.e. altitudinal or upstream-downstream) gradient as a function of the mean changes in range centre, and of the upper and lower range limits between the contemporary and initial periods. The size of the circle represents the absolute changes in range centre along the environmental gradient. Solid circles indicate significant ($p < 0.05$) shifts in range centre, with grey for positive (i.e. shift towards higher elevation or upstream) and black for negative (i.e. shift towards lower elevation or downstream). Blue line in response curves represents the initial distribution and red line the distribution during the contemporary period. Arrows indicate the direction of the shift patterns. Changes can either occur at the upper and lower range limits or at the range centre along this gradient and consist of either expansion or contraction. Patterns C, F and I depict positive shifts that may be considered as intermediate patterns towards the full distributional shift shown in A. Pattern I is a special case of a positive shift, where only the range centre along the gradient moved towards higher elevation or upstream. In contrast, patterns E, H and J depict negative shifts that may be considered as intermediate patterns towards the full negative shift illustrated in B. Patterns D and G depict contrasting changes in both range limits, which may indicate complex responses of species to multiple stressors and/or competitive interactions (Lenoir *et al.*, 2010; Maggini *et al.*, 2011).

upper minus the lower range limits along the above-mentioned gradients.

Analyzing range shifts

As threshold selection is known to strongly influence species distribution modelling (Nenzén & Araùjo, 2011), temporal changes in range centre, upper and lower range limits and overall range extent were evaluated by controlling for this effect. For each species, the shift (i.e. extension or contraction) in each range descriptor was assessed by fitting a linear regression through all the range descriptors obtained for each period with the threshold-setting method and the period as explanatory variables. This shift was then determined by the least-squares mean of the contemporary period-group effect.

Shift patterns were then plotted according to changes in range centre, and in the lower and upper limits along the gradient (see Fig. 2 for theoretical examples), making it possible to visualize directional consistency in species responses. To avoid dealing with shifts that we did not consider as ecologically meaningful (i.e. smaller than the resolution of the hydrographic network used), the average slope and length values of all stream reaches were computed, and supplementary thresholds of 30 m and 2 km were then used to interpret the range shifts along the altitudinal and upstream-downstream gradients, respectively.

To test whether species exhibited differential patterns depending on their distribution along environmental gradients, species were classified as having 'low-', 'mid-' or 'high-' elevation preferences and 'upstream', 'midstream' or 'downstream' preferences, respectively. Species preferences were defined following hierarchical clustering (Euclidean distance and Ward's linkage criterion) based on the range centre and the upper and lower range limits of the initial survey dataset for each gradient (Table 1).

Finally, to find out whether habitat shifts were consistent with potential climate tracking, we compared the distribution shifts for each species with the velocity of climate change at its range centre along altitudinal and upstream-downstream gradients.

Models and analyses were developed using R environment software ver 2.13.0 (R Development Core Team, 2011).

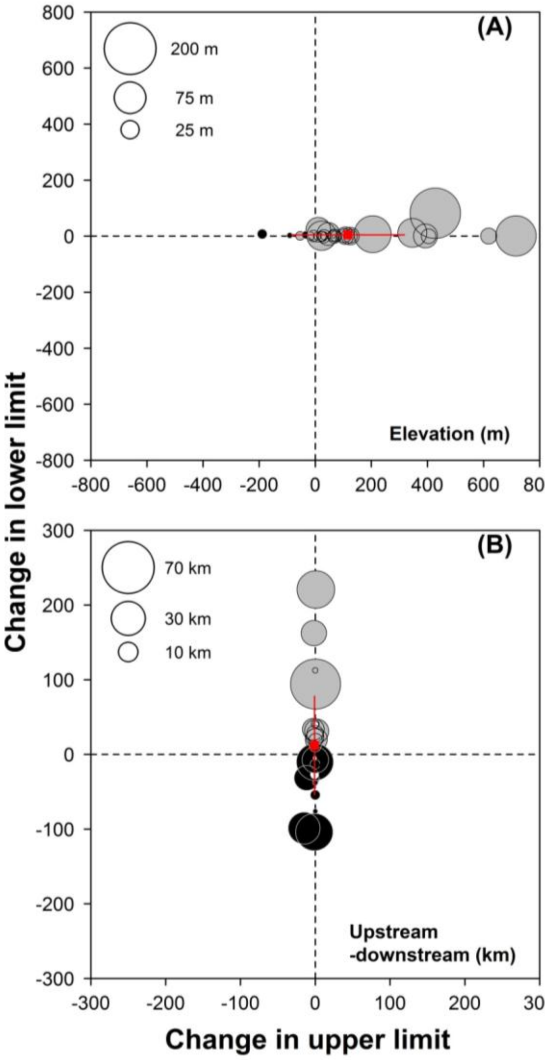

Figure 3 Changes in the upper and lower range limits between the initial and contemporary periods for (A) elevation and (B) upstream-downstream position. Upper limits correspond to high elevation and upstream position. Lower limits correspond to low elevation and downstream position. Each circle represents the value for a stream fish species. The size of the circles indicates differences in species range centre along the gradients. Significant ($P < 0.05$) differences in species range centre are coloured as in Fig. 2: grey for positive (i.e. shift towards higher elevation or upstream) and black for negative (i.e. shift towards lower elevation or downstream) shifts. Red squares and the associated error bars indicate the mean shifts (± SD) in lower and upper limits across all species. Values of range shifts for each species are given in Supporting Information Appendix 4, Table A7.

RESULTS

Climate change velocity

Temporal trends in mean annual temperature and precipitation indicated that the area studied had become warmer (Supporting Information Appendix 1), whereas no trend in precipitation was apparent. On average, the mean annual temperature had increased by about 0.24°C.decade^{-1}, although changes were not consistent across the hydrological network (Supporting Information Appendix 1, Fig. A1). Similarly, the velocity of climate change appeared spatially structured, and particularly along the upstream-downstream gradient were the major shifts were observed for downstream sections. Depending on the gradient considered, the velocity of climate change ranged from -65.2 to 169.5 m.decade^{-1} in elevation (mean: 57.3 m.decade^{-1}), and from -28.6 to 162.6 km.decade^{-1} in stream distance (mean: 14.2 km.decade^{-1}). Nevertheless, the majority of mean annual temperature shifts ranged from 40.6 to 74.3 m.decade^{-1} and 1.1 to 17.3 km.decade^{-1}, respectively, indicating that isotherms moved towards higher elevation and upstream for most French streams and rivers.

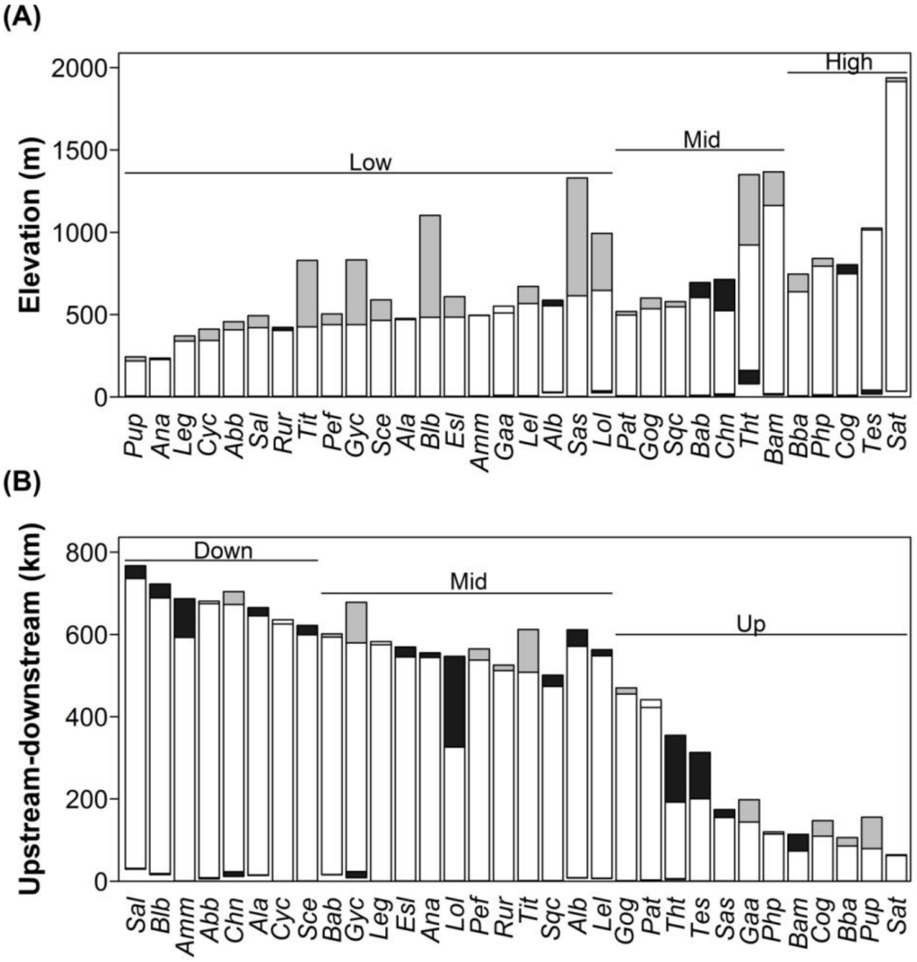

Figure 4 Summary of (A) altitudinal and (B) upstream-downstream range changes across all species in relation to their spatial distribution along these gradients in the initial period. White indicates sections where the initial and contemporary distributions overlapped. Significant ($P < 0.05$) shifts are coloured grey for range expansion and black for contraction. Species codes and spatial distribution preferences along these gradients as in Table 1.

Range shift

The distributional shifts showed directional trends towards higher elevation and upstream position for most species (Fig. 3A, B). Changes higher than 30 m were more common at the upper elevation limit (71.9%) than at the lower limit (3.1%), and only 1 species showed changes at both ends of their range. However, all shifts of the lower limit were relatively negligible compared to those of the upper limit, with mean shifts of 4.9 m and 116.9 m, respectively. All but 7 species exhibited a shift in elevation range centre towards higher elevation, with a mean elevation shift of 26.1 m. Only 4 species exhibited a shift in elevation range centre towards lower elevation, although the magnitude of the shifts toward lower elevation was relatively minor. As a result, when considering changes in range limits higher than 30 m, 78.1% of species actually showed a consistent altitudinal shift, with 17 patterns of range expansion to higher elevation (Fig. 2, pattern C), 1 pattern of full altitudinal shift (Fig. 2, pattern A), and 7 pattern of change in elevation range centre (Fig. 2, pattern I), while 3 species showed a contraction of their upper range limit (Fig. 2, pattern H).

In contrast, changes of > 2 km in the downstream limit were more common (84.4%) than those of the upstream limit (9.4%). Mean shifts in upstream and downstream limits were of 1.0 km downstream and 11.9 km upstream, respectively, and the shift in range centre along this gradient was of 1.2 km upstream. Overall, when considering changes in range limits of more than 2 km, 65.6% of species showed consistent patterns towards upstream positions. The pattern of range contraction (Fig. 2, pattern F) was the one most commonly observed (40.6%), with a mean contraction upstream of both the downstream limit and the range centre of 64.6 km and 13.6 km, respectively. Nevertheless, 5 species exhibited a downstream shift with an expansion of the downstream limit towards a position further downstream (Fig. 2, pattern E), while 2 species showed a downstream shift in range centre (Fig. 2, pattern J).

By comparing range shifts of species according to their distribution along environmental gradients in the initial period, we found that the magnitude of range expansion at the upper elevation range limit was greater for low-elevation species (Fig. 4A). In contrast, contraction along this gradient at either the upper or lower range limits were mostly observed for mid- or high-elevation species. As a result, although most species extended their overall extent, about 30 and 20% of high- and mid-elevation species showed a contraction of their overall extent, respectively. No clear

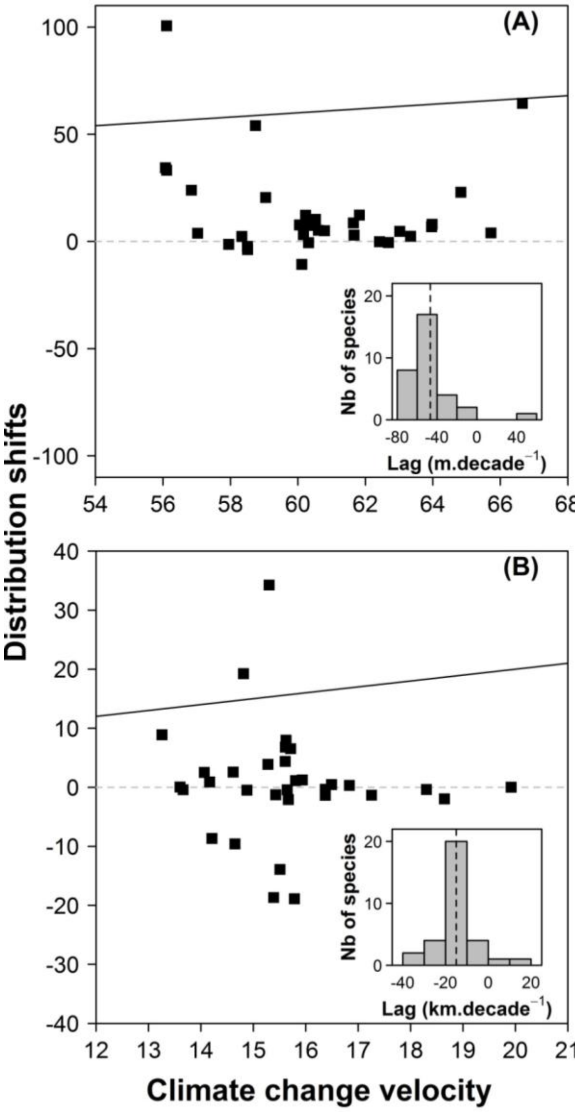

Figure 5 Comparison of distribution shifts with climate change velocity at the species range centre along (A) altitudinal (m.decade^{-1}) and (B) upstream-downstream (km.decade^{-1}) gradients. Positive distribution shifts indicate shifts towards higher elevation or upstream and negative shifts towards lower elevation or downstream. The solid line corresponds to cases where species track perfectly climate change. The histograms show the time lags between shifts in species range centre and the velocity of climate change (i.e. negative values indicate that species are lagging behind climate change).

pattern of range shifts was apparent along the upstream-downstream gradient, although the magnitude of the contraction at the lower range limit was greater for few midstream and upstream species (Fig. 4B). A contraction of the overall extent was commonly observed for all species, although about 40% and 50% of upstream and midstream species showed an expansion related to a downstream shift at their lower range limit. However, about 20% of downstream species showed no changes in their overall extent along this gradient.

The patterns of range shifts were consistent with the expectations based on the velocity of climate change. At the downstream limit, in particular, climate change velocity suggested that species may need to shift at a much faster rate to track climate change than at the upstream limit (Fig. 1D). However, stream fish range shifts lagged far behind expectations along both the elevation and upstream-downstream gradients (Fig. 5). Overall, changes in the spatial distribution of species were directed towards colder conditions with respect to initial climate, but most species have shifted far less than necessary to track the rising annual temperature at their range centres. Indeed, only two species have shifted at a pace sufficient to track temperature change, resulting in mean lags across species of 46.8 $m.decade^{-1}$ and 15.0 $km.decade^{-1}$ along the altitudinal and upstream-downstream gradients, respectively. Nevertheless, the lag behind temperature-based expectations at the species range centre varied considerably among stream fish while no trends with the velocity of climate change was apparent.

DISCUSSION

Our results highlight consistent shifts to higher elevation and upstream in the fish distribution ranges from 1980-1992 to 2003-2009. Increases in elevation range centre appeared to result from colonisations at higher elevations rather than extinctions at low elevations. The mean altitudinal shift (13.7 $m.decade^{-1}$) was consistent with the shifts measured by Hickling *et al.* (2006) for 15 fish species in Britain over a comparable period of time (13.1 $m.decade^{-1}$). Whereas this latter study focused on changes in species elevation range centre, shifts of the upper range limit by 6.1 $m.decade^{-1}$ towards higher elevation were documented for 99 terrestrial species (Parmesan & Yohe, 2003). We found that the shift rate was of greater magnitude (61.5 $m.decade^{-1}$), indicating that stream fish may be more sensitive to climate-induced impacts than other terrestrial organisms. In contrast, upstream movements were greater at the downstream limits (6.3 $km.decade^{-1}$) than at the upstream limits where a mean downstream shift across all species was observed (0.5 $km.decade^{-1}$). Such range contraction resulted in significant shifts in species range centre along this gradient (0.6 $km.decade^{-1}$), but, to the best of our knowledge, no comparable values have been reported in the literature. Similarly to North American streams (Isaak & Rieman, 2013), climate change velocities in French streams indicated that isotherms shifted during the last decades about 40.6 to 74.3 $m.decade^{-1}$ towards higher elevation, and about 1.1 to 17.3 $km.decade^{-1}$ along the upstream-downstream gradient, as air temperature increased by 0.24°$C.decade^{-1}$. Although the magnitude of species distribution shifts observed at range limits was coherent with these expected values, shifts at the centre of species' distributions were of lesser magnitude, particularly along the upstream-downstream gradient. Our findings therefore suggested that species are experiencing greater changes at their range limits than within their range, where larger populations could be more stable and resistant to environmental changes (Brown *et al.*, 1996), resulting in rarely complete but usually transient shifts along environmental gradients, especially over short periods (Maggini *et al.*, 2011).

Under warming conditions, climate change has affected ecosystems in a non-linear way, and species in downstream or lowland (i.e. flat) areas have to cover longer distances to track their climate niche, compared to mountainous regions, where isotherms are highly packed (Loarie *et al.*, 2009). Indeed, our findings provided evidence for such dispersal-driven expansion along the altitudinal gradient, where favourable new conditions at higher elevations prompted the species inhabiting lowland areas to move upward (Hill *et al.*, 2002; Moritz *et al.*, 2008). On the other hand, most species showed a contraction at their lower limit along the upstream-downstream gradient, indicating that climatic stress may be an important determinant of stream fish downstream limits. Given that downstream sections were also the areas where climate has changed most due to the concavity of stream profile (Isaak & Rieman, 2013), geographic variation in the velocity of climate change may explain patterns of range shifts across species distributions. It is therefore likely that stream fish follow climate change through complex modifications of their geographical distributions.

However, although most species shifted in the expected direction, spread rates appeared insufficient to keep pace with changing climate conditions. The velocity of climate change at the species range centre was much greater than the observed distribution shifts, indicating that the response of stream fish actually lags behind climate warming (Devictor *et al.*, 2008; Bertrand *et al.*, 2011; La Sorte & Jetz, 2012). Indeed, mean lags in species response (elevation: 46.8 m.decade^{-1}; upstream: 15.0 km.decade^{-1}) were beyond several order of magnitude the distance already moved by species along the altitudinal and upstream-downstream gradients, respectively. As the velocity of climate change probably already exceeds the rates that species can achieve in colonizing newly suitable habitat, the accumulating delay may have profound consequences on the ability of species to cope with future climate modifications. As the temperature would shift upstream of > 100 km during the next decades (Isaak & Rieman, 2013), our results provided strong empirical support that climate change is now a major threat to freshwater biodiversity (Sala *et al.*, 2000; Heino *et al.*, 2009). Nevertheless, this effect varied considerably among species, such as two species are already experiencing colder temperatures than expected based on isotherms shifts in mean annual temperature, while several species have moved to an unexpected direction. Changes in multiple climatic factors, in addition to mean temperature, may help to explain these conflicting observations (e.g. Burrows *et al.*, 2011; Dobrowski *et al.*, 2013). In particular, the impact of thermal stress may be particularly important for aquatic species such as stream fish because, as ectothermic animals, they are known to be sensitive to extreme temperature conditions (Elliott, 1981; Matthews, 1998). Future studies should therefore assess if shifts in the geographical space of species are related to changes in specific climatic conditions rather than to mean temperature increases.

However, the consistency between directional trends in climate and changing distribution may not be sufficient to demonstrate causation, particularly when there are potential confounding interactions with other drivers of change (Thomas, 2010; Hockey *et al.*, 2011). As a result, movements toward higher elevation and upstream cannot be unambiguously interpreted as a consequence of climate warming, particularly in aquatic systems where dispersal is limited by the structure of the river network. Hence, anthropogenic pressures and climate change may simultaneously influence species range shifts, given the large overlap between 'climate-change-susceptible' and threatened species (Foden *et al.*, 2008). For instance, range retractions might be a consequence of drivers others than climate, as those species are more prone to react to changes in habitat suitability than more generalist species. Alternatively, directions towards previously warmer conditions might be explained by improvement in water quality that occurs over the course of the study period (Glennie *et al.*, 2002; Poulet *et al.*, 2011), especially in downstream sections. In addition, susceptibility of species to diseases or shifting competitive or predator-prey relationships have also been evoked to explain range retractions (Hari *et al.*, 2006; Thomas, 2010), while competition release (Lenoir *et al.*, 2010; Maggini *et al.*, 2011) may have benefited high-range species, allowing them to recolonise the lower periphery of their niche.

Expansion of the upper limit may also be easier to detect than contraction of the lower limit because extinction may be missed or underestimated as a result of the temporary persistence of local populations (Thomas *et al.*, 2006; Doak & Morris, 2010). In this study, we found that sampling success had increased in down to mid upstream-downstream bands over the study period. As a result, the fraction of lower range limits showing either a contraction or an expansion may have been overestimated. Nevertheless, although temporal trends in detectability may simulate range shifts or indeed hide real shifts (Kéry & Plattner, 2007; Tingley & Beissinger, 2009), two pieces of evidence suggested that the patterns observed were more likely to reflect changes in distribution rather than temporal changes in detectability. First, the differences in the mean proportion of species detected appeared to be limited to the downstream areas rather than occurring in the upper areas, where an increase in detection success might artificially suggest downstream shifts but in any case upstream shifts. Second, changes in species-specific detectability were relatively minor, and not related to shifts measured along environmental gradients. They may thus only reflect the increase in the number and abundance of species documented in large rivers over the last decades (Daufresne & Boët, 2007; Poulet *et al.*, 2011).

Freshwater ecosystems contain some of the most imperilled faunas worldwide and advancing our knowledge of the effect of climate change is a key challenge for conservation (Olden *et al.*, 2010). Our approach, which integrates distinct facets of species ranges along environmental gradients, provides evidence that complex modifications of stream fish distribution have occurred over recent decades in France, that were consistent with the geographical variation in the velocity of climate change. However, we found that the degree of climate change exposure alone could not explain much of the differences across species range shifts. Indeed, responses of individual species may not be isolated phenomena, but determined by an array of interacting biological and environmental factors, that are sometimes difficult to predict (Walther, 2010). Moreover, individualistic traits (e.g. dispersal capacity, trophic level) may induce high variability in the consistency of climate response across species (Parmesan, 2006). Although species sharing similar characteristics should be expected to show similar patterns in range shift (Pöyry *et al.*, 2009), recent work has not strongly supported this assertion (e.g. Angert *et al.*, 2011). Additional work is thus needed to further elucidate the mechanisms underlying species responses to a changing climate and to understand the nature of multiple-stressor effects on species populations and local assemblages.

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SUPPORTING INFORMATION

Appendix 1 Climatic trends from 1965 to 2008 and sites characteristics.

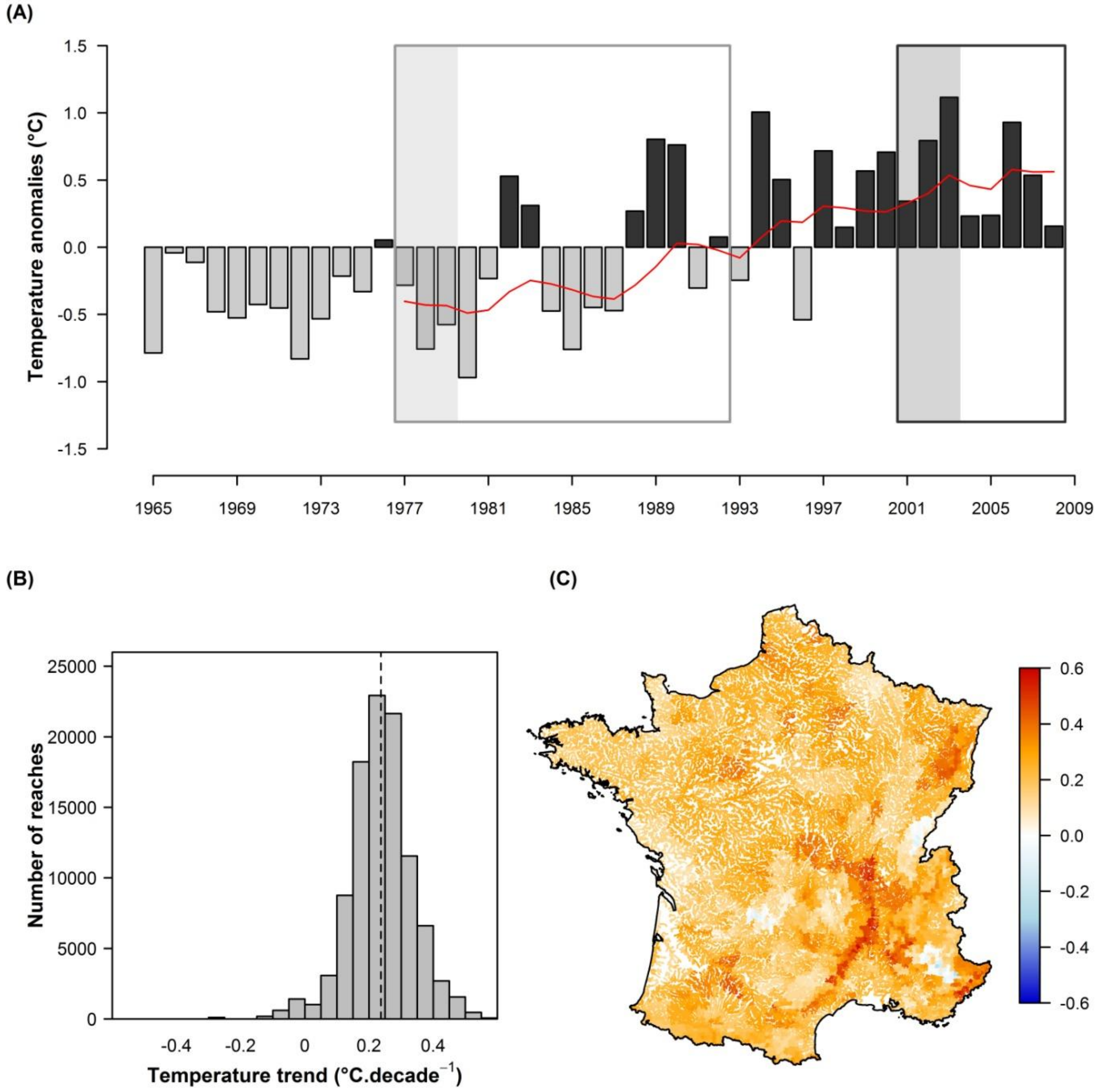

Figure A1 (A) Mean annual temperature anomalies for 1965 to 2008 (using overall air mean temperature as baseline) averaged for 8-km grid climatic data distributed over the entire study area. Grey bars refer to negative anomalies, whereas black bars refer to positive ones. The first period is mainly composed of 'cold' years and the second period of only 'warm' years. No temporal trend was observed within both periods. The red curve is the moving-average with use of a 10-year filter. Black rectangles show the length of the initial and the contemporary periods including the three preceding years, which are indicated by the grey shaded areas. (B) Histogram and (C) spatial distribution of the temporal trends in mean annual temperature (°C.decade^{-1}) along the reaches of the hydrographic network, calculated as the slope of the linear regression of mean annual temperature over time. The dashed line indicates the mean of the differences across all reaches. Air temperature was used as a surrogate of water temperature after applying a scaling factor of 0.8°C.

Table A1 Summary of the environmental conditions of the sampling sites.

	Units	Minimum	Maximum	Mean	SD
Elevation	m	2	2289	298	308
Slope	‰	0.001	380.902	12.301	23.805
Full area drained by the upstream area	km²	0.5	84809	1006.6	4541.1
Cumulated length of the upstream flow network	km	0.1	26732.9	370.7	1633.2
Distance from source	km	0.02	846.21	15.96	78.86

Appendix 2 Temporal variation in the sampling success between initial and contemporary surveys.

For this analysis, we initially refined the datasets to include only sites sampled at least three times during each period. In addition, to determine if the species pool was sufficiently closed during time windows of varying lengths within each period, the test of Otis *et al.* (1978) was used. It compares the mean observed difference between first and last detection of each species to that expected under the assumption of closure, indicating if violation of closure (i.e. gains and losses) has occurred over the period of sampling. We therefore retained for analysis only the sites for which the assumption of closure was not rejected ($P > 0.05$): 177 sites with 4.19 ± 2.39 SD surveys per site and 777 sites with 4.89 ± 1.69 SD surveys per site for the initial and contemporary periods, respectively.

To assess the completeness of the inventory (i.e. the proportion of species detected) for each sampling occasion, we calculated the ratio of observed species richness for a given sampling occasion to estimate species richness for the corresponding site. Species richness was estimated using the maximum of two different non-parametric estimators, based on the frequencies of species in the collection of sampling occasions for a given site: Chao 2 and Jackknife 1 (Colwell & Coddington, 1994). We then fitted a generalized linear mixed-effects model (GLMM), designed to assess the extent of spatial and temporal variation in survey effort that might potentially have affected the proportion of species detected. After having checked for normality, we modelled the proportion of species detected for each sampling occasion according to several characteristics of the samplings using a Gaussian error distribution. To account for the relative uncertainty in species richness estimates, we included the inverse of the standard error of the estimates of species richness as weights in the GLMMs (Meyer *et al.,* 2011). Fixed effects included in the model were season, sampling method (complete, partial or fractional), prospection method (wading, using a boat or mixed) and the number of pass removals as well as the interactions between these factors and the time period. Sampling sites nested within hydrographic basins were specified as a random effect in the model.

To obtain species-specific temporal estimates of detectability, we fitted a single GLMM with a binomial error distribution to the presence-absence data of all the species. We thus modelled the probability that the species seen during at least one survey would also be detected during subsequent surveys in each time period. Season, sampling method, prospection method and the number of pass-removals were included as fixed effects. Sampling sites nested within hydrographic basins and species were specified as random effects in the model. This partially crossed design allowed to account for the possible dependence of species detections induced by shared sites and by the identity of species (Kéry & Plattner, 2007).

The significance of each effect, including interaction terms, was assessed using likelihood ratio tests, with sequential dropping of non-significant terms, starting with a full model (Gelman & Hill, 2006). After model simplification, the fixed effects retained were tested using Wald tests. Models were initially fitted using maximum likelihood estimation, while the estimates of the final model parameters were obtained by re-fitting the model using the restricted maximum likelihood estimation (Pinheiro & Bates, 2000).

Models were fitted using the *nlme* package (Pinheiro *et al.,* 2011) and *lme4* package (Bates *et al.,* 2011) using R environment software version 2.13.0 (R Development Core Team, 2011).

Table A2 Results of GLMM assessing the influence of a set of predictors on the proportion of species detected.

Source of variation	L-ratio X^2	d.f.	*P*	
Random effects				
Basin	15.58479	1	< 0.001	***
Sites (Basin)	2403.733	1	< 0.001	***
Fixed effects				
Season	15.795	3	0.001	**
Sampling method	5.069	2	0.079	.
Prospection method	21.083	2	< 0.001	***
Number of passes	16.909	1	< 0.001	***
Period	0.495	1	0.482	
Season : Period	2.773	3	0.428	
Number of passes : Period	0.449	1	0.503	
Sampling method : Period	3.244	2	0.198	
Prospection method : Period	41.703	2	< 0.001	***

	Estimate (SE)	*z*	*P*	
Intercept	0.542 (0.03)	18.232	< 0.001	***
Season_Spring	< 0.001 (0.008)	-0.002	0.999	
Season_Summer	0.01 (0.006)	1.572	0.116	
Season_Winter	-0.062 (0.02)	-3.059	0.002	**
Sampling_Partial	-0.017 (0.011)	-1.461	0.144	
Sampling_Fractional	-0.026 (0.012)	-2.218	0.027	*
Prospection_Mixed	0.196 (0.055)	3.575	< 0.001	***
Prospection_Wading	0.182 (0.023)	7.788	< 0.001	***
Number of passes	0.033 (0.008)	4.088	< 0.001	***
Prospection_Mixed : Period	-0.187 (0.057)	-3.318	< 0.001	***
Prospection_Wading : Period	-0.137 (0.022)	-6.231	< 0.001	***

Table A3 Results of GLMM assessing the influence of a set of predictors on species-specific detection probability during successive initial surveys.

Source of variation	L-ratio X^2	d.f.	*P*	
Random effects				
Basin	0.735	1	0.391	
Sites (Basin)	157.820	1	< 0.001	***
Species	668.910	1	< 0.001	***
Fixed effects				
Season	5.340	3	0.149	
Sampling method	9.209	2	0.010	*
Prospection method	10.525	2	0.005	**
Number of passes	12.522	1	< 0.001	***

	Estimate (SE)	*z*	*P*	
Intercept	-0.326 (0.322)	-1.011	0.312	
Sampling_Partial	0.241 (0.181)	1.333	0.183	
Sampling_Fractional	-0.334 (0.237)	-1.409	0.159	
Prospection_Mixed	0.308 (0.235)	1.311	0.190	
Prospection_Wading	0.441 (0.157)	2.813	< 0.001	**
Number of passes	0.466 (0.131)	3.545	< 0.001	***

Table A4 Results of GLMM assessing the influence of a set of predictors on species-specific detection probability during successive contemporary surveys.

Source of variation	L-ratio X^2	d.f.	*P*	
Random effects				
Basin	< 0.001	1	0.9978	
Sites (Basin)	996.730	1	< 0.001	***
Species	4765.200	1	< 0.001	***
Fixed effects				
Season	4.560	3	0.207	
Sampling method	0.921	2	0.631	
Prospection method	14.113	2	< 0.001	***
Number of passes	25.166	1	< 0.001	***

	Estimate (SE)	*z*	*P*	
Intercept	0.683 (0.166)	4.112	< 0.001	
Prospection_Mixed	0.055 (0.073)	0.755	0.450	
Prospection_Wading	-0.187 (0.061)	-3.088	0.002	**
Number of passes	0.229 (0.046)	5.014	< 0.001	***

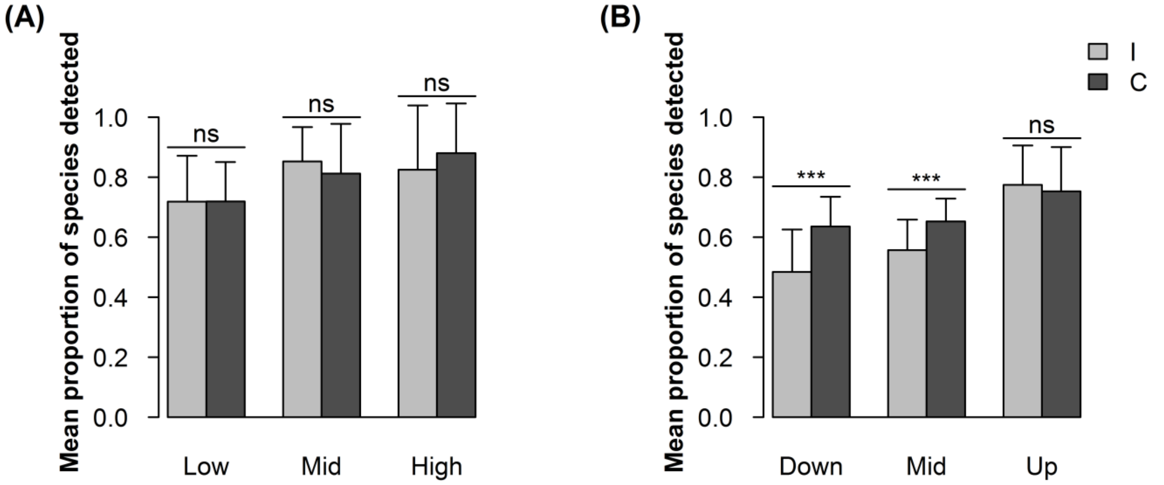

Figure A2 GLMM estimates of the mean proportion of species detected for different (A) altitudinal and (B) upstream-downstream bands and between periods (I = initial; C = contemporary). Altitudinal bands are represented by Low = 0-400 m, Mid = 400-800 m, High = > 800 m and upstream-downstream bands by Down = > 400 km, Mid = 200-400 km, Up = 0-200 km from source. ns = no significant difference, *** highly significant difference (*P* < 0.001) (Wilcoxon ranked test).

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Appendix 3 Performance measures for the initial and the contemporary periods.

Table A5 Mean performance measures of the consensus models calibrated for each species in the initial period. Numbers in brackets indicate standard deviations.

Species	Code	Periode	Prevalence	AUC	TSS	Sensitivity	Specificity
Abramis brama	*Abb*	I	0.08	0.87 (0.01)	0.53 (0.07)	0.69 (0.15)	0.84 (0.09)
Alburnoides bipunctatus	*Alb*	I	0.04	0.89 (0.02)	0.56 (0.12)	0.71 (0.19)	0.85 (0.08)
Alburnus alburnus	*Ala*	I	0.14	0.91 (0.01)	0.64 (0.05)	0.79 (0.1)	0.86 (0.06)
Ameiurus melas	*Amm*	I	0.02	0.91 (0.02)	0.6 (0.19)	0.72 (0.25)	0.88 (0.08)
Anguilla anguilla	*Ana*	I	0.36	0.9 (0.01)	0.63 (0.02)	0.8 (0.04)	0.83 (0.04)
Barbatula barbatula	*Bba*	I	0.54	0.82 (0.01)	0.48 (0.02)	0.78 (0.06)	0.69 (0.06)
Barbus barbus	*Bab*	I	0.16	0.91 (0.01)	0.64 (0.04)	0.8 (0.09)	0.85 (0.05)
Barbus meridionalis	*Bam*	I	0.02	0.98 (0.01)	0.77 (0.17)	0.82 (0.2)	0.95 (0.03)
Blicca bjoerkna	*Blb*	I	0.03	0.91 (0.02)	0.6 (0.12)	0.73 (0.19)	0.87 (0.08)
Chondrostoma nasus	*Chn*	I	0.04	0.91 (0.01)	0.64 (0.11)	0.78 (0.16)	0.86 (0.06)
Cottus gobio	*Cog*	I	0.48	0.84 (0.01)	0.52 (0.02)	0.75 (0.04)	0.76 (0.04)
Cyprinus carpio	*Cyc*	I	0.04	0.78 (0.03)	0.39 (0.09)	0.58 (0.18)	0.81 (0.11)
Esox lucius	*Esl*	I	0.17	0.84 (0.01)	0.51 (0.05)	0.72 (0.1)	0.79 (0.07)
Gasterosteus aculeatus	*Gaa*	I	0.08	0.86 (0.02)	0.52 (0.08)	0.71 (0.16)	0.81 (0.08)
Gobio gobio	*Gog*	I	0.48	0.82 (0.01)	0.49 (0.02)	0.77 (0.05)	0.72 (0.04)
Gymnocephalus cernua	*Gyc*	I	0.03	0.9 (0.02)	0.56 (0.16)	0.69 (0.23)	0.87 (0.08)
Lepomis gibbosus	*Leg*	I	0.08	0.86 (0.02)	0.55 (0.09)	0.73 (0.15)	0.83 (0.07)
Leuciscus leuciscus	*Lel*	I	0.21	0.84 (0.01)	0.52 (0.03)	0.75 (0.09)	0.77 (0.07)
Lota lota	*Lol*	I	0.03	0.93 (0.02)	0.64 (0.14)	0.75 (0.2)	0.89 (0.08)
Parachondrostoma toxostoma	*Pat*	I	0.02	0.94 (0.02)	0.68 (0.17)	0.77 (0.21)	0.91 (0.05)
Perca fluviatilis	*Pef*	I	0.23	0.84 (0.01)	0.5 (0.04)	0.73 (0.09)	0.78 (0.07)
Phoxinus phoxinus	*Php*	I	0.49	0.8 (0.01)	0.45 (0.02)	0.74 (0.04)	0.71 (0.04)
Pungitius pungitius	*Pup*	I	0.06	0.91 (0.01)	0.61 (0.12)	0.75 (0.18)	0.86 (0.07)
Rutilus rutilus	*Rur*	I	0.40	0.87 (0.01)	0.57 (0.02)	0.78 (0.04)	0.79 (0.04)
Salmo salar	*Sas*	I	0.04	0.95 (0.01)	0.7 (0.14)	0.79 (0.18)	0.91 (0.05)
Salmo trutta	*Sat*	I	0.72	0.89 (0.01)	0.59 (0.04)	0.81 (0.06)	0.78 (0.08)
Sander lucioperca	*Sal*	I	0.02	0.91 (0.03)	0.62 (0.15)	0.72 (0.2)	0.9 (0.06)
Scardinius erythrophthalmus	*Sce*	I	0.07	0.81 (0.02)	0.42 (0.07)	0.63 (0.16)	0.79 (0.11)
Squalius cephalus	*Sqc*	I	0.41	0.86 (0.01)	0.57 (0.02)	0.78 (0.04)	0.78 (0.03)
Telestes souffia	*Tes*	I	0.04	0.98 (0.01)	0.81 (0.1)	0.87 (0.13)	0.94 (0.04)
Thymallus thymallus	*Tht*	I	0.01	0.91 (0.03)	0.59 (0.17)	0.71 (0.24)	0.88 (0.09)
Tinca tinca	*Tit*	I	0.12	0.79 (0.01)	0.42 (0.06)	0.67 (0.14)	0.75 (0.09)

Table A6 Mean performance measures of the consensus models calibrated for each species in the contemporary period. Numbers in brackets indicate standard deviations.

Species	Code	Period	Prevalence	AUC	TSS	Sensitivity	Specificity
Abramis brama	*Abb*	C	0.08	0.87 (0.01)	0.54 (0.07)	0.72 (0.14)	0.82 (0.08)
Alburnoides bipunctatus	*Alb*	C	0.14	0.89 (0.01)	0.6 (0.05)	0.77 (0.1)	0.83 (0.05)
Alburnus alburnus	*Ala*	C	0.22	0.91 (0.01)	0.65 (0.03)	0.81 (0.06)	0.84 (0.05)
Ameiurus melas	*Amm*	C	0.06	0.87 (0.02)	0.53 (0.1)	0.72 (0.18)	0.8 (0.09)
Anguilla anguilla	*Ana*	C	0.30	0.92 (0.01)	0.67 (0.02)	0.82 (0.05)	0.85 (0.04)
Barbatula barbatula	*Bba*	C	0.57	0.81 (0.01)	0.48 (0.02)	0.78 (0.04)	0.7 (0.04)
Barbus barbus	*Bab*	C	0.23	0.91 (0.01)	0.67 (0.02)	0.83 (0.05)	0.83 (0.03)
Barbus meridionalis	*Bam*	C	0.03	0.96 (0.01)	0.72 (0.15)	0.79 (0.19)	0.93 (0.05)
Blicca bjoerkna	*Blb*	C	0.09	0.89 (0.01)	0.58 (0.09)	0.74 (0.15)	0.84 (0.08)
Chondrostoma nasus	*Chn*	C	0.09	0.93 (0.01)	0.68 (0.08)	0.8 (0.12)	0.88 (0.05)
Cottus gobio	*Cog*	C	0.41	0.86 (0.01)	0.56 (0.02)	0.77 (0.04)	0.79 (0.04)
Cyprinus carpio	*Cyc*	C	0.07	0.8 (0.02)	0.41 (0.09)	0.63 (0.19)	0.78 (0.12)
Esox lucius	*Esl*	C	0.18	0.85 (0.01)	0.54 (0.04)	0.75 (0.08)	0.79 (0.05)
Gasterosteus aculeatus	*Gaa*	C	0.09	0.83 (0.02)	0.48 (0.06)	0.68 (0.13)	0.8 (0.08)
Gobio gobio	*Gog*	C	0.54	0.84 (0.01)	0.53 (0.03)	0.79 (0.04)	0.74 (0.04)
Gymnocephalus cernua	*Gyc*	C	0.08	0.89 (0.01)	0.59 (0.08)	0.76 (0.14)	0.83 (0.08)
Lepomis gibbosus	*Leg*	C	0.21	0.84 (0.01)	0.51 (0.04)	0.72 (0.1)	0.79 (0.07)
Leuciscus leuciscus	*Lel*	C	0.22	0.84 (0.01)	0.5 (0.03)	0.73 (0.08)	0.77 (0.06)
Lota lota	*Lol*	C	0.01	0.89 (0.03)	0.55 (0.19)	0.7 (0.26)	0.85 (0.1)
Parachondrostoma toxostoma	*Pat*	C	0.03	0.93 (0.01)	0.64 (0.14)	0.75 (0.19)	0.89 (0.06)
Perca fluviatilis	*Pef*	C	0.31	0.82 (0.01)	0.48 (0.03)	0.72 (0.06)	0.76 (0.06)
Phoxinus phoxinus	*Php*	C	0.55	0.8 (0.01)	0.46 (0.02)	0.75 (0.04)	0.71 (0.04)
Pungitius pungitius	*Pup*	C	0.07	0.91 (0.01)	0.61 (0.08)	0.77 (0.15)	0.84 (0.07)
Rutilus rutilus	*Rur*	C	0.43	0.87 (0.01)	0.57 (0.02)	0.77 (0.03)	0.8 (0.03)
Salmo salar	*Sas*	C	0.04	0.94 (0.02)	0.68 (0.12)	0.77 (0.16)	0.91 (0.06)
Salmo trutta	*Sat*	C	0.58	0.88 (0.01)	0.6 (0.02)	0.79 (0.03)	0.8 (0.03)
Sander lucioperca	*Sal*	C	0.03	0.87 (0.02)	0.53 (0.12)	0.69 (0.19)	0.84 (0.09)
Scardinius erythrophthalmus	*Sce*	C	0.13	0.8 (0.02)	0.43 (0.06)	0.67 (0.14)	0.77 (0.09)
Squalius cephalus	*Sqc*	C	0.54	0.88 (0.01)	0.6 (0.02)	0.81 (0.03)	0.79 (0.03)
Telestes souffia	*Tes*	C	0.06	0.94 (0.01)	0.69 (0.1)	0.79 (0.15)	0.9 (0.06)
Thymallus thymallus	*Tht*	C	0.01	0.91 (0.03)	0.55 (0.22)	0.66 (0.3)	0.89 (0.08)
Tinca tinca	*Tit*	C	0.12	0.83 (0.01)	0.49 (0.05)	0.71 (0.1)	0.79 (0.07)

Appendix 4 Range shifts.

Table A7 Changes in the spatial distribution of the species between the initial and the contemporary periods along altitudinal and upstream-downstream gradients. Positive distribution shifts indicate shifts towards higher elevation or upstream and negative shifts towards lower elevation or downstream. Bold indicates significant changes ($P < 0.05$).

		Elevation (m)			**Upstream-downstream (km)**		
Species names	Code	Range center	Lower limit	Upper limit	Range center	Lower limit	Upper limit
Abramis brama	*Abb*	-1.03	-0.1	**48.64**	**2.11**	-6.22	**-3.01**
Alburnoides bipunctatus	*Alb*	**-4.47**	**4.2**	**-34.33**	-0.94	**40.1**	**0.69**
Alburnus alburnus	*Ala*	**9.81**	**0.81**	-6.46	**12.88**	**19.97**	**1.33**
Ameiurus melas	*Amm*	**-20.34**	**-1.46**	1.9	**65.07**	**94.04**	**0.47**
Anguilla anguilla	*Ana*	**4.47**	**0.13**	**7.98**	**-3.76**	**11.28**	**-0.02**
Barbatula barbatula	*Bba*	**23.12**	**2.19**	**106.68**	**0.59**	**-20.33**	**0.29**
Barbus barbus	*Bab*	**-2.63**	**2.41**	**-90.53**	**4.74**	**-7.71**	-0.43
Barbus meridionalis	*Bam*	**102.56**	**6.97**	**204.79**	**1.68**	**40.52**	**0.07**
Blicca bjoerkna	*Blb*	**19.51**	0.04	**618.65**	**12.41**	**33.6**	-2.63
Chondrostoma nasus	*Chn*	**-7.33**	**7.43**	**-189.02**	**-16.48**	**-31.69**	**-11.44**
Cottus gobio	*Cog*	**5.92**	**1.17**	**-54.43**	**-0.75**	**-37.73**	**-0.05**
Cyprinus carpio	*Cyc*	**15.08**	**0.43**	**68.29**	**-35.51**	-10.09	**-0.29**
Esox lucius	*Esl*	**14.6**	**0.13**	**125.45**	**-3.94**	**24.26**	**-0.53**
Gasterosteus aculeatus	*Gaa*	-0.28	**-2.77**	41.27	**-2.56**	**-54.34**	**-0.01**
Gobio gobio	*Gog*	**9.43**	**0.6**	**65.09**	**2.32**	**-14.78**	0.05
Gymnocephalus cernua	*Gyc*	**43.49**	**1.02**	**392.73**	**-26.47**	**-98.88**	**-14.78**
Lepomis gibbosus	*Leg*	**12.89**	**0.49**	**30.8**	**-18.23**	-7.33	**-0.04**
Leuciscus leuciscus	*Lel*	**14.18**	**1.87**	**104.23**	-0.85	**14.92**	-0.64
Lota lota	*Lol*	**63.07**	**11.95**	**346.07**	**36.55**	**220.63**	**0.97**
Parachondrostoma toxostoma	*Pat*	**7.21**	1.01	**21.61**	**4.87**	19	0.54
Perca fluviatilis	*Pef*	-1.14	0	**65.43**	-2.44	**-27.02**	**-0.78**
Phoxinus phoxinus	*Php*	**38.82**	**7.82**	**46.64**	**0.83**	**-5**	**-0.1**
Pungitius pungitius	*Pup*	**7.49**	**-1.07**	**25.91**	**-0.68**	**-76.09**	**-0.01**
Rutilus rutilus	*Rur*	**5.58**	**0.47**	**-18.33**	**-2.6**	**-13.32**	**-0.19**
Salmo salar	*Sas*	**122.35**	**1**	**715.66**	-0.02	**19.56**	-0.07
Salmo trutta	*Sat*	**65.19**	**1.63**	**22.74**	**0.05**	**1.99**	0
Sander lucioperca	*Sal*	**8.86**	**0.2**	**72.9**	**15.16**	**31.09**	2.03
Scardinius erythrophthalmus	*Sce*	**23.29**	**0.26**	**125.41**	**8.31**	**22.71**	-0.28
Squalius cephalus	*Sqc*	**4.38**	**1.13**	**32.39**	**7.34**	**27.73**	-0.24
Telestes souffia	*Tes*	**45.36**	**23.57**	10.93	-0.82	**112.53**	0.08
Thymallus thymallus	*Tht*	**190.97**	**82.11**	**427.86**	**16.86**	**162.35**	**-1.86**
Tinca tinca	*Tit*	**16.27**	**-0.3**	**403.69**	**-35.9**	**-103.91**	**-1.3**

ARTICLE IV (*P_{IV}*)

Grenouillet G & **Comte L** (Under Review**)** Illuminating geographical patterns in species' range shift. Submitted to ***Global Change Biology***.

Illuminating geographical patterns in species' range shifts

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ABSTRACT

Species' range shifts in response to ongoing climate change have been widely documented, but although complex spatial patterns in species' responses are expected to be common, comprehensive comparisons of species' ranges over time have undergone little investigation. Here, we outline a modeling framework based on historical and current species distribution records for disentangling different drivers (i.e. climatic *vs* non-climatic), and assessing distinct facets (i.e. colonization, extinction, persistence, and lags) of species' range shifts. We used extensive monitoring data for stream fish assemblages throughout France, to assess range shifts for 32 fish species between an initial period (1980-1992) and a contemporary one (2003-2009). Our results provide strong evidence that the responses of individual species varied considerably and exhibited complex mosaics of spatial rearrangements. By dissociating range shifts in climatically suitable and unsuitable habitats, we demonstrated that patterns in climate-driven colonization and extinction were less marked than those attributed to non-climatic drivers, although this situation could rapidly shift in the near future. We also found evidence that range shifts could be related to some species' traits, and that the traits involved varied depending on the facet of range shift considered. The persistence of populations in climatically unsuitable areas was greater for short-lived species; whereas the extent of the lag behind climate change was greater for long-lived, restricted-range, and low-elevation species. We further demonstrated that non-climatic extinctions were primarily related to the size of the species' range, whereas climate-driven extinctions were better explained by thermal tolerance. Thus, the proposed framework demonstrated its potential for markedly improving our understanding of the key processes involved in range shifting, and also offers a template for informing management decisions. Conservation strategies would greatly benefit from identifying both the geographical patterns and the species' traits associated with complex modifications of species' distributions in response to global changes.

Keywords: distribution shifts; range limits; colonization; extinction; lag; drivers; climate change; stream fish

INTRODUCTION

Species' distribution shifts in response to contemporary climate change have been documented for many taxa (Root *et al.*, 2003; Parmesan, 2006; Chen *et al.*, 2011), and these distributional shifts can have important ecological implications at various levels of organization. Species' range shifts can elicit evolutionary responses with rapid life-history shifts (Phillips *et al.*, 2010) and changes in neutral evolution (McInerny *et al.*, 2009), species' genetic structure, and diversity patterns (Jezkova *et al.*, 2011; Espíndola *et al.*, 2012). Range shifts can also result in community reorganization (Le Roux & McGeoch, 2008), and lead to no-analog communities, in which species co-occur in previously unknown combinations (Williams & Jackson, 2007), which can have considerable impacts on species interactions and lead to profound alterations of ecosystem functioning and services (Lovejoy & Hannah, 2005; Walther, 2010). Consequently, as it informs both species-specific extinction risks and future changes in ecosystem integrity, understanding the capacity of species to shift geographic ranges in the face of climate change is of crucial importance from a conservation perspective (Angert *et al.*, 2011). To date, although reported range shifts (poleward and upslope) have predominantly been in the direction expected from observed climate changes (Parmesan, 2006), there is also ample evidence of idiosyncratic responses, which limits our ability to predict distributional shifts across species and calls for a better understanding of the processes involved in range shifts (Tingley *et al.*, 2009; Angert *et al.*, 2011; Chen *et al.*, 2011). There is still little consensus about the ability of different species to track changing climates (Angert *et al.*, 2011), and whether species' range shifts are occurring fast enough remains hardly quantifiable. Thus, understanding species' abilities to shift range successfully is crucial for assessing species' vulnerability to climate change, and remains one of the main challenges facing biodiversity conservation.

Several factors are probably responsible for some aspects of the variation observed among the range shifts of individual species. Firstly, ecological responses to climate change may depend on complex patterns of microclimates (Tingley *et al.*, 2012; Bennie *et al.*, 2013), since interactions between several climatic variables and species-specific sensitivities to those variables shape the direction and magnitude of range shifts (Crimmins *et al.*, 2011; VanDerWal *et al.*, 2013). Moreover, patterns of climate change are often highly dynamic and spatially heterogeneous (Burrows *et al.*, 2011; Chen *et al.*, 2011). Geographical topography and variability in climate change can then create both micro-refugia, where species might persist locally (Lenoir *et al.*, 2013), and gaps in climate paths that prevent range expansions and shifts (Lyons *et al.*, 2010; Early & Sax, 2011). Secondly, although it has been argued that range shifts are caused by climate change, non-climatic influences of global change (e.g. regional anthropogenic drivers) can also contribute to differential rates of range shifting (Le Roux & McGeoch, 2008; D'Andrea *et al.*, 2009; La Sorte & Thompson, 2007). Specifically, habitat fragmentation or degradation and land-use changes can both have a marked impact on the ability of species to cope with climate change and, as a result, the ability of species populations to respond is unevenly distributed over space (Hof *et al.*, 2011). Finally, individualistic traits (e.g. physiological tolerances, life-history strategies, habitat requirements) probably underlie the high level of variability in the degree of the response to climate in different species (Parmesan, 2006; Reif & Flousek, 2012). For instance, although the ability to disperse is acknowledged to be of major importance in enabling species to respond successfully to climate change (e.g. Anderson *et al.*, 2009; Hof *et al.*, 2012), recent work has shown that population persistence (i.e. the ability of populations to persist during periods of unfavorable climatic conditions) may in fact play a critical role in determining whether species are able to shift their range along a climate path (Early & Sax, 2011). Ecological specialization could also be an important cause of lags and species-specific rates of range shift, with habitat generalists expanding more rapidly in response to warming than habitat specialists (e.g. Warren *et al.*, 2001; Le Roux & McGeoch, 2008). Thus, the numerous mechanisms and physiological processes behind range shifting act in concert, and give rise to spatially complex and multi-faceted range shifts (Parmesan *et al.*, 2005; Rabasa *et al.*, 2013).

A better understanding of the geographical patterns in species' range shifts could therefore help to refocus strategies from protected areas towards landscape networks that include protected areas, connecting zones, and intermediate landscapes (Opdham & Washer, 2004). For instance, species' range shifts could be enhanced by management measures intended to improve population persistence (e.g. by increasing habitat patch size and connectivity, Lawson *et al.*, 2012). In this context, disentangling population persistence in climatically-suitable areas could be used to provide a better identification of refugia that are likely to sustain viable populations, whereas persistence in areas that are no longer suitable could be used to pinpoint the areas where the species are most at risk. Furthermore, identifying spatial patterns in species' lags behind climate change can also be particularly useful, as the availability and accessibility of colonizable habitats are key factors underpinning species' abilities to shift their ranges successfully (D'Andrea *et al.*, 2009). In the context of species' responses, strategies that encourage the colonization of newly-suitable habitats (e.g. landscape management for habitat corridors or managed relocation) may facilitate range shifts in response to climate change (Ackerly *et al.*, 2010; Early & Sax, 2011).

Previous studies addressing contemporary species' range shifts have mainly used modeling approaches (i.e. correlative or physiologically-based bioclimatic models, Guisan & Zimmerman, 2000) in which the ranges of species are modeled over periods of time to provide the basis for quantitatively assessing the changes in species distributions. In most of these studies, range shifts were assessed by contrasting species' distributions during two periods (i.e. historical versus current), making it possible to determine whether particular species exhibit range expansion (i.e. colonization), range contraction (i.e. extirpation), or a stable range size. However, these studies often rely on rather simplistic descriptors of the geographical distribution of species (e.g. using the range center, or the upper/lower range limits along elevational/latitudinal gradients), which may provide only a limited biological indication of the impact of climate change on geographic ranges (La Sorte & Thompson, 2007). Moreover, so far, relatively few studies have taken the entire ranges of species into account (Lehikoinen *et al.*, 2013) or attempted to detect shifts using several descriptors (e.g. leading and trailing edges, Zhu *et al.*, 2012; Ordonez & Williams, 2013). The comparison between SDMs trained with historical data and projected over time, and independently-constructed, current models has also been previously addressed (e.g. Kharouba *et al.*, 2009; Maiorano *et al.*, 2012). Nevertheless, most of these studies focused primarily on the temporal transferability of the models (e.g. Araújo *et al.*, 2005a; Dobrowski *et al.*, 2011) or niche stability (e.g. Dudei & Stigall, 2010), while the assessment of geographical patterns in range shifts has remained mainly limited to identifying the locations where species are experiencing range expansion, contraction, or stability (e.g. Parra & Monahan, 2008). Therefore, although this would be of great benefit to our understanding of species' responses to recent climate change, comprehensive comparisons of spatial patterns in species' ranges over time remain poorly explored.

Here, we outline a modeling framework based on historical and current records of species distribution intended to disentangle the different drivers (i.e. climatic vs non-climatic) and the diverse facets (i.e. colonization, extinction, range persistence, and lags) of species' range shifts. First, historical and current data were used to model ranges in both periods. Second, we projected current suitable habitats (i.e. potential current ranges) based on the historical models combined with current climate data. Several aspects of geographical range shifts between time periods were then quantified by comparing the historical and current modeled ranges to the projected current ranges. To demonstrate the potential usefulness of this approach, we used extensive monitoring data of stream fish assemblages obtained throughout France to describe changes in species' ranges for 32 fish species between an initial period (1980-1992) and a more recent one (2003-2009). Finally, we tested whether species' traits explained the variability in multi-faceted range shifts of individual species, providing a way towards a deeper understanding of the complex modifications of species' distribution observed in a context of changing climate.

METHODS

Modelling framework

A modeling approach based on historical and current species distribution records was developed to describe species' range shifts. Our framework involved three steps (Fig. 1): (1) modeling historical species' range using historical environmental and distribution records (hereafter referred to as the 'historical model'), (2) projecting the historical model onto the current climatic conditions (hereafter referred to as the 'projected model'), and (3) modeling current species' range using current environmental and distribution records (hereafter referred to as the 'current model'). While historical and current models predict the species' geographical ranges, the range predicted by the projected model should be interpreted as being the current climatically-suitable range. Confronting these three geographical ranges makes it possible to distinguish geographical areas of population persistence, colonization, or extinction, in both climatically suitable and unsuitable habitats, as well as newly-suitable habitats, which have not so far been colonized (see Fig. 1).

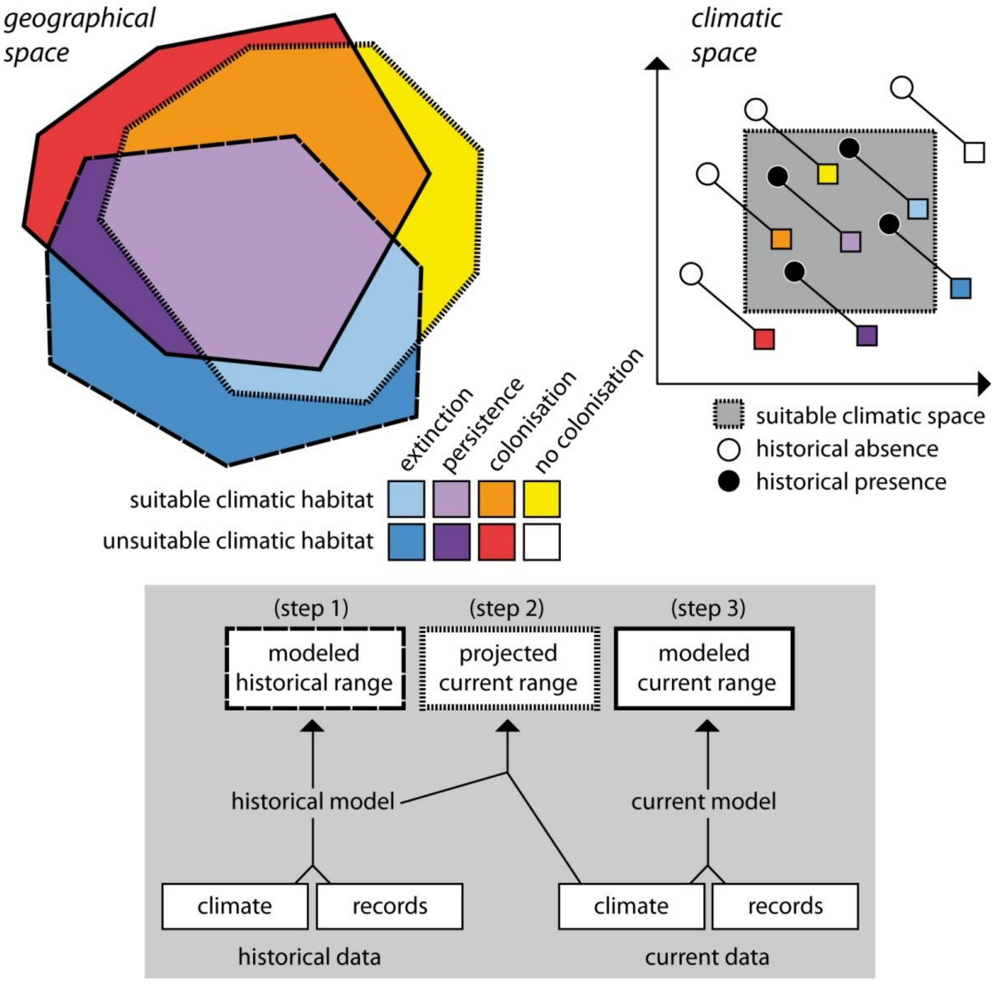

Figure 1 Modeling framework developed to assess how species have changed their geographical ranges and are lagging behind climate change. Comparisons between the modeled historical (dashed line) and current (solid line) ranges, and the projected current climatically suitable (dotted line) range are used to identify distinct facets of range shifts, here illustrated in both the geographical (top left) and climatic (top right) space. Species persistence is shown in light violet (climate deemed to be suitable) and dark violet (climate deemed to be unsuitable, i.e. where the species is likely to be at risk). Extinctions are shown in dark blue (climate-related extinctions) and light blue (extinctions driven by non-climatic factors). Colonizations are shown in orange for newly-suitable habitats (i.e. climate tracking) and in red for climatically-unsuitable habitats (e.g. human-assisted dispersal outside the species' climatic niche). Finally, newly-suitable areas which have not been colonized (i.e. where the species is lagging behind climate change) are shown in yellow.

Species and environmental data

Because of their high sensitivity to thermal conditions, and the facts that they inhabit freshwater habitats where they are confronted by a variety of threats, and that their movements are spatially constrained by the network structure of the drainage basins, stream fish provide particularly relevant model organisms for studying species' range shifts.

Stream fish data were provided by the French National Agency for Water and Aquatic Environments (Onema), the national fisheries organization in charge of protecting and conserving freshwater ecosystems in France. From this electrofishing database (Poulet *et al.*, 2011), we extracted 3549 sites from 1980 to 1992 (referred to below as 'historical surveys'), and 3543 sites from 2003 to 2009 (referred to below as 'current surveys') (see Comte & Grenouillet, 2013). For each period, the selected sites were distributed throughout France and covered the entire range of environmental conditions found in French streams. Data on the presence-absence of fish species were recorded at each site, and we considered only species that were adequately represented in both the historical and current datasets (> 75 presences), for a total of 32 species.

Four habitat variables that were assumed to shape stream fish distributions were used to describe each site. These habitat characteristics consisted of elevation (m), river slope (‰), the entire area drained by the upstream area (km²), and the cumulated length of the upstream flow network (m) (CCM2, Vogt *et al.*, 2007). We then used a principal component analysis (PCA) to eliminate the colinearity between the last two catchment variables and the first axis of the PCA (accounting for 97.80% of the total variability) was kept as a synthetic variable representative of the position along the upstream-downstream gradient.

Six climatic variables were derived from the SAFRAN atmospheric reanalysis over France (8 km grid-data, Le Moigne, 2002): the mean temperature of the coldest and warmest quarters (°C), temperature variability (i.e. CV of the monthly average temperature), cumulated precipitation of the wettest and driest quarters (mm), and precipitation variability. Climatic conditions were averaged across each period, including the three preceding years (e.g. Rowe *et al.*, 2010).

Changes in climate

To assess changes in climate between the two periods, we performed a PCA on the six climatic variables. Changes in climate were quantified by assessing the changes in the position of each reach of the hydrographic network in the climatic space defined by the first two axes (accounting for 81.9% of the total variance). Specifically, we measured the direction (i.e. angular coordinate) and the magnitude (i.e. radial coordinate) of changes in climate for each reach of the network. Beyond global warming, this approach made it possible to identify consistent trends across the reaches, showing more frequent and greater changes towards warmer and thermally more variable conditions (polar diagram, Fig. 3).

Ensemble modelling of species' ranges

For each period and each species, presence-absence data were related to the environmental variables using an ensemble modelling approach (Araújo *et al.*, 2005b) based on eight different species distribution models (SDMs): generalized linear models (GLM), generalized additive models (GAM), multivariate adaptive regression splines (MARS), mixture discriminant analyses (MDA), classification and regression trees (CART), random forest (RF), generalized boosted trees (GBT) and artificial neural networks (ANN). SDMs were built using a random subset of data containing 70% of the sites (i.e. the training dataset), and the remaining 30% of the data (i.e. the testing dataset) were used to evaluate the predictive performance of the models. This split-sample procedure was reiterated 30 times.

For each iteration, we combined the single-SDM predictions by computing the mean value of this ensemble (i.e. 'average model', Marmion *et al.*, 2009). Following Hijmans (2012), the predictive performances of average models were then evaluated using a threshold-independent measure, the calibrated area under the receiver operating curve (cAUC), which controlled for the effect of spatial sorting bias (i.e. inflation of cross-validation results due to spatial autocorrelation).

Finally, the predictions of the average model were computed for the reaches throughout the whole hydrographic network (CCM2, Vogt *et al.*, 2007) and converted into binary values (i.e. presence-absence) using a threshold maximizing the sum of sensitivity and specificity (Liu *et al.*, 2005). Individual species ranges were then mapped, resulting in 30 species ranges modeled for both the historical and current periods.

The same methodology was used to project the historical models onto the current climatic conditions. For each species, the eight single-SDM projections were averaged, evaluated using cAUC, and converted into binary data by using the same threshold values as for the historical predictions, thus resulting in 30 projected species ranges.

Changes in species' range

First, to compare the modeled species' ranges between the two periods, we computed two commonly used measures of the overall change: (1) the difference between the current and historical spatial extents (range sizes) of the species defined as the length of the hydrographic network occupied by the species (Fagan *et al.*,, 2002), and expressed as a percentage of the historical spatial extent, and (2) the dissimilarity between spatial distributions predicted by the historical and current models using the pairwise Jaccard's dissimilarity index (Gower & Legendre, 1986).

For each species and each iteration, we then contrasted the two species' ranges modeled (historical and current), and the projected current range, allowing us to quantify the different facets of species' ranges as described in Fig.1. We computed the length of the hydrographic network corresponding to each of these facets, and we expressed them as a percentage of the historical spatial extent. In addition, we further analyzed changes in species' ranges by mapping them on both geographical and climatic space to provide a better visual assessment of spatial patterns.

Species' trait effects and phylogenetic relatedness

All species were characterized using five traits expected to affect species' range shifts: dispersal ability, life-history strategy, thermal tolerance (i.e. the upper temperature limit), geographical range size and elevational distribution preference (see Table S1 in Supporting Information, Appendix S1 for details of these traits). We tested whether these traits explained the observed variability in range shifts after accounting for the phylogenetic relatedness among species.

First, the phylogeny of the 32 species studied was built on the basis of molecular data obtained from Genbank for three mitochondrial genes (Grenouillet *et al.*, 2011). Sequence data consisted of 1124, 651, and 459 base pairs for cytochrome b, cytochrome oxidase I, and ribosomial 16S sub-unit, respectively. Phylogenetic relationships among species were reconstructed using the Bayesian method under the TVM_I_G substitution model, and the phylogeny estimation implemented with MrBayes and PAUP softwares.

Then, we related species' traits to distinct facets of species' range using phylogenetic generalized least-squares (PGLS) models (Freckleton *et al.*, 2002). These models accounted for the non-independence of data by adjusting the variance/covariance matrix to the phylogenetic relatedness among species using Pagel's λ (i.e. the degree of phylogenetic autocorrelation). More specifically, we focused on four descriptors of range shift: (1) climate-related extinctions, (2) extinctions due to non-climatic drivers, (3) persistence in climatically-unsuitable areas, and (4) lags behind climate change. All the predictors were transformed into z-scores in order to standardize the slope coefficients (β) for comparison across traits.

All models and analyses were developed using R environment software v 2.14.2 (R Development Core Team, 2012).

RESULTS

Model performances between periods

Overall, both the historical and current models showed a good ability to predict the observed species' ranges, with cAUC values among the 32 species ranging from 0.76 to 0.95 (mean = 0.85 ± 0.04), and from 0.78 to 0.93 (mean = 0.85 ± 0.04), respectively (Table S2 in Supporting Information, Appendix S2). No significant difference was observed in predictive performances between the two periods (paired *t*-test, $P = 0.354$). Compared to the current model, the projected model performed significantly worse (paired *t*-test, $P < 0.001$), but showed good predictive performance, with cAUC values ranging from 0.73 to 0.90 (mean = 0.83 ± 0.05).

Changes in species' range

Among the 32 species, 12 species had undergone range contraction while 20 species had experienced range expansion (Table S2 in Supporting Information, Appendix S2). In general, fish species exhibited a gain of area compared to their historic range, with changes in range size ranging from -28.2% to +58.1% (mean = +10.4% ± 0.19). Similarity between the historical and current species' ranges also revealed clear differences between the modeled distributions, which ranged from 0.32 to 0.89 (mean = 0.64 ± 0.12). While changes in species' range were unrelated to differences in model performances for the two periods ($R^2 = 0.018$, $P = 0.459$), dissimilarities between the modeled species' distributions increased with differences in model performance over time ($R^2 = 0.261$, $P = 0.003$).

When the distinct facets of species' range shifts were quantified, we observed contrasted responses among species (Fig. 2). While persistence was the predominant pattern for nearly all of the species (mean = 80.0% of the historical species' range), persistence in climatically-unsuitable areas corresponded, on average, to 8.9% of the historical range and ranged from 0.1 to 54.9% among the 32 species. Lags behind climate change (i.e. newly climatically-suitable areas that remained unoccupied) varied considerably among species, ranging from 0.1 to 125.7% of the historical species' range. Climate tracking (i.e. colonizing newly climatically-suitable areas) had allowed species to expand their historical range by 10.6% on average (range: 0.1-32.4%), whereas climate-related extinctions resulted in range contractions of 5.8% on average (range: 0.0-17.1%). For both the colonization and extinction patterns, the magnitude of the changes in species' range due to non-climatic drivers was significantly greater (paired *t*-tests, $P < 0.001$) than climate-related changes (i.e. 3.2 and 3.7 times higher, respectively).

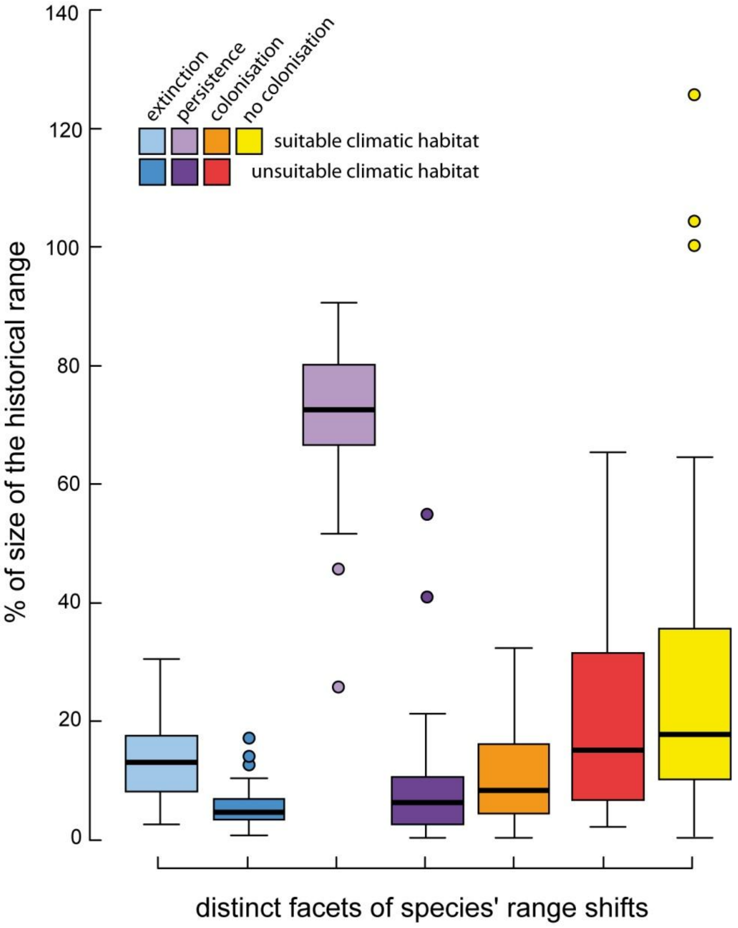

Figure 2 Distinct facets of geographical range shifts between historical and current periods for the 32 fish species studied, expressed as a percentage of the size of the historical range of the species. Color legend as in Fig.1.

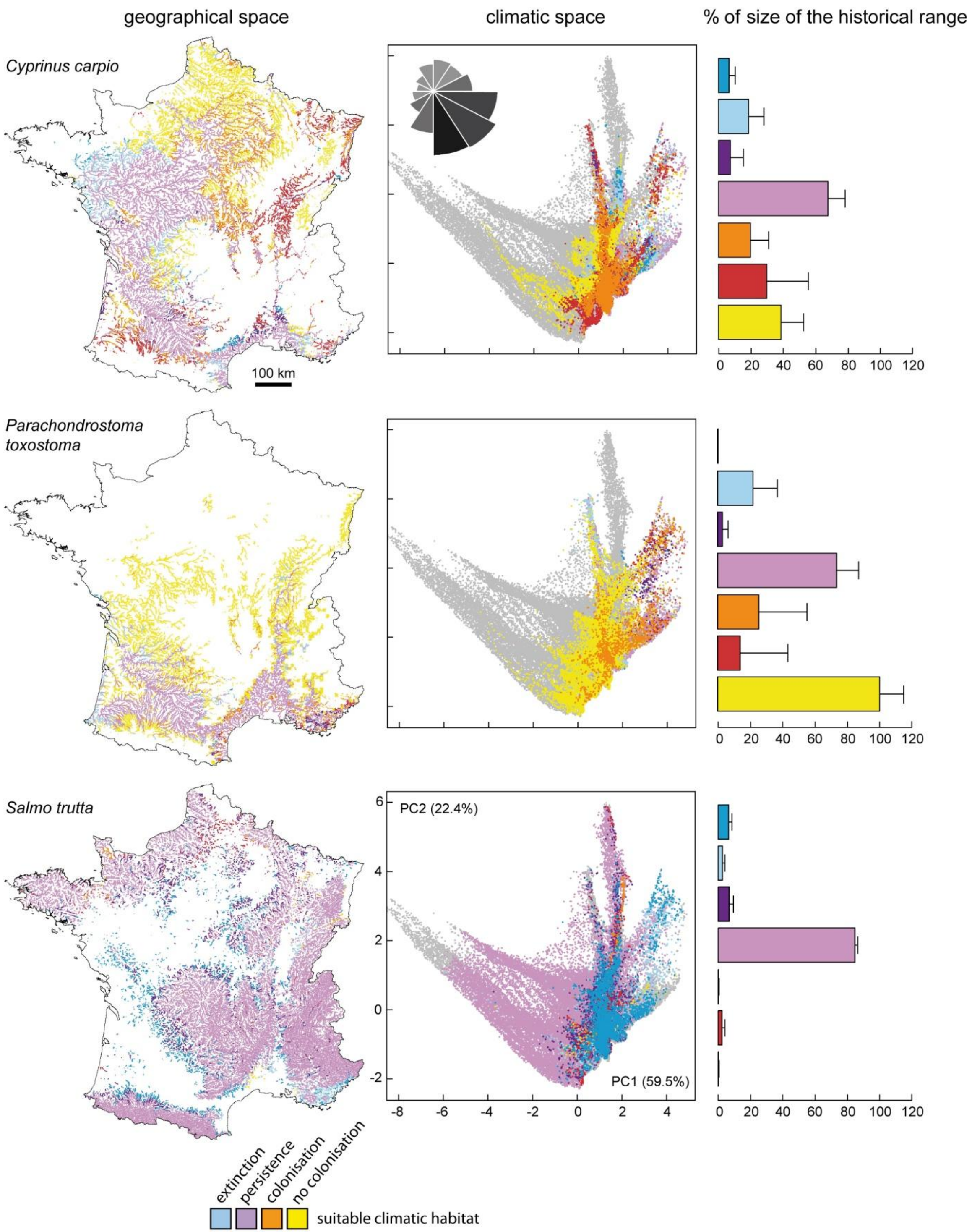

Figure 3 Patterns in species' range shifts over time for three fish species, mapped in both geographical and climatic space. Climatic space was defined by the first two axes (accounting for 81.9% of the total variance) of a principal component analysis performed on the six climatic variables. PC1 represents a gradient from warmer, drier areas (positive loadings) to cooler, wetter areas (negative loadings), whereas PC2 was more strongly associated with temperature variability and contrasted areas with relatively stable conditions (positive loadings) with areas showing greater variation in temperatures (negative loadings). The polar diagram shows the frequencies of occurrence and the directions of climate change between the two periods, with the gray scale proportional to the mean amplitude of the changes for each direction. The percentage of the size of the historical range of the species was quantified for the distinct facets of species' range shifts. Error bars indicate standard deviations across the 30 modeling iterations (see methods). Color legend as in Fig.1.

Spatial patterns in species' range shifts

Following hierarchical clustering based on distinct measures of species' range shifts (Table S2 in Supporting Information, Appendix S2), three species were used to illustrate the spatial patterns in species' responses typical of most of the other species (Fig. 3). *Cyprinus carpio*, a downstream species, showed complex patterns in range shifts. All the distinct facets of species' range shift were represented (by areas of population persistence, colonization, extinction, and lag), and each of these facets displayed clear geographical patterns (i.e. a patchy spatial structure). For instance, large areas of lag behind climate change (characterized by cooler conditions compared to historical distribution) were identified in northern France, while colonizations and extinctions due to non-climatic drivers were more often observed in north-eastern France and north-western France, respectively. Climate tracking was observed for reaches characterized by similar conditions in mean temperature (i.e. low dispersion in climatic space along the first axis, Fig. 3), and for a wide range of conditions in temperature variability. *Parachondrostoma toxostoma*, a species restricted to southern France, persisted in warm reaches of the hydrographical network. This species exhibited lags behind climate change in many reaches located north of its historical distribution, while the species expanded its range in newly climatically-suitable reaches at the edge of its historical distribution. No climate-related extinctions were observed for this species, but a loss of range attributed to non-climatic factors had contracted its historical range by 21.6%. Finally, *Salmo trutta*, a cold-water species, showed large areas of persistence in cold reaches of the hydrographic network. This species exhibited climate-related extinctions and persistence in climatically-unsuitable habitats in the warmest reaches at the edge of its historical distribution, while the few colonization events observed were mainly driven by non-climatic factors.

Species' traits

When accounting for the effect of phylogenetic relatedness among fish species, the magnitude of climate-related extinctions was negatively related to life cycle duration and the species' upper temperature limit (P = 0.019 and 0.026, respectively), revealing that extinctions due to loss in climatic habitat suitability were greater for short-lived and cold-adapted species (Table 1). Extinctions driven by non-climatic factors were negatively related to the species' thermal tolerance and geographical range size (P = 0.016 and 0.002, respectively), resulting in more pronounced range contractions for cold-adapted and restricted-range species. Persistence in climatically-unsuitable areas was significantly (P = 0.003) related to life cycle duration (persistence was greater for short-lived species). Finally, the magnitude of the lags behind climate change was related to life-cycle duration and the two geographical attributes of the species (range size and elevational distribution preference), with significantly greater lags being observed for long-lived, restricted-range and low-elevation species (P = 0.012, 0.003, and 0.002, respectively).

Table 1 Phylogenetic generalized least-squares (PGLS) models testing the relationships between range shifts and species' traits. Changes in species' range included climate-related extinctions, extinctions due to non-climatic drivers, persistence in climatically unsuitable areas, and lags behind climate change. Species' traits included dispersal ability, life-history strategy (i.e. life cycle duration), thermal tolerance (i.e. upper temperature limit), geographical range size, and elevational distribution preference. Slope coefficients (β) and associated P-values (ns, not significant) are given. See Table S1 in Supporting Information, Appendix S1, for details on traits.

	Climate-related extinctions		Non-climatic extinctions		Persistence		Lags	
Species' traits	*β*	*P*	*β*	*P*	*β*	*P*	*β*	*P*
dispersal	-0.012	*ns*	-0.007	*ns*	-0.014	*ns*	0.023	*ns*
life cycle duration	-0.015	0.019	0.030	*ns*	-0.095	0.003	0.063	0.012
thermal tolerance	-0.016	0.026	-0.040	0.016	0.046	*ns*	-0.022	*ns*
range size	-0.002	*ns*	-0.050	0.002	0.059	*ns*	-0.070	0.003
elev. preference	0.003	*ns*	-0.029	*ns*	0.067	*ns*	-0.076	0.002

DISCUSSION

The novel framework presented here demonstrates how dissociating different drivers (i.e. climatic vs non-climatic) and assessing distinct facets (i.e. colonization, extinction, persistence and lags) of species' range shifts can capture the complex mosaics of species' responses and could markedly improve our understanding of key processes involved in range shifts. Although such an approach has already been partially tackled (e.g. Warren *et al.*, 2001), we are not aware of any study that has actually proposed a similar framework.

Our findings provide strong evidence that the responses of individual species varied considerably and they exhibited complex mosaics of range shifts. Such individualistic and spatially-complex range shifts have already been reported in response to changing climates in the past (Graham *et al.*, 1996), and evidence from palaeoecology suggests that climatic micro-refugia have been important in shaping current species' geographical ranges (Sublette Mosblech *et al.*, 2011). Similarly, geographical variation in ongoing climate change is critical in explaining the contemporary differences in the range shifts of individual species (e.g. Ackerly *et al.*, 2010; Chen *et al.*, 2011). Therefore, as both climate change and topographic heterogeneity influence how species modify their distribution (Lyons *et al.*, 2010; Lenoir *et al.*, 2013), we propose that complex geographical patterns in species' responses should be expected to be common and must, therefore, be more intensively explored if we are to better understand and more accurately predict range shifts.

By confronting historical and current modeled ranges and projected current ranges, we have shown in both climatically-suitable and -unsuitable habitats geographical areas of range stability, colonization, extinction, and lags behind climate change. Notably, we have demonstrated that patterns in climate-driven colonization and extinction were of lower magnitude than those attributed to non-climatic drivers. This finding is consistent with a recent meta-analysis of range shifts documented for freshwater fish, which compared both observed and predicted climate-induced changes in fish species' ranges (Comte *et al.*, 2013). These authors conclusively showed that the current rates of change were of greater magnitude than those forecasted to occur under future climate conditions, thus indicating that other drivers of change may be interacting with climate and seriously affecting freshwater fish species. Among these drivers, Alofs *et al.* (2013) recently noted that human-mediated dispersal could be strongly influencing range shifts in fish species. Previous studies have also suggested that synergetic effects between ongoing climate change and regional anthropogenic drivers (e.g. habitat destruction and fragmentation concomitant with land-use changes) could have a marked impact on species' abilities to shift their ranges (La Sorte & Thompson, 2007; Hof *et al.*, 2011). This is of particular interest as it means that range shift forecasts based solely on climate variables may profoundly underestimate future changes in species' distribution. However, few studies have quantitatively assessed how human influence and species' range shifts are correlated (Laliberte & Ripple, 2004), and we strongly recommend that further research be carried out in order to investigate the combined effects of climate change and other regional drivers on species' ranges.

After accounting for phylogenetic relatedness among species, we also found evidence that range shifts could be related to some particular traits of species, and that the traits involved varied depending on the facet of range shifts considered. We showed that population persistence and lags behind climate change were related to life cycle duration, whereas lags also appeared to be related to the geographical attributes of the species. Numerous empirical studies have assessed whether species' traits are linked to recent shifts in geographical ranges (e.g. Perry *et al.*, 2005; Lenoir *et al.*, 2008; Pöyry *et al.*, 2009), but these studies have often reported weak or non-existent relationships (Angert *et al.*, 2011; Crimmins *et al.*, 2011). For instance, Angert *et al.* (2011) failed to identify any consistent effect of geographic range size on recent range shifts, although this trait is the one most often correlated to extinction risk (Cardillo *et al.*, 2008). In contrast, when dissociating climatic and non-climatic drivers of extinctions, we demonstrated that non-climatic extinctions were primarily related to species' range size, while climate-driven extinctions were better explained by species' thermal tolerance. These findings suggest that the weak relationships reported so far could partly result from the fact that (1) these traits are expected to differ fundamentally depending on which threatening processes predominate (e.g. Isaac & Cowlishaw, 2004; Bromham *et al.*, 2012), and (2) most of the documented range shifts cannot unambiguously be attributed to climate change, because of possible confounding effects (e.g. Popy *et al.*, 2010). However, climate change is already beginning to exacerbate other extrinsic threats (Brook *et al.*, 2008), and species' vulnerability is likely to shift from anthropogenic effects in the near term to climate change in the near future (Zhu *et al.*, 2012). In addition, our results caution against over-optimistic conclusions about the vulnerability of species to climate change as lags in extinction and immigration could lead to more severe long-term effects as a result of extinction debts and immigration credits (Jackson & Sax, 2010). We therefore argue that the framework proposed here offers a template for informing management decisions and a promising way to better describe, understand, and predict complex modifications of species' distribution in response to global changes.

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SUPPORTING INFORMATION

Appendix S1 Species’ traits expected to affect range shifts.

Table S1 Description of species’ traits and modalities.

Trait	Modality	Description
Body length	-	Total body length in adults (mm)
Larval length	1	< 4.2mm
	2	4.2-6.3mm
	3	> 6.3mm
Shape factor	-	Ratio of total body length to maximum body depth
Swimming factor	-	Ratio of the minimal depth of the caudal peduncle to maximum caudal fin depth
Fecundity	1	< 10000 oocytes
	2	10000-100000 oocytes
	3	> 100000 oocytes
Spawn time	1	1
	2	> 1
Egg diameter	1	< 1.35 mm
	2	1.35-2 mm
	3	> 2 mm
Life span	1	< 8 years
	2	8-15 years
	3	> 15 years
Female maturity	1	< 2 years
	2	2-3 years
	3	3-4 years
	4	4-5 years
	5	> 5 years
Parental care	1	No protection
	2	No protection with nest or egg hiders
	3	nest or egg hiders
Incubation period	1	< 7 days
	2	7-14 days
	3	> 14 days
Upper temperature limit	-	Upper limit of the optimal temperature range (°C)
Range size	-	% of total network length in the historical period
Elevational distribution preference	1	Low
	2	Medium
	3	High

From these traits, we defined species' ability to disperse by using one axis from a principal co-ordinates analysis (PCoA) based on four morphological traits: body sizes in adults and larvae, and ratios describing the hydrodynamic profile of the fish (shape factor) and their capacity for sustained swimming (swimming factor). For life-history strategies, we used the first axis (interpreted as life cycle duration) of a PCoA based on seven traits: female fecundity, spawn time, egg diameter, life span, female maturity, length of incubation period and parental care. Species' preferences along elevational gradient were defined following hierarchical clustering (Euclidean distance and Ward's linkage criterion) based on the range centre and the upper and lower range limits (Comte & Grenouillet, 2013).

Appendix S2. Model performances and changes in species' range between the historical and current periods.

Table S2 Predictive performances (cAUC) of the average models calibrated for each species, range changes (i.e. differences in spatial extent expressed as a percentage of the historical extent) and range similarities between current and historical periods. Numbers in brackets indicate standard deviations across the 30 modelling iterations. Three clusters (C1-C3) were defined following a hierarchical clustering based on the Ward's method with the Euclidean distance on the different descriptors of species' range shifts as defined in Fig. 1.

Species	**Historical cAUC**	**Current cAUC**	**Range change**	**Similarity**	**Cluster**
Abramis brama	0.849 (0.021)	0.839 (0.021)	-1.3% (0.258)	0.322 (0.058)	C3
Alburnoides bipunctatus	0.866 (0.027)	0.867 (0.017)	-2.7% (0.203)	0.378 (0.034)	C3
Alburnus alburnus	0.891 (0.012)	0.894 (0.013)	+7.8% (0.183)	0.238 (0.040)	C3
Ameiurus melas	0.865 (0.042)	0.847 (0.019)	+22.0% (0.357)	0.434 (0.068)	C1
Anguilla anguilla	0.891 (0.010)	0.909 (0.012)	+14.2% (0.162)	0.259 (0.044)	C1
Barbatula barbatula	0.808 (0.012)	0.799 (0.016)	+29.7% (0.270)	0.314 (0.087)	C1
Barbus barbus	0.894 (0.013)	0.892 (0.014)	-5.6% (0.126)	0.213 (0.031)	C3
Barbus meridionalis	0.929 (0.045)	0.923 (0.033)	+28.4% (0.458)	0.398 (0.078)	C1
Blicca bjoerkna	0.875 (0.030)	0.850 (0.024)	+36.6% (0.453)	0.401 (0.079)	C1
Chondrostoma nasus	0.871 (0.035)	0.905 (0.021)	-24.4% (0.181)	0.360 (0.075)	C3
Cottus gobio	0.828 (0.011)	0.849 (0.012)	+23.0% (0.272)	0.330 (0.054)	C3
Cyprinus carpio	0.756 (0.033)	0.776 (0.026)	+26.6% (0.451)	0.498 (0.063)	C1
Esox lucius	0.829 (0.019)	0.840 (0.017)	-8.7% (0.126)	0.243 (0.035)	C3
Gasterosteus aculeatus	0.832 (0.023)	0.776 (0.031)	-10.9% (0.267)	0.425 (0.052)	C2
Gobio gobio	0.811 (0.012)	0.819 (0.018)	+4.1% (0.167)	0.244 (0.041)	C3
Gymnocephalus cernua	0.853 (0.044)	0.867 (0.021)	+24.4% (0.386)	0.426 (0.071)	C3
Lepomis gibbosus	0.836 (0.027)	0.829 (0.015)	+4.3% (0.203)	0.388 (0.034)	C3
Leuciscus leuciscus	0.824 (0.017)	0.825 (0.013)	-8.5% (0.156)	0.261 (0.047)	C3
Lota lota	0.901 (0.035)	0.788 (0.079)	+34.8% (0.913)	0.615 (0.084)	C2
Parachondrostoma toxostoma	0.881 (0.056)	0.894 (0.028)	+11.8% (0.497)	0.417 (0.080)	C2
Perca fluviatilis	0.826 (0.016)	0.811 (0.015)	-6.7% (0.176)	0.261 (0.054)	C3
Phoxinus phoxinus	0.780 (0.014)	0.785 (0.017)	+15.8% (0.148)	0.401 (0.032)	C1
Pungitius pungitius	0.873 (0.025)	0.884 (0.018)	+33.9% (0.300)	0.368 (0.060)	C3
Rutilus rutilus	0.860 (0.012)	0.845 (0.015)	-9.2% (0.110)	0.209 (0.036)	C3
Salmo salar	0.910 (0.028)	0.893 (0.033)	+58.1% (0.536)	0.560 (0.052)	C1
Salmo trutta	0.870 (0.017)	0.866 (0.015)	-6.5% (0.050)	0.112 (0.022)	C3
Sander lucioperca	0.864 (0.061)	0.835 (0.036)	+40.8% (0.613)	0.454 (0.089)	C1
Scardinius erythrophthalmus	0.773 (0.030)	0.786 (0.020)	+4.1% (0.334)	0.381 (0.068)	C3
Squalius cephalus	0.849 (0.011)	0.862 (0.020)	+4.3% (0.134)	0.214 (0.029)	C3
Telestes souffia	0.948 (0.026)	0.925 (0.020)	-1.1% (0.259)	0.381 (0.054)	C3
Thymallus thymallus	0.856 (0.047)	0.838 (0.048)	+23.5% (0.698)	0.684 (0.046)	C1
Tinca tinca	0.778 (0.020)	0.812 (0.019)	-28.2% (0.159)	0.427 (0.063)	C3

ARTICLE V (P_V)

Comte L & Grenouillet G (Under Review) Species’ traits and phylogenetic conservatism of climate-induced range shifts. Submitted to ***Nature Communications***.

Species' traits and phylogenetic conservatism of climate-induced range shifts

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ABSTRACT

Understanding climate-induced range shifts is crucial for biodiversity conservation. However, no general consensus has so far emerged about the mechanisms involved, and the role of phylogeny in shaping species' responses has so far been poorly explored. Here, we investigated whether species' traits are phylogenetically related to the elevational shifts at the trailing and leading edges documented in aquatic environments. We demonstrate that these shifts are predicted by different combinations of traits. We found that whereas range expansions were underpinned by evolutionarily labile traits, notably life-history strategy and range size, range retractions were clustered within the phylogeny due to a high level of conservatism in thermal tolerance. These findings emphasize that considering various facets of range shifts in the light of evolutionary histories could enhance our understanding of how species respond to climate change and thus improve the assessment of species' vulnerability.

Keywords: distribution shifts; range limits; warming; vulnerability; colonisation; extinction

INTRODUCTION

Evidence is accumulating that ongoing climate change is causing many species to shift their geographic ranges drastically so as to remain within their ancestral environment (i.e. niche-tracking) (Chen *et al.*, 2011; La Sorte & Jetz, 2012). However, we still know little about how the evolutionary history of traits (i.e. phylogeny) constrains species' ability to niche-tracking. Species have been continuously exposed to climate change throughout their evolutionary history, and climate changes in the past have resulted in lineage-specific extinction rates (McKinney, 1997; Roy *et al.*, 2009). Therefore, determining the characteristics that underlie species' sensitivity and/or vulnerability to climate change is crucial for the development of effective conservation and management strategies (Angert *et al.*, 2011; Williams *et al.*, 2008). Present-day geographical biodiversity patterns have been strongly shaped by two distinct processes affecting range dynamics: the expansions and contractions caused by Pleistocene glacial-interglacial cycles (Davis & Shaw, 2001; Roy *et al.*, 2001). As a result, population dynamics at the edges of the distribution range are critical in determining the vulnerability of species to changing climate and, ultimately, for their long-term persistence: colonisation by leading populations (i.e. cold limits at high elevation and latitude) (La Sorte & Jetz, 2012; Thomas, 2010), and extirpation of trailing populations (warm limits at low elevation and latitude) (Cahill *et al.*, 2013; Hampe & Petit, 2005).

The selective responses of species to climate change are underpinned by the interplay between several biological, physiological and ecological traits (Box 1). Despite recent advances (Angert *et al.*, 2011), there is no general consensus about the effects of species' traits on range expansion, and the mechanisms driving the response of trailing populations have so far been poorly explored (Chessman, 2009; Felde *et al.*, 2013). Identifying the phylogenetic signal in range shifts may help us to decipher the mechanisms underlying differences in how species' respond to climate change (Willis *et al.*, 2008). Conservatism of range shifts at the leading and trailing edges of the distribution can be expected to be driven by the degree of phylogenetic clustering of the traits involved in the response to climate change (Roy *et al.*, 2009). At the trailing edge, range contraction is expected to be phylogenetically clustered. Indeed, thermal tolerances are strongly conserved along the phylogeny (Hoffmann *et al.*, 2013), although trophic interactions or traits promoting local persistence could enhance the variability of temperature-dependent extinction at the trailing edge (Box 1). In contrast, colonisation at the leading edge depends strongly on multiple dispersal traits that are subjected to various selection pressures, ultimately leading to decreasing phylogenetic signal (Phillips *et al.*, 2010; Stevens *et al.*, 2010). Indeed, morphological traits linked to dispersal ability (e.g. mobility through body size) are commonly conserved along the phylogeny, whereas several behavioural and ecological traits related to dispersal efficiency (e.g. the degree of habitat specialisation should decrease the habitat available for the species) are thought to be more evolutionarily labile (Blomberg *et al.*, 2003; Losos, 2008). Consequently, we expected to find little or no phylogenetic clustering of range expansion at the leading edge. As far as we are aware, however, the effect of evolutionary constraints on how species track shifting climate has so far remained largely unexplored.

Here, we used range shifts documented in freshwater environments to assess whether phylogenetic patterns in range shifts at the leading and trailing edges along an elevational gradient resulted from conservatism of the traits involved in how fish species' respond to climate change. Stream fishes provide ideal model organisms for studying climate-induced range shifts because of their ectothermic physiology, their relatively-short generation times and the fact that their distribution is constrained within hydrographic networks, thus promoting directional shifts. Specifically, we aimed (*i*) to test whether range-shifting species were phylogenetically more closely related than would be expected by chance alone, and (*ii*) to confront several non-exclusive theoretical expectations (Box 1) of the extent to which traits were phylogenetically related to range shifts at the contracting and expanding limits. As far as we are aware, this is the first time that species' shifts at both range limits have been related to different combinations of traits and shown to exhibit different phylogenetic correlation patterns. This provides novel evidence that divergent mechanisms underlie how species are responding to current climate changes by shifting their ranges.

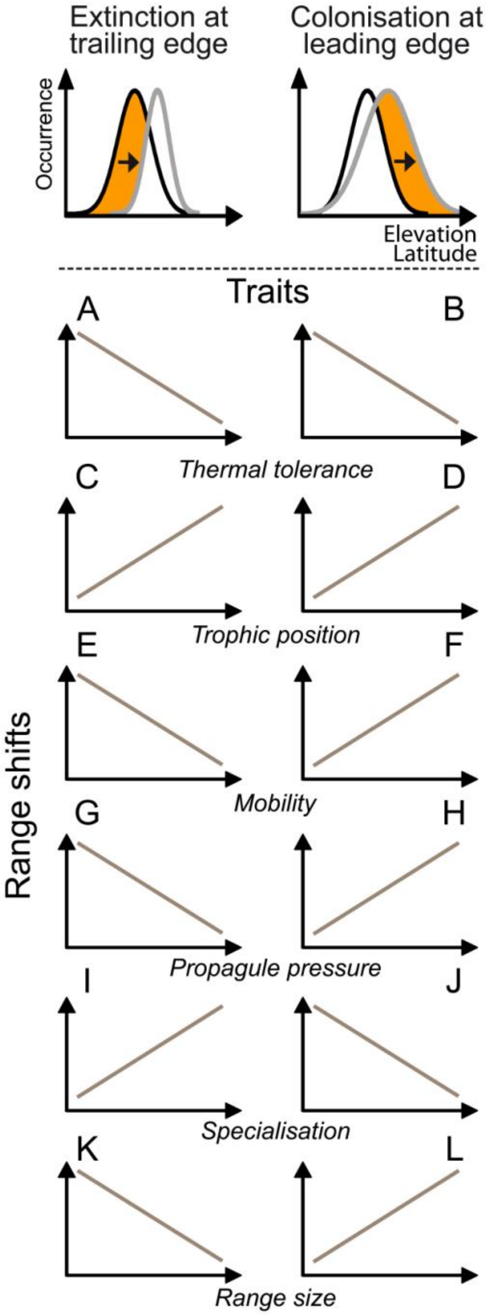
Box 1 Representative subset of predictions about the effects of species’ traits on the climate-induced range shifts of ectotherms.

Contemporary climate change is driving widespread colonisation at the leading edge and extinction at the trailing edge, resulting in range shifts upslope and polewards (Chen *et al.*, 2011; La Sorte & Jetz, 2012).

Ectotherms are especially vulnerable to climate change, because their physiology is directly influenced by temperature. Thermal preferences coincide with temperatures that maximise fitness, and individual performance rapidly drops outside the optimal range (Deutsch *et al.*, 2008; Huey *et al.*, 2012). Thermal tolerance is the principal trait driving extinctions or shifts to cooler habitats (A, B) (Pörtner & Knust, 2007; Sinervo *et al.*, 2010). These effects could also be indirect, since climate change modifies the architecture of food webs as a result of the differing thermal sensitivities of interacting species (Cahill *et al.*, 2013; Pörtner & Knust, 2007). Although the outcome depends on a complex interplay of species responses at different trophic levels (Walther *et al.*, 2002), these impacts are amplifies along the food chain, and are greater at higher trophic positions (C, D). Additional traits can, however, delay extinction at the trailing edge or impede colonisation at the leading edge, although acting in opposite directions (McKinney & Lockwood, 1999; Williams *et al.*, 2008).

At the trailing edge, where thermal physiology or biotic interactions limit range-edge populations, even a small degree of warming has major consequences (Deutsch *et al.*, 2008; Huey *et al.*, 2012). Given the rate and magnitude of changes in climate, these populations may have a limited capacity to cope with new climatic conditions (Hoffmann *et al.*, 2013; Loarie *et al.*, 2009). Nevertheless, mobility capacity and propagule pressure (i.e. the quantity and frequency of dispersing individuals) may enable species to temporarily compensate for local extinctions caused by adverse climatic conditions (E, G) (McKinney & Lockwood, 1999; Trakhtenbrot *et al.*, 2005). Alternatively, thermal stress can be buffered through adaptation, acclimatization and/or behavioural adjustments (Huey *et al.*, 2012), so that the extinction risk may be greater for environmentally-specialized species, and especially significant for range-restricted species (I, K) (Hoffmann *et al.*, 2013).

At the leading edge, dispersal limitations can prevent range expansion since successful colonisation relies on the propensity to disperse, the ability to disperse, and the establishment of propagules outside the current species distribution (Stevens *et al.*, 2010). A wide range of traits is involved, including mobility, propagule pressure, environmental requirements (e.g. resource and habitat specialisation) and geographical range of species (F, H, J, L) (Davis & Shaw, 2001; Stevens *et al.*, 2010; Trakhtenbrot *et al.*, 2005).



METHODS

Species' range shifts

To identify the mechanisms involved in species' range shifts, we used shifts of the lower (i.e. trailing edge) and upper (i.e. leading edge) altitudinal limits previously documented for 32 species of stream fish over two periods of time (1980-1992 and 2003-2009) (Comte & Grenouillet, 2013). This study identified systematic range shifts for most species towards higher altitudes, which were consistent with geographic variations in climate change velocities observed across the French hydrographic network, thus providing strong support that stream fish are currently tracking recent climate warming. Range shifts were reported as mean rates of displacement towards higher elevations in meters, based on spatial distributions described using species distribution models. These models allowed to account for uncertainty in comparing range limits over time based on data sets that had not originally been collected explicitly in order to detect range shifts. Species' distribution data were taken from surveys conducted in all the major hydrographic basins of France, and covered the entire range of environmental conditions of French rivers and streams. Species' ranges were mapped at the scale of stream reaches (i.e. 2 km lengths) throughout the whole French hydrographic network for each time period and each species using an ensemble modelling approach combining several modelling and threshold-setting methods. Overall, all models demonstrated high predictive performances, with a mean AUC value of 0.88 (± 0.05 SD). In addition, no link was found between the variations in species detectability and distribution changes over time. Based on these maps, the lower and upper range limits were calculated to be 2.5 and 97.5%, respectively, of the altitudes where the species were predicted to be present. The shifts were then determined by the least-squares mean of the 2003-2009 period-group effect of the linear regressions relating the measures of range limits and time periods, after accounting for the variability arising from methodological choices (Comte & Grenouillet, 2013).

Phylogeny

We used a phylogeny reconstructed from molecular data on European stream fish (Grenouillet *et al.*, 2011) as our phylogenetic hypothesis (Fig. 1a). Phylogenetic relationships were reconstructed on the basis of three mitochondrial genes (cytochrome b, cytochrome oxidase I and ribosomial 16S sub-unit). Sequence data were obtained from Genbank and consisted of 2234 base pairs (i.e. 1124, 651 and 459 for cytochrome b, cytochrome oxidase I and 16S sub-unit, respectively). The phylogeny was reconstructed using the Bayesian method under the TVM_I_G substitution model, and the phylogeny estimation implemented with MrBayes and PAUP software.

Species' traits

We used 16 different traits to test our theoretical expectations (Box 1) - (see Appendix S1 in Supporting Information for details).

As temperature can act as an inhibiting stress by affecting several different functions, we used two thermal tolerance traits: the upper limit of the optimal temperature range (*upper temperature limit*), defined as the range over which feeding occurs and there are no external signs of abnormal behaviour, and the optimal spawning temperature (*spawning temperature*). We did not use thermal tolerance range *per se* as this information is in short supply for most species, and so we were unable to test specific hypotheses related to the degree of thermal specialisation (but see below *niche breadth*).

The *trophic position* trait was defined as herbivorous, omnivorous, invertivorous, invertivorous-carnivorous to piscivorous.

Despite being difficult to estimate directly, the ability of species to disperse is often estimated for actively dispersing organisms from their morphological characteristics (Trakhtenbrot *et al.*, 2005). In particular, body size is closely correlated with the greatest dispersal distance an active disperser is able to achieve (Jenkins *et al.*, 2007). We therefore included two traits related to body size: that in adults (*body length*) and that in larvae (*larval length*), and two ratios describing the hydrodynamic profile of the fish (*shape factor*) and their capacity for sustained swimming (*swimming factor*). Colinearity between these traits was reduced using a principal co-ordinates analysis (PCoA), and mobility was summarised by the first two axes. The first axis (*mobility PC1*) was interpreted as the larval mobility, and the second (*mobility PC2*) as the adult mobility (Table S4). As the ratios had very skewed distributions, they were log-transformed prior to the analysis.

We used seven traits related to life-history: female *fecundity* (number of oocytes), *spawn time*, *egg diameter* at hatching, *life span*, *female maturity*, length of *incubation period* and *parental care*. We then used the first two axes of a PCoA to summarize these seven traits, the first axis (*life-history PC1*) being positively correlated to propagule pressure and describing the rate of population turnover (i.e. fecundity and life cycle duration), and the second (*life-history PC2*) being negatively correlated to propagule pressure and describing the position of the species along the r-K continuum (i.e. reproductive capacity and development time) (Table S4).

To describe environmental specialisation, we used the outlying mean index analysis (OMI; Doledec *et al.*, 2000) to estimate the *niche breadth*, calculated as the standard deviation of the environmental space used by each species in the initial period along the main axes of the OMI including three environmental variables (slope, elevation, and upstream-downstream position). This niche axis was considered to reflect the tolerance of a wide range of abiotic conditions, including climatic factors, and therefore interpreted as habitat generalisation as well as thermal generalisation.

Range size was estimated as the percentage of the total length of the network predicted to be occupied by the species in the initial period.

Overall, this led us to keep nine variables summarizing the characteristics of species. Although the dependence of thermal tolerance on physiology could lead to interdependence of several of these traits, all remaining correlations between traits were found to be less than 0.65 using phylogenetic analyses (see below).

Statistical analyses

The phylogenetic signal, meaning the tendency of closely-related species to share more similar values than species drawn at random from the tree (Losos, 2008), was evaluated using Pagel's λ (Harvey & Purvis, 1991). Under a Brownian motion model, where species inherit their traits from ancestors, but then slowly diverge by small random amounts and at a constant rate through time, λ is expected to be equal to one. Alternatively, a λ value of zero implies that there is no phylogenetic dependence, while $0 < \lambda < 1$ corresponds to some degree of trait lability. Pagel's λ is a statistically powerful

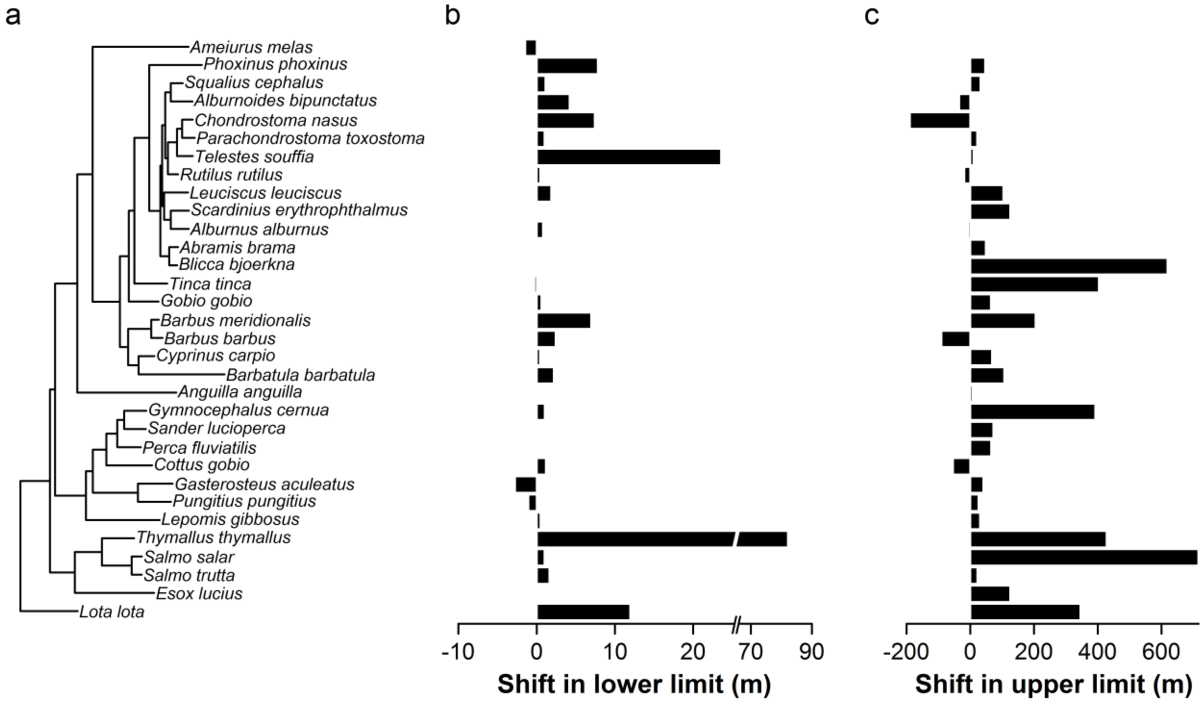


Figure 1 Relationships between the (a) molecular phylogeny and the species' range shifts in (b) the lower and (c) the upper altitudinal limits.

index for measuring whether data exhibit phylogenetic signal, performing better than other indices (Freckleton *et al.*, 2002; Münkemüller *et al.*, 2012), and accounting for phylogenetic non-independence in correlative analyses according to processes other than pure Brownian motion (Harvey & Purvis, 1991). We used this index and its associated likelihood ratio test (Freckleton *et al.*, 2002) to test whether the phylogenetic signal in lower and upper shifts as well as in species' traits differed significantly from a null model of phylogenetic dependence (i.e. no phylogenetic signal; $\lambda = 0$), and in subsequent correlative analyses (see below).

The expected relationships between range shifts and species' traits were tested using phylogenetic generalized least squares (PGLS), which accounted for data non-independence by adjusting the variance/covariance matrix to the phylogenetic relatedness among species using Pagel's λ. All the predictors were transformed to z-scores to standardize the slope coefficients (β) in order to compare the relative strength of the predictors. We constructed all the combinations of models for a maximum of three predictors, in accordance with the general rule of thumb limiting the number of predictors to one-tenth of the number of observations (i.e. 32 species). We used the Akaike information criterion adjusted for small sample size (AICc) for multimodel inference (Burnham & Anderson, 2004). We performed model averaging accounting for model uncertainty by averaging the slope coefficients (β) across all models with ΔAICc ≤ 2 from the model with the lowest AICc, using Akaike weights (w_i), and including zeros when predictors did not occur in a particular model.

However, to control for the effects of confounding factors that are likely to influence species' range shifts, we first regressed the values of range shifts against two covariates: the degree of exposure to climate change, estimated as the median of the change in the annual temperature between the two time periods experienced by a species in its initial distribution, and the degree of anthropogenic manipulation, scored from one to four to reflect their use in aquaculture, as bait or as gamefish (see Appendix S1 for details). Multimodel inference was then performed on the residuals. As some species may occupy areas where climate has changed faster than that occupied by other species, the change in temperature in the initial species' range was included to control for the fact that differing degrees of exposure to recent climate change may have resulted in different degrees of physiological stress, and consequently in different impacts (Williams *et al.*, 2008). In addition, human commercial or recreational activities may give species more opportunities to move into previously unsuitable habitats (i.e. human-mediated dispersal), leading to range expansions, or conversely reduce species' persistence (i.e. human-induced species loss), leading to range contraction. This procedure was repeated for both range shift measures (i.e. the lower and upper altitudinal limits), making it possible to test the influence of species' traits on their responses to climate change, while controlling for the effect of other confounding factors.

Models and analyses were developed using R environment software v 2.13.0 (R Development Core Team, 2011) using the packages *ape* and *nlme*.

RESULTS

Range shifts in the lower altitudinal limit were phylogenetically conserved ($\lambda = 1.00$; $P = 0.01$), indicating that species persisting at their trailing edge were more closely related than would be expected by chance (Fig. 1b). The phylogenetic selectivity of extinction at the lower altitudinal limit was correlated with phylogenetically-conserved traits (Table 1). As expected, thermal tolerance, and especially the upper temperature limit, had a preponderant and negative effect on the magnitude of retreat of the lower altitudinal limit (Fig. 2a; Table 1). More cold-water species (i.e. those characterised by a low upper thermal limit) have suffered from local extinction at their lower altitudinal limit than warm-water species. Similarly, niche breadth, range size, and mobility all had weak but negative effects on extinction at the lower altitudinal limit.

Table 1 Phylogenetic conservatism (Pagel's λ) and model selection for PGLS built to investigate the relationships between shifts in the lower and upper altitudinal limits and species traits. ● indicates a trait that was included in the model. w_i is the model weight, and R^2 is calculated as in eq. 2.3.16 (Judge *et al.*, 1985).

	Phylogenetic	Model selection									
	conservatism	Lower limit				Upper limit					
Trait	λ	M1	M2	M3	M4	M1	M2	M3	M4	M5	M6
Optimal temperature	0.85**	●*	●*		●*			●			●
Spawning temperature	0.82**									●	
Trophic position	0.9***					●*			●*		●*
Mobility PC1	1***								●		
Mobility PC2	0.83*				●						
Life-history PC1	0										
Life-history PC2	0.382					●**	●**	●**	●	●**	●*
Niche breadth	0			●							
Range size	0		●			●**	●**	●**		●**	
wi	-	0.39	0.25	0.21	0.15	0.2	0.18	0.17	0.14	0.14	0.10
R^2	-	0.14	0.18	0.11	0.16	0.47	0.42	0.44	0.31	0.46	0.31

$^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

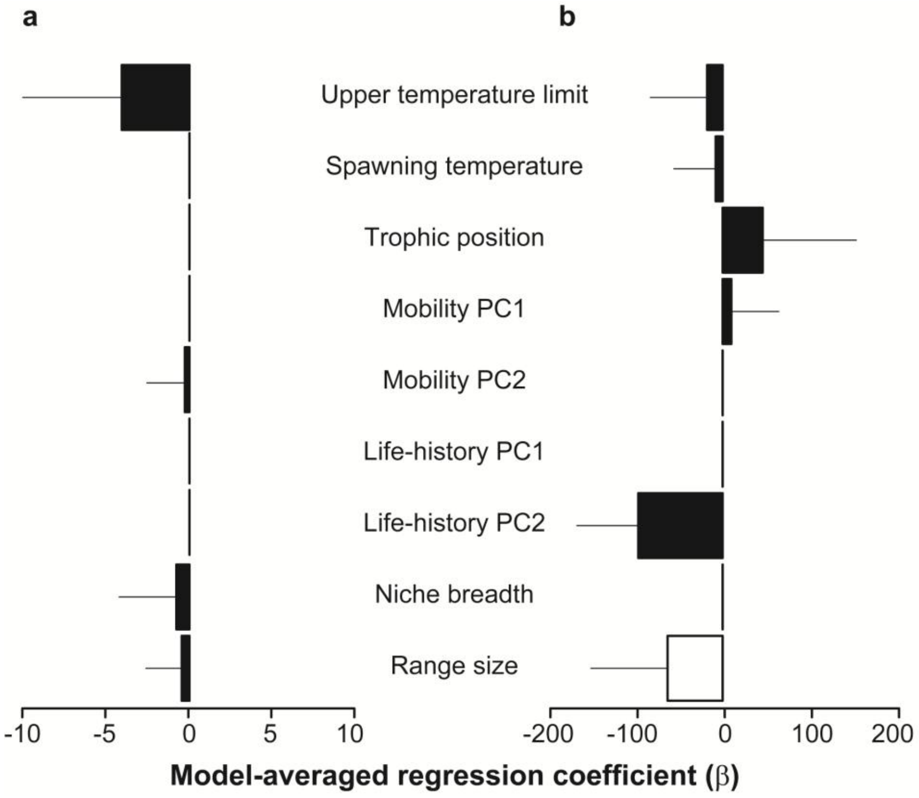


Figure 2 Model-averaged slope regression coefficients standardized to z-scores for PGLS relating shifts in (a) the lower and (b) the upper altitudinal limit to species' traits. Bars are confidence interval. Colours indicate whether the results supported the expected relationships: black for 'yes', white for 'no'.

In contrast to our lower limit results, shifts in the upper altitudinal limit (i.e. the ability of species to colonize newly suitable habitats) were not phylogenetically related ($\lambda = 0.10$; $P = 0.78$) (Fig. 1c). Interestingly, shifts at the upper altitudinal limit were best predicted by life-history strategy and range size, which both have a weak phylogenetic signal (Fig. 2b; Table 1). Species with high propagule pressure showed the greatest shifts (i.e. r-strategists, *life-*

history PC2). Contrary to expectations, range size was negatively correlated to the magnitude of shifts at the upper altitudinal limit. The trophic position also appeared to be a strong predictor of shifts, with piscivorous species showing higher rates of expansion. Finally, species' shifts also appeared to be dependent on thermal tolerances, with cold-water species exhibiting higher shifts at their upper altitudinal limit than warm-water species.

Overall, all the models explained non-trivial amounts of variability in range shifts ($R^2 = 0.11\text{-}0.47$; Table 1).

DISCUSSION

Changes in species' distributions are multifaceted and complex (Parmesan *et al.*, 2005), and disentangling the underlying mechanisms driving these range shifts has proven to be difficult. Here, we show for the first time that contrary to what is commonly assumed (McKinney & Lockwood, 1999; Williams *et al.*, 2008), the impacts of climate change at the trailing and leading edges of the species' ranges are driven by dissimilar mechanisms. We demonstrate that the vulnerability of species could be informed by evolutionary considerations, as we found a close convergence between the phylogenetic patterns in climate-induced range shifts and the degree of conservatism in the related species' traits. Furthermore, this study reveals that range shifts are related to shared ecological traits, which is consistent with theoretical expectations about species' abilities to cope with climate change (Thuiller *et al.*, 2005). Our findings support the hypothesis that to a large extent thermal tolerance, a highly phylogenetically conserved trait, determines range contraction at the trailing edge. In contrast, life history traits and range size, two evolutionarily labile traits related to species' dispersal and establishment abilities, are critical to explaining range expansions at the leading edge. The work presented here highlights the need to consider different facets of species' responses if we are to develop a consensual predictive framework for vulnerability assessment, which has so far often been overlooked, and demonstrate that taking into account the evolutionary history of species is important in attempting to understand the mechanisms underlying range shifts. This suggests that predictive studies would greatly benefit from investigating the phylogenetic selectivity of the biological consequences of future climate change, coupled with the traits involved, in order to generalise the patterns of the relationships between the vulnerability of species and their ecological properties.

To date, testing simple relationships between range shifts and species' traits has not been a successful approach in elucidating the mechanistic causes of range dynamics during climate warming (Angert *et al.*, 2011; Crimmins *et al.*, 2011; Tingley *et al.*, 2012). Given that the sensitivity of species depends on regional patterns of exposure to climate change (Thuiller *et al.*, 2005; Tingley *et al.*, 2012), our methodological framework controlling for these effects could help to disentangle these mechanisms (Willis *et al.*, 2008). Nonetheless, the failure of most empirical studies to identify a clear relationship between species range shifts and their traits may stem from inconsistencies in the way range shifts are assessed (i.e. changes in range size: Warren *et al.* (2001), range centre: Crimmins *et al.* (2011), warm limit: Moritz *et al.* (2008); Perry *et al.* (2005) or cold limit: Felde *et al.* (2013)). The lack of consensus has been previously suggested to result from different mechanisms acting at the opposite ends of species' distributions (Angert *et al.*, 2011). By identifying several traits with contrasting phylogenetic patterns that correlated with the evolutionary conservatism of both colonisation and extinction at the leading and trailing edge, our results strongly support that contention, revealing the importance of studying the dynamics of both contracting and expanding limits.

Extinctions at the trailing edge display high levels of phylogenetic conservatism and correlate with thermal tolerance, a highly-conserved trait likely to reflect the direct influence of climate change. This phylogenetically-selective pattern of extinctions supports both paleontological observations and predictions, suggesting that species losses are not randomly distributed across the tree of life (Roy *et al.*, 2009; Thuiller *et al.*, 2011). To the extent that local extinction drives the global extinction of species (McKinney, 1997), the phylogenetic non-randomness in range contraction documented here suggests the evolutionary history of species is an important determinant of extinction risk. Thermal tolerance curves are negatively skewed; minor changes such as small increases in temperature can lead to sharp declines in growth rate for populations living close to their thermal optima, precipitating extinctions (Huey *et al.*, 2012), which may be exacerbated by interaction with oxygen limitation for aquatic organisms (Pörtner & Knust, 2007). The generality of our finding is verified by concordant range contractions observed for thermal sensitive macroinvertebrates in Australia (Chessman, 2009) and lizards in Mexico (Sinervo *et al.*, 2010). This pattern supports the assertion that cold-adapted taxa are likely to face increased extinction risk as they cannot evolve rapidly enough to cope with climate change due to evolutionary constraints on their thermal tolerance (Hoffmann *et al.*, 2013; Sinervo *et al.*, 2010).

In contrast to our trailing edge analyses, the lack of phylogenetic clustering in range shifts at the leading edge largely reflects the fact that ecological traits promoting colonisation abilities are not shared by close relatives. This may suggest that strong environmental filters have favoured convergence for similar suites of traits for species in distant clades, enabling them to track climate niches better. For example, we found that the species that are expanding their range tend to be fast-developing species, which are better equipped for coping with habitat instability (Southwood, 1977). Several studies have identified a similar correlation (Moritz *et al.*, 2008; Perry *et al.*, 2005). Nevertheless, evidence from palaeoecology also suggests that establishing new ranges as the climate changes involves a great deal more than the dispersal of a propagule ahead of the advancing species front (Davis & Shaw, 2001). Here, we demonstrate that the interplay between the direct (thermal tolerance) and indirect (trophic position) sensitivity to climate change, dispersal ability and habitat availability plays an important role in determining the current magnitude of range expansion. In particular, greater expansions were associated with narrowly-distributed species. The explanation of this finding lies in the following characteristics facing widely distributed species: the limited availability of newly suitable habitats, and the existence of topographic variations within the species range that can provide microrefugia with suitable climates (Hof *et al.*, 2011). Species with restricted ranges are therefore more likely to be sensitive to climate change, irrespective of their colonisation abilities, whereas more widely-distributed species are likely to be more tolerant (Thuiller *et al.*, 2005). Nonetheless, our results suggest that on expanding range limits evolutionary change in life history traits might arise that accelerate range expansion (Hill *et al.*, 2012; Phillips *et al.*, 2010).

However, the mechanisms identified here provide an informed, but incomplete vision of how species respond to climate change by shifting their ranges. The dynamics of range shifts is further structured by the spatial distribution of suitable habitats, which is often patchy, and naturally- or anthropogenically-fragmented (Opdam & Wascher, 2004), and can lead to differential time lags in climate tracking (Chen *et al.*, 2011). Changes in other confounding factors may also help to enhance our ability to predict range shifts (Angert *et al.*, 2011; Comte & Grenouillet, 2013; Warren *et al.*, 2001). The predictive science of range shifts would thus greatly benefit from coupling species' characteristics with extrinsic factors such as the spatial distribution and availability of habitats. In addition, consistent with other studies, the lower performance of the models predicting the magnitude of range contractions compared to that of range expansions (Felde *et al.*, 2013; Tingley *et al.*, 2012) also raises the possibility of other broadly-applicable mechanisms of the response to climate change. Along with shifts in range limits, phenology is likely to be influenced by a rise in temperature, which can potentially drive phylogenetically-biased patterns of species loss (Willis *et al.*, 2008). Thus, although the best explanation of trailing edge retreat is underpinned by the temperature tolerance of species, the pattern of phylogenetic selectivity in extinction might not be solely attributable to progressively increasing overruns of climate thresholds. These results point towards the critical need to find out whether other traits may also be influencing the phylogenetic pattern of extinction documented here.

Finally, our results combined with those of previous studies (Roy *et al.*, 2009; Willis *et al.*, 2008) prove that phylogenetic history provides useful insights into how species and communities are likely to respond to future climate change. Although range expansion may facilitate adaptation to changing environmental conditions and buffer the effects of climate change (Davis & Shaw, 2001), trailing edge populations are crucial in determining long-term species persistence (Hampe & Petit, 2005). Climate-induced impacts may therefore be especially significant for cold-adapted species with reduced propagule pressure, for which colonisation of the leading populations may only trivially offset the extinction of trailing populations. In the near future, large-scale patterns of biodiversity could be greatly modified owing to the spatially-selective reshuffling of species assemblages, not only as the result of an incursion of species into higher latitudes and elevations - which usually contain fewer species - but also because of a drop in phylogenetic diversity in the most exposed habitats. Extinction usually befalls species displaying synergistic combinations of extinction-promoting traits (e.g. a high degree of specialisation, narrow range), triggering a loss of phylogenetic and taxonomic diversity both within (alpha diversity) and between (beta diversity) regions where these species are unique (Winter *et al.*, 2009). Given that very little is known about the relative effects of range expansion and contraction on biodiversity patterns at large spatial scales, the consequences of species' range shifts on taxonomic and phylogenetic diversity deserves further attention.

If phylogenetic clustering in species' responses to climate change is a generalised phenomenon, phylogeny could be a useful predictive tool in conservation applications. It provides a simple way to integrate species' differences across multiple traits, and helps to elucidate the underlying mechanisms that determine how species respond to climate change (Pau *et al.*, 2011). In angiosperms, the extinction risk has demonstrated to be also correlated with phenological response traits linked to species' evolutionary history (Willis *et al.*, 2008). The strength of the evolutionary conservatism in species' responses can be used to project forward species' sensitivities to future climate change in under-studied communities, for which little information may be available about species' traits, where it offers a more effective predictive tool than trait-based approaches. Conservation biologists would benefit greatly from projecting future phylogenetic extinction selectivity at various taxonomic scales in order to prioritise taxa with the greatest potential vulnerability, while simultaneously considering their phylogenetic uniqueness in conservation decisions (McKinney, 1997).

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SUPPORTING INFORMATION

Appendix 1 Species' traits and additional variables

Table S1 Description of species' traits and modalities.

Trait	Code	Modality	Description
Upper temperature limit	Opt_Tpmax	-	Upper limit of the optimal temperature range (°C) (Elliott, 1981, Elliott, 1995, Tissot & Souchon, 2010)
Spawning temperature	SP_tp	-	Optimal spawning temperature (°C)
Trophic position	TP	1	Herbivorous
		2	Omnivorous
		3	Invertivorous
		4	Invertivorous-carnivorous
		5	Piscivorous
Body length	BL	-	Total body length from the mouth to the fork of the tail (mm)
Larval length (at emergence)	LL	1	≤ 4.2mm
		2	4.2-6.3mm
		3	> 6.3mm
Shape factor	SH	-	Ratio of total body length to maximum body depth (Poff & Allan, 1995)
Swimming factor	SW	-	Ratio of the minimal depth of the caudal peduncle to maximum caudal fin depth (Poff & Allan, 1995)
Range size	range_size		% of total network length in the initial period
Niche breadth	niche_breadth	-	Niche breadth on the first axis of the Outlying Mean Index (OMI) based on 3 environmental variables: slope, elevation and upstream-downstream position
Fecundity (# oocytes)	FE	1	≤ 10,000
		2	10,000-100,000
		3	> 100,000
Spawn time (Nb.)	ST	1	1
		2	> 1
Egg diameter (at hatching)	ED	1	< 1.35 mm
		2	1.35-2 mm
		3	> 2 mm
Life span	LS	1	< 8 years
		2	8-15 years
		3	> 15 years

Table S1
(continued)

Variable	Code	Modality	Description
Female maturity	MA	1	1-2 years
		2	2-3 years
		3	3-4 years
		4	4-5 years
		5	≥ 5 years
Parental care	PC	1	No protection
		2	No protection with nest or egg hiders
		3	nest or egg hiders
Incubation period	IP	1	≤ 7 days
		2	7-14 days
		3	> 14 days

Table S2 Description of additional variables and modalities.

Variable	Code	Modality	Description
Temperature change	change_tp	-	Change in mean annual temperature experienced by species at their initial distribution (°C)
Human interest	human_use	-	Sum of the scores of use (0 or 1) for aquaculture, as bait or as gamefish (Froese & Pauly, 2012)

Table S3 Matrix of traits and additional variables for the 32 stream fish species. Details of traits and variables are given in Table S1 and S2.

Species name	**change_tp**	**human_use**	**Opt_Tpmax**	**SP_tp**	**range_size**	**niche_breadth**	**TP**	**BL**	**LL**	**SH**	**SW**	**FE**	**ST**	**ED**	**LS**	**MA**	**PC**	**IP**
Abramis brama	0.81	3	26	16	17.60	1.91	2	400	2	2.81	0.33	3	1	2	3	4	1	2
Alburnoides bipunctatus	0.83	2	24	17.5	14.23	1.12	2	110	3	3.58	0.31	1	2	2	1	2	1	2
Alburnus alburnus	0.77	2	30	21.5	16.93	1.77	3	135	2	4.92	0.36	1	2	2	1	2	1	2
Ameiurus melas	0.76	2	35	21.5	17.05	2.64	2	250	1	4.43	0.37	1	1	2	2	2	3	2
Anguilla anguilla	0.70	2	29	18.5	28.07	1.21	4	650	1	17.8	1	3	1	1	3	5	1	1
Barbatula barbatula	0.85	0	28	8	42.86	0.89	3	100	1	6.5	0.58	1	2	1	1	2	1	3
Barbus barbus	0.82	1	32	16.5	17.52	1.31	3	500	1	5.23	0.3	2	1	2	3	5	1	2
Barbus meridionalis	0.82	1	25	16.5	11.67	0.27	3	250	-	5.63	0.33	2	2	1	1	1	1	3
Blicca bjoerkna	0.88	0	25	20	12.13	1.73	3	250	2	3.23	0.27	3	2	2	2	3	1	1
Chondrostoma nasus	0.88	0	24	11	12.68	1.55	1	300	3	5.03	0.32	2	1	3	2	3	1	2
Cottus gobio	0.99	0	26.5	8.5	32.80	0.61	3	125	3	4.38	0.39	1	1	3	1	2	3	3
Cyprinus carpio	0.72	2	32	19	22.94	2.51	2	500	2	3.13	0.42	3	2	2	3	4	1	1
Esox lucius	0.86	2	24	11.5	23.23	1.82	5	750	3	5.2	0.31	2	1	3	3	3	1	2
Gasterosteus aculeatus	1.00	0	20	14.5	19.49	1.05	4	60	1	4.48	0.19	1	2	2	1	1	3	2
Gobio gobio	0.75	1	30	14.5	38.13	1.48	3	120	2	6.09	0.4	1	2	2	1	2	1	3
Gymnocephalus cernua	0.86	2	25	12	11.88	1.28	4	120	1	4.67	0.34	3	2	1	1	2	1	2
Lepomis gibbosus	0.65	1	30	19	24.65	2.19	4	150	1	2.41	0.42	2	2	1	2	2	3	1
Leuciscus leuciscus	0.87	2	25	9.5	21.69	1.34	3	250	3	4.87	0.32	2	1	2	2	3	1	3
Lota lota	0.97	1	21.2	5.3	11.89	1.95	5	400	1	5.47	0.36	3	1	1	3	4	1	3
Parachondrostoma toxostoma	0.65	1	25	11.5	10.67	0.81	1	225	3	4.41	0.4	2	1	2	2	4	1	2
Perca fluviatilis	0.89	2	27	11.5	27.44	2.00	5	275	2	3.3	0.32	2	1	2	3	4	1	2
Phoxinus phoxinus	0.71	1	25	15	40.29	0.91	2	80	1	5.26	0.32	1	2	2	1	2	1	2
Pungitius pungitius	0.89	0	24	11	18.32	0.47	3	60	1	5.83	0.17	1	1	1	1	1	3	3
Rutilus rutilus	0.86	2	25	14	33.66	1.73	2	275	2	3.66	0.29	2	1	2	2	2	1	2
Salmo salar	0.64	2	20	8	6.06	0.72	5	700	3	4.3	0.31	1	1	3	2	5	1	3
Salmo trutta	0.77	2	19	9.5	67.59	1.30	4	325	3	4.21	0.38	1	1	3	2	3	1	3
Sander lucioperca	0.78	2	30	13	10.62	1.96	5	500	1	5.2	0.26	3	1	1	2	4	3	2
Scardinius erythrophthalmus	0.85	2	28	20.5	22.56	2.61	2	225	2	2.95	0.36	3	2	2	2	3	1	1
Squalius cephalus	0.79	1	24	9.5	34.85	1.61	2	400	3	3.97	0.36	3	2	2	2	3	1	1
Telestes souffia	0.90	0	18	13.5	13.32	0.45	2	150	-	4.95	0.29	1	1	2	2	3	1	1
Thymallus thymallus	0.84	2	18	9.5	11.12	0.58	4	300	3	4.9	0.3	1	1	3	1	3	1	3
Tinca tinca	0.87	2	26	21	27.31	1.90	2	300	2	4	0.46	3	2	1	2	3	1	1

Table S4 Correlations between species traits and the first two axes of the PCoA. Percentages in parentheses indicate the relative contribution of the axes to the PCoA.

		Correlation	
	Trait	PC 1	PC 2
Mobility		(31.7%)	(19.5%)
	Body length	-0.01	0.74
	Larval length	0.89	0.47
	Shape factor	-0.56	0.44
	Swimming factor	-0.22	0.37
Life-history		(26.7%)	(23.3%)
	Fecundity	0.70	-0.56
	Spawn time	-0.47	-0.84
	Egg diameter	0.07	0.55
	Life span	0.91	0.03
	Female maturity	0.84	0.14
	Incubation period	-0.42	0.67
	Parental care	-0.40	0.18

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ANNEXE I (A_I)

Paz-Vinas I, **Comte L**, Chevalier M, Dubut V, Veyssière C, Grenouillet G, Loot G & Blanchet S (2013) Combining genetic and demographic data for prioritizing conservation actions: insights from a threatened fish species. ***Ecology and Evolution*** 3: 2696–2710.

Combining genetic and demographic data for prioritizing conservation actions: insights from a threatened fish species

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ABSTRACT

Prioritizing and making efficient conservation plans for threatened populations requires information at both evolutionary and ecological timescales. Nevertheless, few studies integrate multidisciplinary approaches, mainly because of the difficulty for conservationists to assess simultaneously the evolutionary and ecological status of populations. Here, we sought to demonstrate how combining genetic and demographic analyses allows prioritizing and initiating conservation plans. To do so, we combined snapshot microsatellite data and a 30-year-long demographic survey on a threatened freshwater fish species (*Parachondrostoma toxostoma*) at the river basin scale. Our results revealed low levels of genetic diversity and weak effective population sizes (<63 individuals) in all populations. We further detected severe bottlenecks dating back to the last centuries (200-800 years ago), which may explain the differentiation of certain populations. The demographic survey revealed a general decrease in the spatial distribution and abundance of *P. toxostoma* over the last three decades. We conclude that demo-genetic approaches are essential for (1) identifying populations for which both evolutionary and ecological extinction risks are high; and (2) proposing conservation plans targeted towards these at risk populations, and accounting for the evolutionary history of populations. We suggest that demo-genetic approaches should be the norm in conservation practices.

Keywords: conservation genetics; species distribution models; rivers; *Parachondrostoma toxostoma*; bottleneck; demographic survey; temporal trends

INTRODUCTION

Prioritizing and making appropriate plans to manage and conserve threatened species is a complex task. Global changes simultaneously affect multiple facets of individual species, making predictions difficult (Margules & Pressey, 2000; McMahon *et al.,* 2011). For instance, global changes such as habitat fragmentation or climate change can affect the genetic diversity (Olivieri *et al.,* 2008; Blanchet *et al.,* 2010), the demographic dynamics (Julliard *et al.,* 2004; Dunham *et al.,* 2008), the evolution of life-history traits (Conover *et al.,* 2009; Blanchet & Dubut, 2012) and/or the spatial distribution of species (Parmesan, 2006; Buisson *et al.,* 2008). Accordingly, the conservation biologists' toolbox includes several methods which emerged from multiple disciplines such as population genetics, population ecology, and biostatistics (Guisan & Zimmermann, 2000; Green *et al.,* 2005; Excoffier & Heckel, 2006). Nevertheless, most conservation studies focus on a single facet of species health (e.g. the genetic diversity), and hence provide only partial information for biodiversity management and conservation (Frankham, 2010; Geist, 2011; Loss *et al.,* 2011).

Integrative studies are, however, increasingly acknowledged as being valuable from a conservation standpoint (Purvis & Hector, 2000; Geist, 2011; Loss *et al.,* 2011). For instance, at the community level, Devictor *et al.* (2010) showed that there was a strong spatial mismatch between phylogenetic, functional and taxonomic measures of bird biodiversity. These measures provide different but complementary information, suggesting that reserve designs should be optimized accordingly (Devictor *et al.,* 2010). Similarly, at the population level, diverse measures classically used to assess the health of a population (e.g. effective population size, abundance and dispersal rate) provide complementary information that should be integrated into common analyses to set efficient conservation plans (e.g. Osborne *et al.,* 2010; Osborne *et al.,* 2012). For instance, demographic monitoring programs (hereafter, DMPs) provide useful information regarding the ecological status of populations and enable predictions on future distributions under global change scenarios, whereas population genetics studies (hereafter, PGSs) obtain information regarding the evolutionary status of populations and their potential resistance to rapid environmental changes (Smith & Bernatchez, 2008). Because evolutionary and ecological time-scales and processes are sometimes confounded (Carroll *et al.,* 2007), it is of prime importance to merge evolutionary and ecological information to (1) identify the populations that need to be prioritized for conservation actions; and (2) implement effective long-term management and conservation of endangered populations (Osborne *et al.*, 2012).

The use of population genetics in biodiversity conservation has increased considerably in the last decades (Frankham, 2010). Low genetic diversity in natural populations has been generally associated with pervasive effects such as inbreeding depression, loss of evolutionary potential and the accumulation of deleterious mutations (Saccheri *et al.,* 1998; Frankham, 2010). These effects theoretically increase extinction risks, and are expected to be stronger in populations under anthropogenic or natural stresses (Spielman, 2004). Accordingly, PGSs generally aim at (1) describing the genetic status of populations (i.e. genetic diversity and structure assessed during a snapshot survey, Schwartz *et al.,* 2007); (2) identifying historical and contemporary factors affecting the genetic diversity of populations (Manel *et al.,* 2003; Dubut *et al.,* 2012); and (3) inferring past and contemporary demographic parameters such as effective population sizes (N_e) (Storz & Beaumont, 2002). Although PGSs provide key information about demographic processes, linking genetics and population demography remains tricky (Osborne *et al.,* 2012). For instance, the link between N_e and census population size (N_c) is notoriously difficult to assess (Luikart *et al.,* 2010; Palstra & Fraser, 2012; Belmar-Lucero *et al.,* 2012), and genetic bottlenecks (i.e. strong decreases in N_e) can be detected even in the absence of demographic bottlenecks (Broquet *et al.,* 2010; Chikhi *et al.,* 2010). Furthermore, the effects of particular threats may be undetected through PGSs due to the lag time that often exists between an ecological cause and its evolutionary consequence (Landguth *et al.,* 2010).

Analyses based on demographic data can overcome some of these gaps (Nichols & Williams, 2006; Lindenmayer *et al.,* 2010). DMPs provide information about the current status of populations by allowing the inference of key demographic parameters such as abundance and/or occurrence (Royle & Dorazio, 2006). Combined with time series analyses, DMPs also permit the investigation of temporal trends and hence the identification of the causes and consequences of population declines or changes in spatial distribution (Daufresne *et al.*, 2004). Additionally, these surveys are useful for the early detection of the effects of threats on populations as well as 'ecological surprises' (Doak *et al.*, 2008), which is notoriously difficult using only PGSs (Julliard *et al.*, 2004; Lindenmayer *et al.*, 2010). Finally, long-term and large spatial-scale surveys are of prime interest and may allow predictions about the future status of populations in a changing world through the use of species distribution models for instance (Guisan & Zimmermann, 2000).

In this study, we attempt to demonstrate how combining PGSs and DMPs provides baseline information for prioritizing and initiating management and conservation plans. We focused on an endangered freshwater fish species (i.e. the South-west European nase *Parachondrostoma toxostoma*, Vallot 1837) which is considered vulnerable throughout its restricted native range (i.e. Southern France, Crivelli, 2006). We used a microsatellite dataset gathered at the river basin scale (i.e. the Garonne river basin, South-Western France) to (1) describe the genetic diversity and structure of *P. toxostoma* populations, and (2) detect and quantify both contemporary and past N_e (i.e. contraction or reduction in N_e over time), as well as to date main changes in *Ne* following the last glacial maximum (i.e. ~10,000 years ago). In parallel, we used a demographic survey performed at the same spatial scale over the last three decades to (3) identify temporal trends in species abundance at the Garonne river basin scale; and (4) assess the current spatial distribution of the species and changes in the distribution over the last three decades.

METHODS

Biological model

Parachondrostoma toxostoma is a threatened freshwater fish species of the Cyprinidae family endemic to France and Switzerland, where its native range area is restricted to the Rhône, Adour and Garonne river basins. This species is listed as vulnerable in the IUCN red list, in the Annex II of the European Union Habitats Directive and in Appendix III of the Bern Convention (Crivelli, 2006). The range of the species has been strongly reduced due to water pollution, habitat fragmentation by dams and weirs, artificial water releases and hybridization with a non-native species, Chondrostoma nasus (Costedoat *et al.*, 2007). Our study focuses on the Garonne river basin, which hosts the major stock of pure *P. toxostoma* (i.e. not introgressed by the *C. nasus* genome). This highlights the urge for conservation actions directed towards the Garonne drainage in order to preserve the *P. toxostoma* species.

Population genetics study

Sampling design

Ninety-two sampling sites belonging to 34 rivers of the Garonne river basin were investigated using electro-fishing in 2010 and 2011 (Figure S1). We did not catch *P. toxostoma* at 76 sites. Two hundred and 30 individuals of *P. toxostoma* were sampled at sixteen sites (Table 1, Figure 1). Thus, we assume that these sixteen sites are representative of the current *P. toxostoma* populations. However, due to the low numbers of individuals captured at some sampling sites, individuals from sites belonging to the same river were pooled for subsequent analyses. All genetic analyses were therefore conducted at the river level (n_{RIVER} = 9). A small fragment of pelvic fin was collected and stored in 90% ethanol. Individuals were all released alive at their sampling site.

Genotyping

We used a salt-extraction protocol to extract genomic DNA from pelvic fins (Aljanabi & Martinez, 1997). Fifteen microsatellite loci previously developed and/or evaluated for *P. toxostoma* (Dubut *et al.*, 2010) were co-amplified using two multiplexed Polymerase Chain Reactions (PCRs) (see Table S1 for details on loci and primers concentrations). PCR amplifications were performed with 5-20 ng of genomic DNA and using the QIAGEN® Multiplex PCR Kit (Qiagen, Valencia, CA, USA). PCRs were carried out under conditions described by Dubut *et al.* (2010). Genotyping was performed on an ABI PRISM™ 3730 Automated Capillary Sequencer (Applied Biosystems, Foster City, CA, USA) at the

'Génopole Toulouse Midi-Pyrénées' (France). Allele sizes were scored using the software GENEMAPPER® v.4.0 (Applied Biosystems).

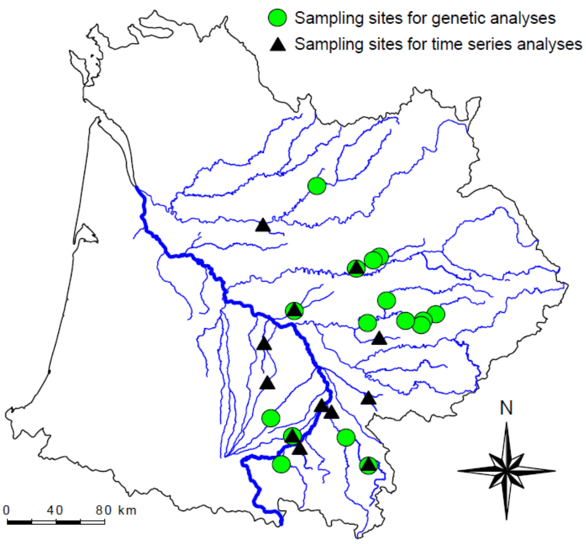

Figure 1 Map of the Garonne river basin (South-Western France) representing (1) sites where *Parachondrostoma toxostoma* was sampled for the genetic analyses (green circles) and (2) sites that have been selected for analyses of temporal trends in population abundances (black triangles).

Table 1 *Parachondrostoma toxostoma* sampling sites information.

River		Location	Latitude	Longitude	PGS	$N_{(PGS)}$	DMP	$Y_{(DMP)}$
ARRATS	ARR	Aubiet	N 43°38'48"	E 0°46'45"	−	−	**X**	13
AUROUE	AUR	L'isle-Bouzon	N 43°54'32"	E 0°43'45"	−	−	**X**	13
AVEYRON	AVE	Feneyrols	N 44°07'52"	E 1°48'51"	**X**	5	−	−
		Monteils	N 44°17'09"	E 2°00'07"	**X**	4	−	−
ARIEGE	ARI	Vénerque	N 43°26'13"	E 1°26'15"	−	−	**X**	8
PETITE BARGUELONNE	BAR	Montbarla	N 44°12'34"	E 1°03'40"	**X**	9	**X**	17
CELE	CEL	Boussac	N 44°35'46"	E 1°55'02"	**X**	7	−	−
		Sainte Eulalie	N 44°35'36"	E 1°52'25"	**X**	8	−	−
		Sauliac-sur-Célé	N 44°31'09"	E 1°42'58"	**X**	25	**X**	11
COUZE	COU	Bayac	N 44°48'16"	E 0°43'45"	−	−	**X**	14
ELLE	ELL	Terrason-Lavilledieu	N 45°08'51"	E 1°15'37"	**X**	25	−	−
GARONNE	GAR	Muret	N 43°27'36"	E 1°19'52"	−	−	**X**	10
HERS	HER	Besset	N 43°05'03"	E 1°50'24"	**X**	4	**X**	10
		Calmont	N 43°17'10"	E 1°37'59"	**X**	25	−	−
LOUGE	LOU	Fousseret	N 43°16'27"	E 1°04'07"	**X**	8	**X**	13
SALAT	SAL	Touille	N 43°04'38"	E 0°58'05"	**X**	25	−	−
SAVE	SAV	Espaon	N 43°25'20"	E 0°51'21"	**X**	18	−	−
VENDINELLE	VEN	La Salvetat Lauragais	N 43°32'22"	E 1°48'15"	−	−	**X**	18
VERE	VER	Cahuzac-sur-Vère	N 43°59'12"	E 1°53'43"	−	−	**X**	17
VIAUR	VIA	La Calquière	N 44°09'12"	E 2°12'15"	**X**	13	−	−
		Saint Just	N 44°07'24"	E 2°21'57"	**X**	23	−	−
		Navech	N 44°09'25"	E 2°23'18"	**X**	25	−	−
		Serres	N 44°12'29"	E 2°31'25"	**X**	6	−	−
VOLP	VOL	Plan	N 43°10'16"	E 1°07'07"	−	−	**X**	8

PGS (for Point Genetic Study) indicates whether the site has (**X**) or not (−) been sampled for genetic analyses. $N_{(PGS)}$ indicates the number of individuals sampled *per* site for genetic analyses. DMP (for Demographic Monitoring Program) indicates whether the site has (**X**) or not (−) been selected for analyses of temporal trends in abundance. $Y_{(DMP)}$ indicates the number of years considered in the time series.

Descriptive genetic analyses

The presence/absence of large allele dropouts and null alleles was determined using the software MICRO-CHECKER 2.3 (Van Oosterhout *et al.*, 2004). Departures from Hardy-Weinberg (HW) equilibrium were estimated using the program GENEPOP v4.0 (Rousset, 2008). Levels of significance for HW were adjusted using the False Discovery Rate (FDR) procedure (Benjamini & Hochberg, 1995). Linkage disequilibrium among loci within sites was tested with the program FSTAT 2.9.3.2 (Goudet, 1995).

The mean number of alleles per site, the average observed (H_o) and expected (H_e) heterozygosity over loci, as well as H_o and H_e per loci per site were estimated using ARLEQUIN 3.5 (Excoffier & Lischer, 2010). We used a rarefaction procedure, as implemented in the software ADZE 1.0 (Szpiech *et al.*, 2008), to estimate allelic richness (Petit *et al.*, 1998) for each site, considering minimum sample sizes of $N = 8$ and $N = 18$ individuals.

Population structure

A Bayesian model-based clustering approach was used to search for the occurrence of independent genetic groups (i.e. clusters, K) in our dataset (as implemented in STRUCTURE 2.3.3; Pritchard *et al.*, 2000; Falush *et al.*, 2003, 2007; Hubisz *et al.*, 2009). The burn-in length of the Markov Chain Monte Carlo (MCMC) was set to 50,000 followed by 200,000 iterations. The admixture model and the correlated allele frequencies model were used with priors on population sampling location (Hubisz *et al.*, 2009). Ten runs were conducted for each K value, with K ranging from 1 to 9. We used CORRSIEVE 1.6.2 (Campana *et al.*, 2011) to combine two approaches aiming at determining K: the ΔK test (Evanno *et al.*, 2005) and the ΔF_{st} test (Campana *et al.*, 2011).

To further assess the levels of genetic differentiation among *P. toxostoma* sites, two different indices were estimated: pairwise F_{st} (Weir & Hill, 2002) and the unbiased pairwise D_{est} (Jost 2008), calculated using ARLEQUIN 3.5 and SMOGD (Crawford 2010) respectively.

Demographic history inference and current N_e estimation

We used two different approaches for inferring past changes in the effective population size (i.e. expansions or contractions) of *P. toxostoma*.

The first method, implemented in the BOTTLENECK v1.2.02 software (Cornuet & Luikart, 1996; Piry, 1999), uses summary statistics of the genetic diversity to assess significant deviations from mutation/drift equilibrium. Significant heterozygosity excesses are considered as evidence of recent bottlenecks, whereas significant heterozygosity deficiencies can be interpreted as signals of recent population expansion (Luikart & Cornuet, 1998). We performed analyses considering two different microsatellite evolution models: the Stepwise Mutation Model (SMM) and the Two-Phase Model (TPM). For the latter, we set the percentage of multi-step mutations at 30%. We tested the significance of mutation/drift equilibrium deviations for the two models using Wilcoxon's signed rank tests. To account for multiple comparisons, we applied the FDR procedure (Benjamini & Hochberg, 1995). The second method is the full-likelihood Bayesian approach implemented in the program MSVAR 1.3 (Beaumont, 1999; Storz & Beaumont, 2002). This coalescent-based method relies on a hierarchical Bayesian model to detect, date and quantify past demographic changes. The model assumes that a stable, closed population of ancestral size N_1 increased or decreased exponentially to its current size N_0 (i.e. its current N_e) over a time interval of T_a years. This method uses all the information contained in the data and lognormal priors to infer the parameters of the model $\Phi = \{N_0, N_1, T_a, \theta\}$, where $\theta = 4N_0\,\mu$ and μ is the mutation rate. The posterior probability density of Φ is assessed via MCMC algorithms. Microsatellite loci are assumed to be independent and to evolve under a strict SMM. For each river-scale analysis, we performed four independent runs of $5\text{x}10^9$ steps, considering different starting values and means for priors and hyperpriors for each run (Goossens *et al.*, 2006). We set a generation time of 3 years for *P. toxostoma* (Keith *et al.*, 2011). Parameters were thinned with an interval of $5\text{x}10^4$ steps, resulting in output files with $1\text{x}10^5$ values. We discarded the first 10% of the chains as burn-in to prevent bias induced by the starting values on parameter estimation. The convergence of the MCMC chains was checked with the Gelman and Rubin analysis implemented in the R package CODA (Gelman & Rubin, 1992; Plummer *et al.*, 2006). For each analysis, posterior parameter values obtained by the four independent runs were pooled together and subsequently used to calculate the median and the 5-95% quartiles for N_0, N_1 and T_a. We also calculated these statistics for the ratio $\log_{10}(N_0/N_1)$. Negative values of this ratio indicate that the population has experienced a decrease in effective population size, while positive values characterize demographic expansions. This approach was also used to estimate a current N_e at the Garonne river basin scale. To do so, we ran MSVAR by pooling all individuals from all rivers in a single analysis. At such a scale, estimates of current N_e were compared to those estimated using the linkage-disequilibrium-based approach implemented in LDNe (Waples & Do, 2008). LDNe was not used at the river scale due to its propensity to give negative N_e estimates (which are interpreted as infinity estimates, Waples & Do, 2008) for most rivers. MSVAR 1.3 runs were performed on an ALTIX ICE 8200 EX and UV computer cluster (Silicon Graphics International, Fremont, CA, USA) hosted by the CALMIP group at the University Paul Sabatier (Toulouse, France).

Demographic monitoring data

Database description

We used the surveillance monitoring database of the French National Agency for Water and Aquatic Environments (i.e. ONEMA) to carry out demographic trend and species distribution analyses. This database includes an extensive spatio-temporal set of monitoring surveys of French freshwater fish populations, representative of all fish assemblages and covering varying degrees of anthropogenic disturbances (Poulet *et al.,* 2011). Surveys were conducted according to standard electro-fishing procedures (Poulet *et al.,* 2011). We used this database to (1) identify temporal trends in population abundance of *P. toxostoma* at 12 sampling locations; (2) assess the current spatial distribution of this species in the Garonne river basin; and (3) investigate whether the spatial distribution of this species in the Garonne river basin has declined or expanded over the last three decades.

Temporal trends in abundance

From this dataset, we selected all sites belonging to the Garonne river basin that have been sampled and investigated for *P. toxostoma* abundance for at least eight years. This resulted in the selection of twelve sites (Table 1, Figure 1) for which time series ranged between eight and eighteen years and occurred between 1991 and 2010. As sampling procedures were standardized over years, abundances (expressed as the number of individuals per m²) were directly comparable across years. It is noteworthy that (1) this database and the genetic database have been gathered during independent research projects; and (2) *P. toxostoma* is relatively rare in this area (Figure S1), which both explain why demographic and genetic data are not available for all sites (see Table 1). Some sites for which long-term demographic data were available have been unsuccessfully sampled for genetic, and inversely, some sites where genetic data were available had time series that were not long enough to be analyzed (i.e. < 8 years).

First, we assessed the strength and significance of temporal trends at these sites, by using a modified Mann-Kendall trend test that we independently applied to each time series (Hamed & Rao, 1998). In this test, the Mann-Kendall's S statistic (Kendall, 1962) provide an estimate of the strength of the association between time and the response variable, while accounting for temporal autocorrelation present in a time series (Hamed & Rao, 1998).

Second, we assessed whether or not these twelve time series showed an overall significant trend. For this purpose, we performed a meta-analysis (Gurevitch & Hedges, 1993) on the twelve Mann-Kendall's trend statistics S calculated in the first step. We applied a mixed linear model approach using maximum likelihood, in which we assumed that the twelve time series included in the meta-analysis share a common effect size with a random variation among the twelve time series.

Current spatial distribution and recent distribution changes

We used the database described above to assess changes in the spatial distribution of *P. toxostoma* on the Garonne river basin over two distinct periods, separated by a time span of ten years (i.e. 'past period': 1980-1992, and 'current period': 2003-2009). To account for potential sampling bias when comparing spatial distributions over time based on datasets not originally collected for this purpose (Shaffer *et al.,* 1998; Shoo *et al.,* 2006), we modeled the spatial distribution of the species across the

French hydrographic network as a function of several climatic and environmental variables.

Accurately modeling species distribution requires performing analyses at the entire species range scale, so as to encompass all environmental conditions (Austin, 2007). Therefore, for both time periods, initial models were calibrated at the French scale. We selected 3549 sites sampled over the 1980-1992 period and 3543 sites sampled over the 2003-2009 period scattered across France (see Figure S2). The occurrence of the species was modeled independently for both time periods as a function of habitat and climatic data strongly related to fish spatial distributions (Buisson *et al.*, 2008): elevation (*m*), slope (‰), upstream-downstream position (*G*), mean temperature of the coldest quarter (°C), mean temperature of the warmest quarter (°C), temperature variability, cumulated precipitations of the wettest quarter (mm), cumulated precipitations of the driest quarter (mm) and precipitation variability (Hijmans *et al.*, 2005).

To account for uncertainty in estimating species range, we used a modeling approach allowing us to produce maps of species habitat suitability (e.g. Puschendorf *et al.*, 2009; Grenouillet *et al.*, 2011). Specifically, we used an ensemble modeling approach based on a consensus model averaging the probabilities of occurrence predicted by eight single-species distribution models (Marmion *et al.*, 2009), as well as three threshold-setting methods allowing the conversion of occurrence probabilities into binary data (i.e. presence or absence, Liu *et al.*, 2005), and 30 iterations (see Appendix S1 for details on models' implementation).

The calibrated models set at the French scale were then used to predict the binary predictions of occurrence of the species for the two distinct periods in the hydrographic network of the Garonne river basin. The spatial distribution of the species for each time period was calculated as the length of the hydrographic network occupied by the species (e.g. Fagan, 2002) in the Garonne river basin (expressed in % of the total network length). However, because the ability to detect changes in the spatial distribution of species may be confounded by the uncertainty arising from methodological strategies (e.g. threshold effect, Nenzén & Araújo, 2011), temporal changes in the occupied stream length were evaluated using a linear model that controlled for the threshold effect. A linear model was thus fitted to the spatial distribution of *P. toxostoma* in both periods where the threshold-setting method and the period were used as explanatory variables. The change (i.e. extension or contraction) was then provided by the least-squares means intercepts of the contemporary period-group effect. Temporal trends analyses and spatial distribution models have been developed under the R environment software 2.13.0 (R Development Core Team, 2011).

RESULTS

Population genetics study

Descriptive genetic analyses

After applying the FDR controlling procedure, no null alleles were detected in our dataset, there were no significant deviations from HW for any loci or any population (Table S2, Table S3), and we failed to detect significant linkage disequilibrium between pairs of loci (Table S4).

Overall, genetic diversity estimates were low (Figure 2A, 2B, Table S3). Loci were weakly polymorphic at the basin scale (2-6 alleles per locus), with some loci being monomorphic at the river scale (na = 1; Table S2). Average H_e and H_o values across loci within rivers were moderately low (H_e = 0.320-0.450; H_o = 0.315-0.482), as well as mean number of alleles and allelic richness estimates (AR_8 = 1.868-2.536 alleles per river; AR_{18} = 2.147-3.037) (Figure 2A, 2B, Table S3). It is noteworthy that the Save River (SAV) displayed the lowest genetic diversity estimates (Figure 2A, 2B, Table S3).

Population structure

The ten runs of the Bayesian clustering analysis were convergent. The ΔK and ΔF_{st} tests revealed three distinct clusters K = 3 (Figure 3A-3B). Most of the populations were hardly differentiable and were characterized by the occurrence of a main cluster, whose frequency range was from 62% (CEL) to 98% (VIA). Only SAV and HER were discriminated from the rest of the Garonne river basin, each site corresponding to a distinct cluster (Figure 3C). Overall, genetic differentiation values between rivers were weak to moderate and ranged between 0.003-0.244 and 0.003-0.281 for F_{st} and D_{est} respectively (Table 2). All but five pairwise F_{st} values were significant (Table 2).

The stronger differentiations were found between SAV/VIA (F_{st} = 0.244; D_{est} = 0.097) and SAV/BAR (F_{st} = 0.117; D_{est} = 0.281).

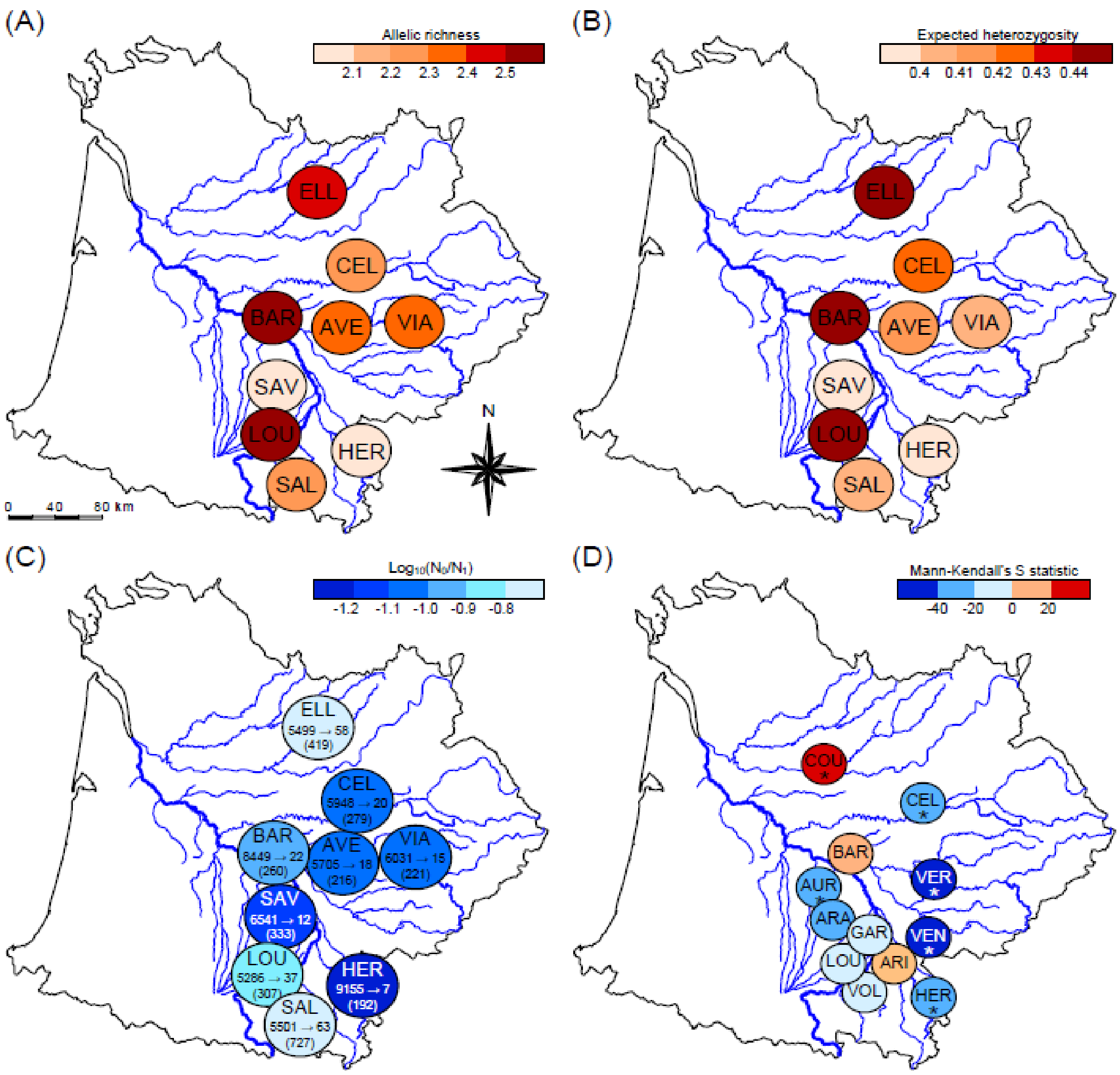

Figure 2 Maps representing (A) the allelic richness per population considering a minimum sample size of 8 (color scale), (B) the expected heterozygosity per population (color scale) (C) the past effective population size (N_1; left number in the bubbles, see also Table S6), the current effective population size (N_0; right number in the bubbles, see also Table S6), the time of the beginning of the bottlenecks (in years backward in time; numbers in brackets, see also Table S6) and the magnitude of bottlenecks (i.e. $\mathrm{Log}_{10}(N_0/N_1)$: color scale, see also Table S6), and (D) the value of the Mann-Kendall's S statistic (color scale) and the significance of Mann-Kendall trend tests for each time series: Asterisks (*) denote significant (i.e. $P < 0.05$) temporal trends. For all panels, the three-letter code in each bubble corresponds to the river codes (see Table 1).

Demographic history inference and current N_e estimation

According to the BOTTLENECK software, and after corrections for multiple tests, there was no significant evidence for demographic changes in the Garonne river basin (Table S5). On the contrary, the MSVAR analyses revealed significant signals of bottleneck in all rivers (Figure 2C, Table S6). The magnitude of these bottlenecks, as indicated by the median values of the $\log_{10}(N_0/N_1)$ ratio, ranged between -0.705 (ELL) and -1.345 (HER) (Figure 2C, Table S6). Overall, N_0 estimates (i.e. the current N_e of populations) were similar across rivers, with medians ranging from 7 (HER) to 63 individuals (SAL). Concerning ancestral population sizes (N_1), median values ranged from 5286 (LOU) to 9155 individuals (HER) (Figure 2C, Table S6). These bottlenecks were estimated to have occurred between 192 (HER) and 727 years ago (SAL). The MSVAR method has often been considered as more powerful than the BOTTLENECK method (Williamson-Natesan 2005; Girod *et al.*, 2011), which may explain the discrepancy observed between these two methods.

The analysis performed at the Garonne river scale confirmed the low estimates of current N_e found at the river scale. Indeed, at this scale, MSVAR provided an estimate of 147 individuals (5%-95% quartiles: 35.6-534.4) in the whole drainage, whereas LDNe provided a global estimate of 74.6 individuals (95% CI: 54.4-104.6).

Demographic monitoring data

Temporal trends in abundance

Five out of the twelve populations (i.e. HER, VEN, AUR, CEL, VER) showed a significant negative trend ($P < 0.05$; $S < 0$), one population (COU) showed a significant positive trend ($P < 0.01$; $S = 23$) whereas the remaining six populations (VOL, LOU, ARI, GAR, ARR, BAR) showed no significant trend in abundance (Figure 2D, Table S7). Overall, the mixed model meta-analysis revealed a significant ($P < 0.001$) negative trend indicating a global decrease in the abundance of *P. toxostoma* populations in the Garonne river basin.

Modeling species distribution

The stream length occupied by the species was estimated at 24.0% (±2.5 SE) of the total river basin stream length in 1980-1992 (Figure 4A) and 20.9% (±2.6 SE) in 2003-2009 (Figure 4B). This represented an overall decrease of 3.2% ($P < 0.01$) with respect to the whole river basin, and of 13.1% of *P. toxostoma*'s 1980-1992 distribution (Figure 4C, Figure 5). The habitat suitability for the species decreased in the middle part of the river basin between the 1980-1992 and 2003-2009 periods (Figure 4).

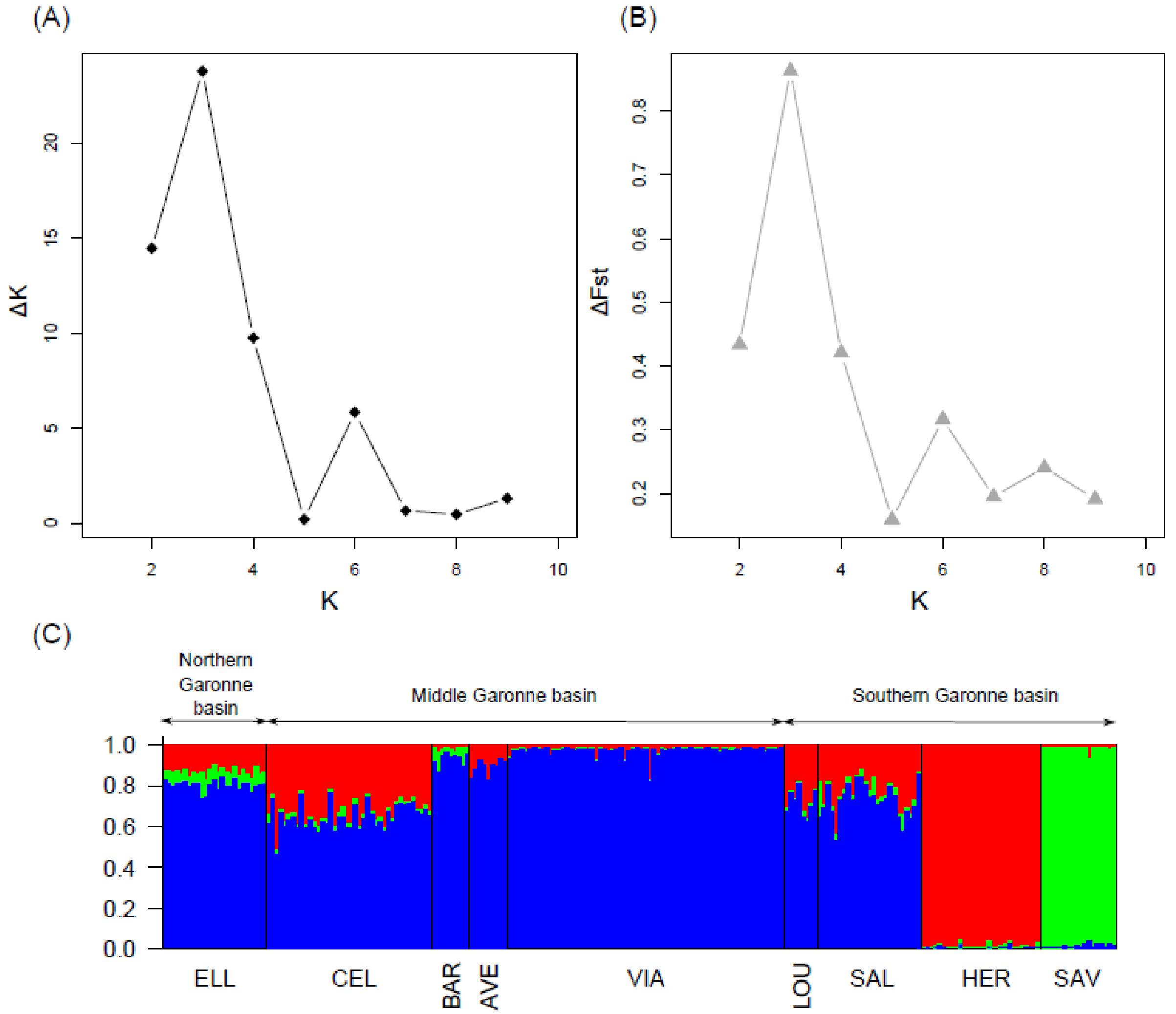

Figure 3 Analysis of the population structure of *Parachondrostoma toxostoma* in the Garonne river basin. (A) and (B) represent the results from ΔK and ΔF_{st} tests respectively. (C) is a barplot representing the results of the Bayesian clustering analysis of microsatellites using STRUCTURE for K = 3.

Table 2: Population pairwise F_{st} (upper half-matrix) and pairwise D_{est} (lower half-matrix) values calculated between all rivers (denoted by their three-level code).

Code	AVE	BAR	CEL	ELL	HER	LOU	SAL	SAV	VIA
AVE	–	**0.117**	**0.067**	**0.070**	**0.042**	0.013 ^{ns}	**0.014**	**0.109**	0.005 ^{ns}
BAR	0.056	–	**0.102**	**0.052**	**0.054**	**0.025**	**0.026**	**0.130**	**0.017**
CEL	0.018	0.031	–	**0.023**	**0.023**	0.003 ^{ns}	**0.012**	**0.089**	**0.010**
ELL	0.035	0.008	0.003	–	**0.032**	0.008 ^{ns}	**0.014**	**0.115**	**0.008**
HER	0.132	0.165	0.077	0.096	–	**0.069**	**0.068**	**0.077**	**0.122**
LOU	0.054	0.057	0.029	0.029	0.019	–	0.004 ^{ns}	**0.114**	**0.050**
SAL	0.049	0.096	0.033	0.034	0.013	0.024	–	**0.090**	**0.037**
SAV	0.262	0.281	0.221	0.230	0.241	0.265	0.228	–	**0.244**
VIA	0.026	0.093	0.044	0.034	0.033	0.015	0.010	0.097	–

For pairwise F_{st}, significant values at level 0.05 after false discovery rate (FDR) correction are in bold. Nonsignificant pairwise F_{st} are denoted by ns.

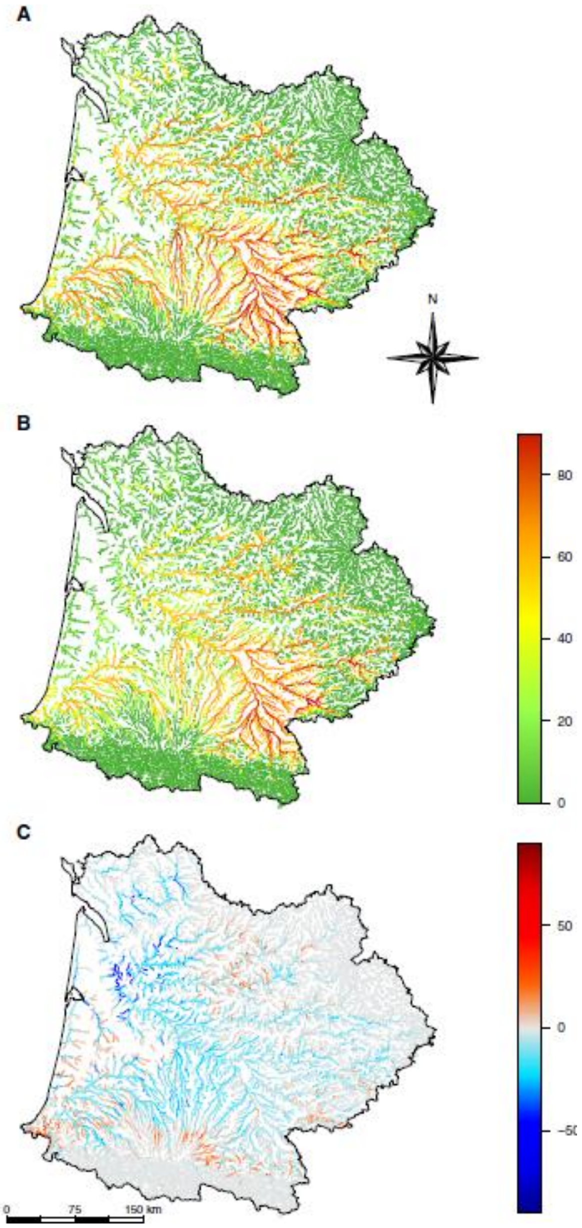

Figure 4 Spatial distributions of *Parachondrostoma toxostoma* modeled for (A) 1980–1992 and (B) 2003–2009 periods, and differences between these two distributions (C). The agreement between presence–absence predictions (i.e. habitat suitability) was measured by summing the 90 predictions (threshold × iteration) for each reach of the Garonne river basin for each period, with color scale varying from green (no predicted presence) to red (90 predicted presences). The differences in the spatial distribution of the species were expressed with a color scale varying from blue (90 presences predicted only for 1980–1992) to red (90 presences predicted only for 2003–2009).

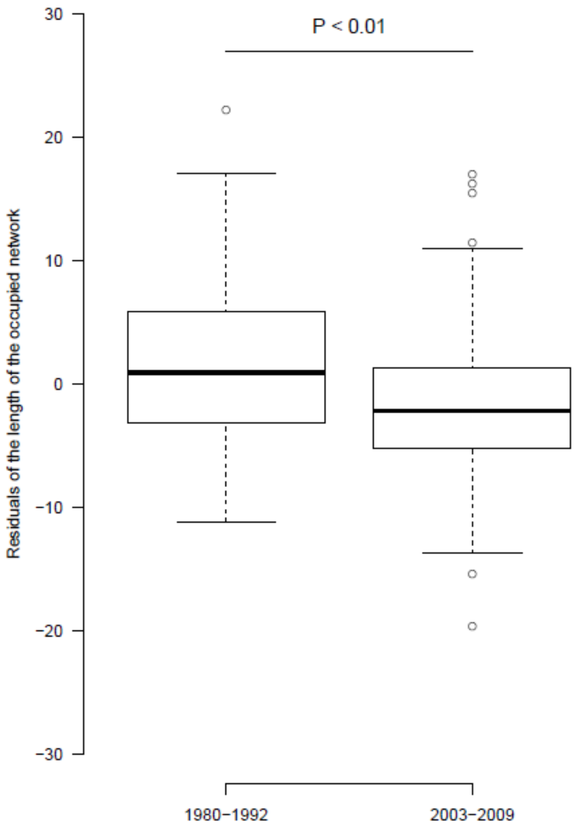

Figure 5 Boxplots of the length of the occupied network by

Parachondrostoma toxostoma in the Garonne river basin modeled for the periods 1980–1992 and 2003–2009. The length of the occupied network was the residuals of a linear regression linking the length of occupied network in both periods with the threshold setting method effect.

DISCUSSION

What did we learn from genetic data?

Using a full-likelihood Bayesian approach (as implemented in MSVAR, Storz & Beaumont, 2002), we showed that all *P. toxostoma* populations have experienced significant decreases in effective population size (N_e), with reductions of more than 99% of their pre-bottleneck long-term N_e. We further showed that: (1) in all populations, bottlenecks started 192-727 years ago, and are hence relatively recent (i.e. within the last millennium); and (2) all populations show extremely low current N_e. Attempting to identify the causes of such bottlenecks would be highly speculative without further data and analyses. If natural causes (climatic or hydrological shifts) cannot be ruled out, anthropogenic causes are also likely (i.e. the first mill weirs date back from the 12th century, Blanchet *et al.,* 2010). It is noteworthy that the bottlenecks highlighted here are ‘species-specific’ rather than ‘basin-specific’, given that for four other sympatric cyprinid fish species (i.e. *Squalius cephalus*, *Leuciscus burdigalensis*, *Gobio gobio* and *Phoxinus phoxinus*), Paz-Vinas *et al.* (2013) demonstrated that bottlenecks were older (approximatively 2000-6000 years ago) and of different magnitudes than those detected for *P. toxostoma*. We can hence reasonably conclude that the bottlenecks inferred here occurred during the last millennium and affected specifically *P. toxostoma* populations.

Descriptive analyses revealed low levels of genetic diversity for all populations. Indeed, all diversity indices were up to approximately 3.3 times lower than those calculated for populations of other cyprinid fish species co-occurring with *P. toxostoma* in the Garonne river basin (Blanchet *et al.,* 2010). They were all also remarkably lower than those calculated for *P. toxostoma* populations from the Rhône river basin (see Dubut *et al.,* 2010). As an example, some microsatellite markers were monomorphic in certain populations, whereas these same markers were highly polymorphic in populations from the Rhône river basin (Dubut *et al.,* 2010). Similarly, Costedoat *et al.* (2005) demonstrated that the diversity measured at mitochondrial genes for *P. toxostoma* was also significantly lower in the Garonne river basin than in the Rhône river basin, a result that may be a consequence of the recent colonization of the Garonne river basin from the Rhône river basin (i.e. approximately 57,000 years ago, Costedoat *et al.* 2005). Although the relatively poor genetic diversity found in the Garonne river basin probably has an important phylogeographical basis (Costedoat *et al.,* 2005), it may reflect the more recent (200-700 years ago) and severe bottlenecks that we detected.

Finally, our PGS also highlighted that *P. toxostoma* populations in the Garonne river basin were relatively homogeneous from a genetic standpoint. Indeed, most populations formed a single cluster with relatively low genetic differentiation within this cluster. This result suggests that these populations constitute a single panmictic unit at the basin level. There were however two noticeable exceptions to this general pattern; the Hers and Save Rivers were genetically differentiated from all other populations. These two populations also demonstrated the lowest contemporary N_e values, the lowest genetic diversities (i.e. H_e, H_o and AR), and the strongest bottlenecks. Altogether, this indicates that these populations may be discriminated from others (1) because gene flow between these populations and others are weak; and/or (2) because genetic drift and inbreeding were particularly high in these populations, causing divergence from other populations in the Garonne river basin.

To summarize, PGS provided a precise description of the current genetic state of *P. toxostoma* populations from the Garonne river basin. Overall, these results clearly indicate that long-term management should integrate the fact that the evolutionary potential of the species in this geographic area may be weak.

What did we learn from demographic data?

Using time series abundance data at twelve locations, we found an overall demographic decrease of *P. toxostoma* populations that occurred in the last three decades. Evidence of a demographic decrease was further supported by comparing the *P. toxostoma* occurrence at the basin scale between two periods (1980-1992 and 2003-2009). This analysis revealed a significant decrease in the distribution range of *P. toxostoma*, representing 13.1% of the 1980-1992’s distribution. These results confirm that over the range of the species, there is a decreasing trend in abundance (Crivelli, 2006; Poulet *et al.,* 2011). This decrease contrasts with the increase in occurrence, abundance and density of several sympatric species at the French scale such as *Barbus barbus* or *Gobio gobio* (Daufresne & Boët, 2007; Poulet *et al.,* 2011). Despite this range-wide trend, we showed that not all local populations were subjected to a significant demographic decrease, since some of them display no particular trends, and one population even showed a significant demographic increase. There was no clear spatial pattern regarding these site-specific trends (see Figure 2D). However, such site-specific analysis provides a basis for further analyses exploring the regional and/or local causes of demographic trends in the Garonne river basin. Indeed, a comparison implying healthy versus non-healthy (from a demographic point of view) populations may highlight the leading environmental factors affecting the demography of this species.

To summarize, DMPs provided insights into the demographic dynamics and changes in the spatial distribution of *P. toxostoma* in the Garonne river basin, which indicates that this species is ecologically weakened in this area, and thus restoration plans should be engaged to ensure the persistence of populations.

Synthesis, implications and conclusions: The conservation gain of combining genetic and demographic data

Synthesis

The history of *P. toxostoma* in the Garonne river basin is relatively recent and began ~57,000 years ago, when it colonized the Garonne from the Rhône river basin (Costedoat *et al.,* 2005). Our results suggest that populations exhibited relatively large long-term N_e (approximately 5,000-8,000 individuals per population) until severe and recent (~800 to 200 years ago) demographic collapses entailed N_e of less than a few hundred (sometimes less than a dozen) individuals. This means that very small numbers of effective breeders are currently sustaining populations in the Garonne river basin. This history led to genetically impoverished *P. toxostoma* populations in the Garonne river basin. Although most populations are genetically homogeneous, these demographic collapses also led to local differentiation in the Garonne river basin. In a more recent timeframe (i.e. the last two decades), we showed that this species experienced a global decrease in census size (N_c) over the entire Garonne river basin, although that some populations remained demographically stable or even increased locally. This recent decrease in N_c was accompanied by a significant reduction of its spatial distribution over the Garonne river basin. Because both N_e and N_c are reduced in these populations, *P. toxostoma* in the Garonne river basin is confronted with a combination of ecological and evolutionary extinction risks, which reinforces its status of vulnerable species in the IUCN red list, and supports the implementation of conservation plans.

Implications

Our results illustrate how combining genetic and demographic approaches is useful to target and to prioritize conservation and management plans for endangered populations. A main weakness of our study resides in the few number of sampling points common to both temporal trend and genetic analyses. However, this fact may well be the standard for most studies focusing on rare and threatened species. We therefore provide recommendations considering two cases. In the first case, both demographic and genetic are available at the sampling site level. In this case, combining genetic and demographic approaches allows identifying priority populations as those (1) having the lowest genetic diversity and N_e; and (2) being subjected to a significant and recent decrease in N_c. For instance, we identified the Hers River as a priority population since both genetic and demographic indices are weak. In this case, we propose conservation strategies involving a program of stocking from broodstock stemming from healthy populations, combined with the restoration of habitat and connectivity with other rivers. Healthy populations are those with stable N_c and higher N_e (such as the Petite Barguelonne and Louge rivers). In the second case, only one of the two metrics is available at the sampling site level. In this case, prioritizing conservation plans is less straightforward. For instance, some populations (e.g. the Vendinelle River) were subjected to a sharp decrease in N_c in recent years, however no data are yet available regarding genetic diversity and N_e dynamics. In this case, managers can conduct a genetic monitoring of these populations to help clarify the populations' status. On the other hand, some populations (e.g. the Save River) have low N_e and low genetic diversity, but lack temporal data regarding N_c. In this case, it is impossible to get the temporal trend of the populations. Thus, invoking the precautionary principle, we propose considering these populations as conservation priority.

Conclusion

To conclude, we showed how combining analyses based on point genetic studies and demographic monitoring programs (i.e. a ‘demo-genetic approach’) reveal complementary information underlying different processes operating at different timescales. Demo-genetic approaches allow (1) identification of ‘at risk’ populations; (2) prioritizing conservation and management actions; and (3) proposing plans that account for the evolutionary history and potential of populations. We hence argue that demo-genetic approaches should be the norm in conservation practices. Indeed, these surveys would allow not only prioritizing and initiation of conservation plans (this study), but would also allow the evaluation of dispersal and connectivity through the use of genetic-based inference methods (Broquet & Petit, 2009), as well as evaluation of the effectiveness of conservation plans (Schwartz *et al.*, 2007; Osborne *et al.*, 2012). We hope that this study will motivate conservation ecologists to invest in genetic monitoring, and conversely, conservation geneticists to initiate long-term demographic surveys.

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SUPPORTING INFORMATION

Appendix S1 Current spatial distribution and recent distribution changes.

The occurrence of *P. toxostoma* was recorded at each site from 1 to 19 times during the 1980-1992 period and from 1 to 14 times during the 2003-2009 period, resulting in 4533 and 7548 sampling occasion records, respectively (see Figure S1).

Independent models were then implemented to model the occurrence of the species in each time period based on a single sampling occasion records (i.e. presence or absence) randomly chosen for each site. We used a ensemble modeling approach allowing to account for variability associated to methodological choices and data quality (e.g. Puschendorf *et al.,* 2009; Grenouillet *et al.,* 2011).

Specifically, to account for the variability related to the modeling method, we followed the procedure applied in Marmion *et al.* (2009) by averaging the probabilities of occurrence predicted by eight single-species distribution models: Generalized Linear Models (GLM), Generalized Additive Models (GAM), Multivariate Adaptive Regression Splines (MARS), Mixture Discriminant Analyses (MDA), Classification And Regression Trees (CART), Random Forest (RF), Generalized Boosted Trees (GBT) and Artificial Neural Networks (ANN).

Models were calibrated on 70% of the sampling occasion records, while the remaining 30% were used for evaluation and threshold selection. Three common threshold-setting methods were then applied to find the thresholds that offer the best trade-off to convert occurrence probabilities into binary data (i.e. presence or absence, Liu *et al.,* 2005). Specifically, we used threshold values maximizing the sum of sensitivity and specificity, sensitivity equaling specificity and maximizing Kappa. Finally, we accounted for the variability due to the quality of the calibration dataset by repeating 30 times with 30 different sampling occasion datasets the different steps of the modeling process.

Therefore, we ultimately obtained 90 final modeled species distributions for each period resulting from 30 iterations, and 3 thresholds that we used to estimate the extent of the spatial distribution of *P. toxostoma* in both time periods.

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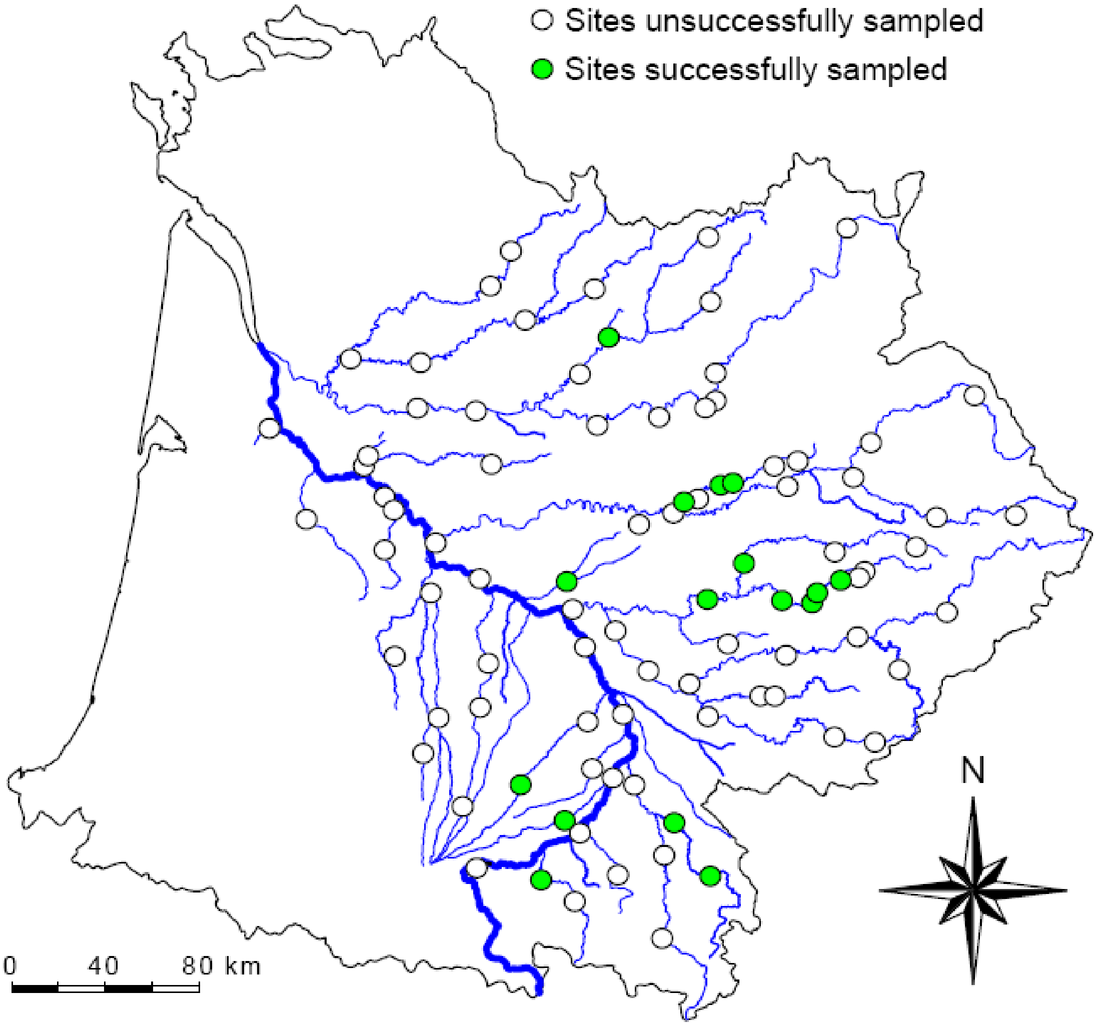

Figure S1 Map of the Garonne river basin (South-Western France) representing (i) sites where *P. toxostoma* was unsuccessfully sampled for genetic analyses (white circles) and (ii) sites where *P. toxostoma* was successfully sampled for genetic analyses (green circles).

Table S1 Information on microsatellite loci and multiplexed PCR used in this study.

Locus	GenBank Accession ID	Ref.	Fluorescent dye	Multiplex Kit	Primers concentration
BL1-30	FJ468353	Dubut *et al.* (2009a)	6-FAM	1	100 nM
Rser10	AJ312850	Dawson *et al.* (2003)	6-FAM	1	100 nM
LleC-090	FJ601722	Dubut *et al.* (2009b)	6-FAM	1	100 nM
LceC1	AY962241	Larno *et al.* (2005)	HEX	1	100 nM
BL1-61	FJ468351	Dubut *et al.* (2009a)	HEX	1	75 nM
Ca1	AF277573	Dimsoski *et al. (*2000)	ATTO550	1	300 nM
N7K4	AJ566138	Mesquita *et al.* (2003)	ATTO550	1	100 nM
CtoA-256	GU254032	Dubut *et al.* (2010)	6-FAM	2	150 nM
BL1-2b	FJ468347	Dubut *et al.* (2009a)	6-FAM	2	100 nM
Rru4	AB112740	Barinova *et al.* (2004)	6-FAM	2	100 nM
Lsou34	EF209012	Muenzel *et al.* (2007)	HEX	2	75 nM
LleA-029	FJ601714	Dubut *et al.* (2009b)	HEX	2	100 nM
CtoF-172	GU254034	Dubut *et al.* (2010)	ATTO550	2	100 nM
Lsou05	EF209002	Muenzel *et al.* (2007)	ATTO550	2	100 nM
BL1-T2	FJ468348	Dubut *et al.* (2009a)	ATTO550	2	100 nM

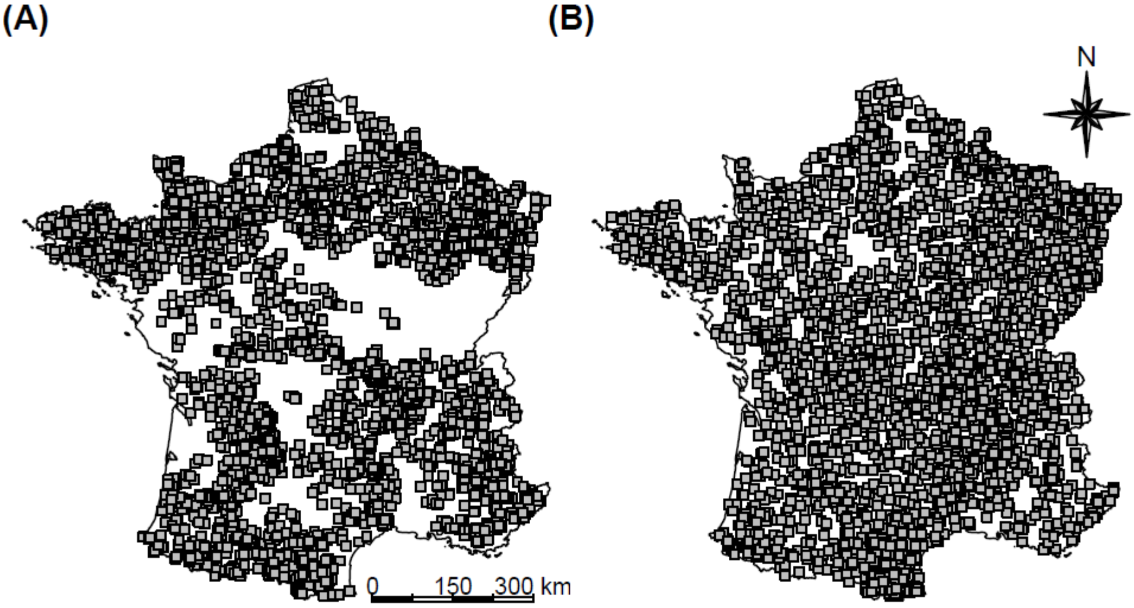

Figure S2 Maps representing sites where the occurrence of *P. toxostoma* was recorded (A) from 1 to 19 times during the 1980-1992 period and (B) from 1 to 14 times during the 2003-2009 period.

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Table S2 Observed number of alleles (*na*), expected (H_e) and observed (H_o) heterozygosities and departures from Hardy-Weinberg equilibrium (F*is*) for all loci and populations of *P. toxostoma*. No significant departures from Hardy-Weinberg equilibrium were found after applying Benjamini & Hochberg (1995) false discovery rate corrections. N indicates the sample size.

	Code	AVE	BAR	CEL	ELL	HER	LOU	SAL	SAV	VIA
Locus	N	9	9	40	25	29	8	25	18	67
BL1-30	*na*	3	3	3	4	3	4	3	2	3
	He	0.370	0.426	0.266	0.316	0.451	0.328	0.150	0.486	0.293
	Ho	0.444	0.333	0.275	0.360	0.552	0.375	0.120	0.500	0.254
	Fis	-0.143	0.273	-0.021	-0.119	-0.206	-0.077	0.217	0	0.141
BL1-61	*na*	3	2	3	3	3	4	4	4	3
	He	0.364	0.278	0.464	0.442	0.216	0.328	0.314	0.542	0.343
	Ho	0.444	0.333	0.500	0.480	0.241	0.375	0.280	0.667	0.254
	Fis	-0.164	-0.143	-0.066	-0.065	-0.101	-0.077	0.130	-0.204	0.268
LleC-090	*na*	6	6	4	6	3	4	5	4	6
	He	0.716	0.531	0.502	0.571	0.267	0.539	0.610	0.497	0.685
	Ho	0.778	0.667	0.500	0.560	0.310	0.625	0.640	0.389	0.657
	Fis	-0.028	-0.200	0.017	0.040	-0.146	-0.094	-0.030	0.244	0.049
LceC1	*na*	2	2	2	2	3	2	2	2	2
	He	0.346	0.346	0.469	0.480	0.492	0.375	0.493	0.494	0.468
	Ho	0.444	0.222	0.600	0.400	0.586	0.500	0.560	0.444	0.328
	Fis	-0.231	0.407	-0.268	0.186	-0.175	-0.273	-0.116	0.128	0.305
Ca1	*na*	4	6	6	6	4	5	5	3	6
	He	0.599	0.790	0.748	0.781	0.662	0.633	0.723	0.370	0.773
	Ho	0.667	0.778	0.750	0.600	0.690	0.625	0.600	0.222	0.761
	Fis	-0.055	0.074	0.010	0.251	-0.025	0.079	0.190	0.424	0.023
Rser10	*na*	2	2	2	2	2	2	2	2	2
	He	0.475	0.346	0.455	0.295	0.498	0.469	0.480	0.494	0.322
	Ho	0.556	0.444	0.600	0.280	0.586	0.250	0.480	0.556	0.373
	Fis	-0.111	-0.231	-0.307	0.072	-0.161	0.517	0.020	-0.097	-0.152
N7K4	*na*	5	5	6	6	4	4	6	3	5
	He	0.667	0.654	0.740	0.757	0.526	0.734	0.798	0.286	0.712
	Ho	0.556	0.889	0.700	0.800	0.586	0.750	0.840	0.222	0.746
	Fis	0.223	-0.306	0.066	-0.037	-0.097	0.046	-0.033	0.249	-0.041
Rru4	*na*	3	2	3	5	2	3	4	3	4
	He	0.290	0.346	0.496	0.546	0.384	0.625	0.253	0.249	0.510
	Ho	0.111	0	0.525	0.680	0.241	0.625	0.280	0.167	0.463
	Fis	0.652	1	-0.045	-0.225	0.386	0.067	-0.087	0.354	0.100
Lsou34	*na*	1	2	2	2	2	2	1	1	1
	He	0	0.494	0.049	0.180	0.034	0.117	0	0	0
	Ho	0	0.444	0.050	0.200	0.035	0.125	0	0	0
	Fis	NA	0.158	-0.013	-0.091	NA	NA	NA	NA	NA
Lsou05	*na*	4	4	4	5	2	3	4	2	4
	He	0.624	0.593	0.434	0.663	0.400	0.477	0.545	0.153	0.569
	Ho	0.889	0.778	0.500	0.600	0.414	0.500	0.560	0.167	0.582
	Fis	-0.376	-0.258	-0.139	0.116	-0.018	0.018	-0.008	-0.063	-0.016
LleA-029	*na*	4	4	6	5	6	6	6	2	5
	He	0.568	0.642	0.591	0.568	0.710	0.734	0.663	0.475	0.399
	Ho	0.667	0.778	0.550	0.600	0.759	0.875	0.600	0.667	0.388
	Fis	-0.116	-0.155	0.081	-0.036	-0.051	-0.126	0.116	-0.378	0.036
CtoF-172	*na*	1	1	2	1	1	1	1	1	1
	He	0.568	0.642	0.591	0.568	0.710	0.734	0.663	0.475	0.399
	Ho	0.667	0.778	0.550	0.600	0.759	0.875	0.600	0.667	0.388

	Fis	NA	NA	NA	NA	NA	NA	NA	NA	NA
CtoA-256	*na*	2	2	2	2	2	2	2	2	2
	He	0.475	0.401	0.500	0.471	0.462	0.469	0.497	0.198	0.486
	Ho	0.333	0.556	0.550	0.600	0.379	0.250	0.360	0.222	0.409
	Fis	0.351	-0.333	-0.088	-0.254	0.196	0.517	0.294	-0.097	0.166
BL1-T2	*na*	3	4	3	4	2	2	2	3	3
	He	0.426	0.624	0.528	0.566	0.366	0.490	0.385	0.554	0.395
	Ho	0.556	0.667	0.525	0.600	0.276	0.286	0.280	0.500	0.388
	Fis	-0.250	-0.011	0.019	-0.041	0.263	0.478	0.291	0.126	0.025
BL1-2b	*na*	1	2	1	2	1	2	2	1	2
	He	0	0.278	0	0.039	0	0.117	0.077	0	0.138
	Ho	0	0.333	0	0.040	0	0.125	0.080	0	0.149
	Fis	NA	-0.143	NA	NA	NA	NA	-0.021	NA	-0.073

Table S3 Mean observed (H_o) and expected (H_e) heterozygosities, mean number of alleles over loci (NA), allelic richness (AR_8 for a minimum sample size of 8 individuals; AR_{18} for a minimum sample size of 18 individuals) and departures from Hardy-Weinberg equilibrium (F*is*) for each *P. toxostoma* population. Numbers inside brackets represent the standard deviation for H_o and H_e. N indicates the sample size.

Code	N	H_o	H_e	NA	AR_8	AR_{18}	F*is*
AVE	9	0.395 (0.239)	0.418 (0.253)	2.933	2.375	–	-0.030 ^{ns}
BAR	9	0.450 (0.198)	0.476 (0.210)	3.133	2.536	–	-0.012 ^{ns}
CEL	40	0.418 (0.234)	0.423 (0.237)	3.267	2.289	2.712	-0.049 ^{ns}
ELL	25	0.445 (0.237)	0.454 (0.242)	3.667	2.466	3.037	0.002 ^{ns}
HER	29	0.364 (0.223)	0.371 (0.226)	2.667	2.028	2.306	-0.017 ^{ns}
LOU	8	0.429 (0.222)	0.458 (0.237)	3.067	2.501	–	0.087 ^{ns}
SAL	25	0.399 (0.259)	0.407 (0.264)	3.267	2.294	2.798	0.072 ^{ns}
SAV	18	0.320 (0.208)	0.329 (0.214)	2.333	1.868	2.141	0.044 ^{ns}
VIA	67	0.406 (0.236)	0.409 (0.238)	3.267	2.307	2.751	0.063 ^{ns}

^{ns} = non-significant departure from Hardy-Weinberg proportions

Table S4 P-values for the linkage disequilibrium test for each pair of loci and population. The adjusted significance threshold value for 5% nominal level is $\alpha = 0.000048$.

Locus1	Locus2	AVE	BAR	CEL	ELL	HER	LOU	SAL	SAV	VIA	All
BL1-30	BL1-61	0.842	0.024	0.922	0.715	0.719	0.287	1.000	0.571	0.369	0.599
BL1-30	LleC-0	1.000	0.818	0.007	0.766	0.026	0.681	0.889	0.905	0.349	0.155
BL1-30	LceC1	0.365	1.000	0.636	0.227	0.864	1.000	1.000	0.166	0.633	0.768
BL1-30	Ca1	0.935	1.000	0.410	0.396	0.755	0.179	0.142	0.185	0.925	0.493
BL1-30	Rser10	0.844	1.000	0.707	0.535	1.000	0.504	0.019	0.642	0.906	0.900
BL1-30	N7K4	1.000	0.612	0.975	0.857	0.977	1.000	0.226	0.216	0.267	0.885
BL1-30	Rru4	1.000	0.054	0.335	0.503	0.046	0.344	0.176	0.197	0.209	0.030
BL1-30	Lsou34	NA	0.619	1.000	0.064	1.000	0.374	NA	NA	NA	0.143
BL1-30	Lsou05	0.759	0.326	0.526	0.586	0.649	0.497	0.578	0.803	0.724	0.698
BL1-30	LleA-0	0.938	0.969	0.213	0.439	0.806	0.359	0.511	0.516	0.852	0.756
BL1-30	CtoF-1	NA	NA	0.276	NA	NA	NA	NA	NA	NA	0.276
BL1-30	CtoA-2	0.179	0.447	0.481	0.872	0.068	1.000	0.566	1.000	0.765	0.467
BL1-30	BL1-T2	0.810	0.920	0.545	0.323	0.743	0.285	1.000	0.951	0.972	0.966
BL1-30	BL1-2b	NA	0.762	NA	1.000	NA	1.000	1.000	NA	1.000	0.948

BL1-61	LleC-0	0.823	0.641	0.401	0.852	0.197	1.000	0.965	0.823	0.256	0.786
BL1-61	LceC1	1.000	1.000	0.980	0.729	0.078	1.000	0.627	0.427	0.498	0.768
BL1-61	Ca1	0.570	1.000	0.238	0.465	0.206	0.717	0.827	0.146	0.036	0.063
BL1-61	Rser10	0.823	1.000	0.121	0.145	0.812	1.000	0.877	0.566	0.034	0.222
BL1-61	N7K4	0.136	0.570	0.625	0.841	0.020	0.648	0.666	0.645	0.585	0.364
BL1-61	Rru4	0.217	1.000	0.476	0.567	0.702	0.330	0.901	0.081	0.085	0.185
BL1-61	Lsou34	NA	1.000	0.251	0.424	1.000	0.369	NA	NA	NA	0.325
BL1-61	Lsou05	0.861	0.525	0.995	0.036	0.621	0.717	0.025	0.482	0.760	0.256
BL1-61	LleA-0	0.570	0.858	0.290	0.912	0.957	0.358	0.324	0.800	0.270	0.598
BL1-61	CtoF-1	NA	NA	1.000	NA	NA	NA	NA	NA	NA	1.000
BL1-61	CtoA-2	0.400	1.000	0.418	0.211	0.368	1.000	0.767	0.341	0.603	0.397
BL1-61	BL1-T2	0.336	0.856	0.684	0.576	1.000	0.037	0.762	0.221	0.392	0.448
BL1-61	BL1-2b	NA	1.000	NA	0.517	NA	1.000	0.194	NA	0.169	0.264
LleC-0	LceC1	1.000	0.954	0.261	0.566	0.196	1.000	0.825	0.641	0.307	0.615
LleC-0	Ca1	0.398	1.000	0.461	0.935	0.973	1.000	0.675	0.466	0.976	0.983
LleC-0	Rser10	0.133	0.527	0.594	0.783	0.839	0.568	0.381	0.082	0.090	0.125
LleC-0	N7K4	1.000	1.000	0.201	0.018	0.465	1.000	0.238	0.022	0.599	0.058
LleC-0	Rru4	0.414	0.834	0.431	0.962	0.004	0.677	0.513	0.567	0.391	0.338
LleC-0	Lsou34	NA	0.790	1.000	0.803	1.000	1.000	NA	NA	NA	0.923
LleC-0	Lsou05	0.538	0.817	0.786	0.561	0.162	0.913	0.403	1.000	0.624	0.700
LleC-0	LleA-0	0.389	0.612	0.401	0.215	0.784	1.000	0.527	0.227	0.651	0.422
LleC-0	CtoF-1	NA	NA	1.000	NA	NA	NA	NA	NA	NA	1.000
LleC-0	CtoA-2	1.000	1.000	0.751	0.247	0.502	0.573	0.645	1.000	0.228	0.651
LleC-0	BL1-T2	1.000	0.479	0.915	0.483	1.000	0.272	0.872	0.817	0.756	0.966
LleC-0	BL1-2b	NA	1.000	NA	1.000	NA	1.000	0.134	NA	0.137	0.318
LceC1	Ca1	0.709	0.438	0.420	0.002	0.649	0.144	0.529	0.847	0.776	0.184
LceC1	Rser10	0.166	0.289	0.202	0.094	0.746	0.659	0.542	0.474	0.004	0.022
LceC1	N7K4	1.000	0.903	0.881	0.620	0.105	0.658	0.829	0.365	0.163	0.490
LceC1	Rru4	1.000	0.661	0.903	0.919	0.523	1.000	0.073	0.945	0.516	0.906
LceC1	Lsou34	NA	0.854	1.000	0.808	0.450	1.000	NA	NA	NA	0.846
LceC1	Lsou05	0.573	0.721	0.232	0.978	0.428	0.258	0.708	1.000	0.110	0.584
LceC1	LleA-0	1.000	0.905	0.693	0.119	0.533	1.000	0.945	1.000	0.356	0.867
LceC1	CtoF-1	NA	NA	1.000	NA	NA	NA	NA	NA	NA	1.000
LceC1	CtoA-2	0.377	1.000	0.278	0.499	0.785	1.000	0.947	0.156	0.960	0.947
LceC1	BL1-T2	1.000	0.113	0.061	0.188	0.539	0.314	0.609	0.927	0.440	0.172
LceC1	BL1-2b	NA	0.404	NA	1.000	NA	1.000	0.484	NA	0.400	0.446
Ca1	Rser10	0.565	1.000	0.131	0.491	0.827	1.000	0.806	1.000	0.858	0.909
Ca1	N7K4	0.399	1.000	0.343	0.802	0.214	1.000	0.556	0.673	0.570	0.375
Ca1	Rru4	1.000	1.000	0.527	0.784	0.781	1.000	0.355	0.087	0.746	0.703
Ca1	Lsou34	NA	0.281	0.769	0.793	0.683	0.625	NA	NA	NA	0.533
Ca1	Lsou05	1.000	1.000	0.030	0.938	0.785	0.070	0.391	0.677	0.524	0.378
Ca1	LleA-0	0.548	1.000	0.582	0.607	0.677	1.000	0.377	0.789	0.784	0.751
Ca1	CtoF-1	NA	NA	0.177	NA	NA	NA	NA	NA	NA	0.177
Ca1	CtoA-2	1.000	1.000	0.106	0.008	0.807	1.000	0.318	0.462	0.478	0.213
Ca1	BL1-T2	0.922	1.000	0.077	0.900	0.088	0.504	0.223	0.504	0.144	0.051
Ca1	BL1-2b	NA	0.498	NA	0.279	NA	0.619	0.533	NA	0.959	0.744
Rser10	N7K4	1.000	1.000	0.709	0.822	0.019	1.000	0.732	0.191	0.601	0.645
Rser10	Rru4	0.726	1.000	0.575	0.120	0.430	0.798	0.541	1.000	0.730	0.737
Rser10	Lsou34	NA	1.000	0.100	0.416	0.171	0.494	NA	NA	NA	0.170
Rser10	Lsou05	0.207	0.528	0.468	0.904	0.476	1.000	0.223	0.376	0.292	0.454
Rser10	LleA-0	0.571	0.271	0.212	0.367	0.780	1.000	0.216	0.508	0.382	0.255
Rser10	CtoF-1	NA	NA	1.000	NA	NA	NA	NA	NA	NA	1.000
Rser10	CtoA-2	1.000	1.000	0.798	0.830	0.288	0.771	0.640	0.785	0.023	0.624
Rser10	BL1-T2	1.000	0.713	0.010	0.878	0.202	1.000	0.306	0.789	0.284	0.344

Rser10	BL1-2b	NA	0.525	NA	1.000	NA	1.000	0.262	NA	1.000	0.787
N7K4	Rru4	0.420	0.608	0.770	0.945	0.472	1.000	0.265	0.246	0.629	0.705
N7K4	Lsou34	NA	0.270	0.633	0.605	0.033	1.000	NA	NA	NA	0.241
N7K4	Lsou05	0.532	0.616	0.866	0.928	0.582	0.449	0.839	0.714	0.770	0.904
N7K4	LleA-0	1.000	0.312	0.578	0.930	0.929	1.000	0.678	0.829	0.319	0.809
N7K4	CtoF-1	NA	NA	0.650	NA	NA	NA	NA	NA	NA	0.650
N7K4	CtoA-2	0.713	0.275	0.891	0.233	0.533	0.485	0.814	0.260	0.535	0.524
N7K4	BL1-T2	0.808	0.731	0.370	0.482	0.118	0.324	0.989	0.368	0.402	0.342
N7K4	BL1-2b	NA	0.349	NA	0.287	NA	1.000	0.552	NA	0.253	0.311
Rru4	Lsou34	NA	1.000	1.000	0.943	1.000	1.000	NA	NA	NA	0.998
Rru4	Lsou05	0.751	0.447	0.038	0.883	0.960	1.000	0.715	1.000	0.715	0.807
Rru4	LleA-0	0.311	0.614	0.696	0.126	0.425	1.000	0.777	0.514	0.824	0.657
Rru4	CtoF-1	NA	NA	0.123	NA	NA	NA	NA	NA	NA	0.123
Rru4	CtoA-2	0.287	0.167	0.401	0.315	0.102	0.797	0.607	0.200	0.151	0.058
Rru4	BL1-T2	0.560	0.663	0.804	0.344	0.859	0.575	0.592	0.405	0.799	0.885
Rru4	BL1-2b	NA	1.000	NA	0.161	NA	1.000	0.483	NA	0.729	0.464
Lsou34	Lsou05	NA	0.288	0.073	0.702	1.000	0.250	NA	NA	NA	0.078
Lsou34	LleA-0	NA	0.586	0.417	0.799	1.000	0.749	NA	NA	NA	0.657
Lsou34	CtoF-1	NA	NA	1.000	NA	NA	NA	NA	NA	NA	1.000
Lsou34	CtoA-2	NA	0.380	0.490	1.000	1.000	1.000	NA	NA	NA	0.602
Lsou34	BL1-T2	NA	0.394	1.000	0.646	1.000	0.629	NA	NA	NA	0.684
Lsou34	BL1-2b	NA	0.214	NA	1.000	NA	1.000	NA	NA	NA	0.398
Lsou05	LleA-0	0.693	0.966	0.104	0.045	0.912	1.000	0.203	0.451	0.479	0.172
Lsou05	CtoF-1	NA	NA	1.000	NA	NA	NA	NA	NA	NA	1.000
Lsou05	CtoA-2	0.096	0.450	0.154	0.800	0.817	1.000	0.030	0.553	0.597	0.173
Lsou05	BL1-T2	1.000	0.921	0.002	0.223	0.753	0.284	0.723	0.462	0.272	0.085
Lsou05	BL1-2b	NA	0.165	NA	0.563	NA	0.496	0.493	NA	0.810	0.508
LleA-0	CtoF-1	NA	NA	1.000	NA	NA	NA	NA	NA	NA	1.000
LleA-0	CtoA-2	0.850	0.456	0.037	0.614	0.315	1.000	0.114	1.000	0.338	0.092
LleA-0	BL1-T2	1.000	1.000	0.918	0.177	0.662	1.000	0.974	0.113	0.245	0.842
LleA-0	BL1-2b	NA	1.000	NA	1.000	NA	1.000	0.802	NA	0.850	0.996
CtoF-1	CtoA-2	NA	NA	1.000	NA	NA	NA	NA	NA	NA	1.000
CtoF-1	BL1-T2	NA	NA	0.594	NA	NA	NA	NA	NA	NA	0.594
CtoF-1	BL1-2b	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
CtoA-2	BL1-T2	0.663	1.000	0.679	0.862	0.927	0.886	0.120	0.928	0.539	0.923
CtoA-2	BL1-2b	NA	1.000	NA	0.390	NA	0.497	1.000	NA	0.316	0.448
BL1-T2	BL1-2b	NA	0.060	NA	0.086	NA	0.620	0.642	NA	0.009	0.0004

NA = comparison for which no contingency table was computable.

Table S5 Results for the Wilcoxon's sign rank test computed by BOTTLENECK for each river and for the TPM and SMM microsatellite mutation models. Significant H_e excesses are evidences of recent population decreases. Significant H_e deficiencies can be interpreted as recent signals of demographic expansion. ^{ns} means that there is not a significant deviation from mutation/drift equilibrium (P > 0.05); ***** indicates a significant deviation from mutation/drift equilibrium ($P \leq 0.05$). No significant H_e deviation has been found after the application of false discovery rate procedure (Benjamini & Hochberg, 1995).

	TPM		SMM	
Code	Wilcoxon excess	Wilcoxon deficiency	Wilcoxon excess	Wilcoxon Deficiency
AVE	0.788 ^{ns}	0.235 ^{ns}	0.945 ^{ns}	0.065 ^{ns}
BAR	0.148 ^{ns}	0.866 ^{ns}	0.500 ^{ns}	0.524 ^{ns}
CEL	0.163 ^{ns}	0.852 ^{ns}	0.596 ^{ns}	0.428 ^{ns}
ELL	0.476 ^{ns}	0.548 ^{ns}	0.879 ^{ns}	0.134 ^{ns}
HER	0.122 ^{ns}	0.892 ^{ns}	0.446 ^{ns}	0.580 ^{ns}
LOU	0.643 ^{ns}	0.380 ^{ns}	0.892 ^{ns}	0.121 ^{ns}
SAL	0.500 ^{ns}	0.527 ^{ns}	0.706 ^{ns}	0.318 ^{ns}
SAV	0.259 ^{ns}	0.765 ^{ns}	0.604 ^{ns}	0.425 ^{ns}
VIA	**0.047***	0.960 ^{ns}	0.527 ^{ns}	0.500 ^{ns}

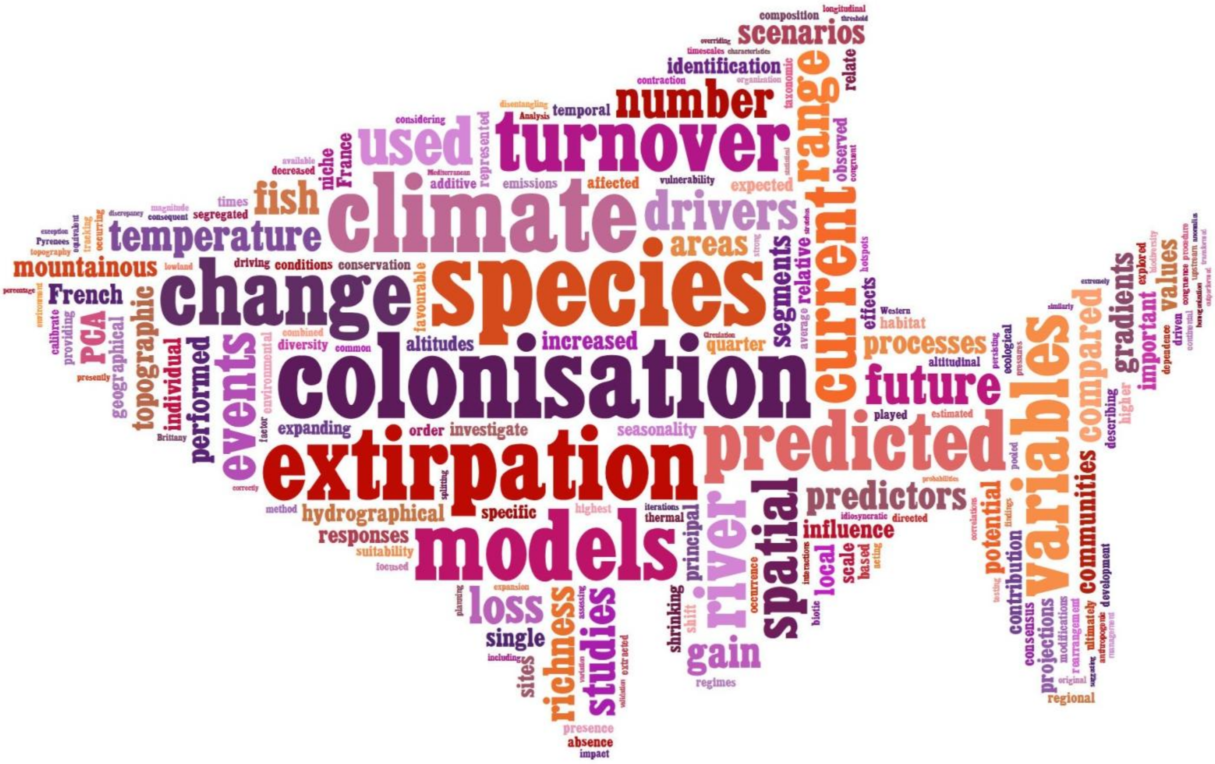
Table S6 Median, 5% and 95% quartile values calculated for N_0 (the current effective population size), N_1 (the past effective population size), T_a (the time of the beginning of the demographic change, in years backwards from the present) and $Log_{10}(N_0/N_1)$ (the magnitude of the demographic change) for each river, through the posterior distributions obtained with MSVAR 1.3. Negative values of the ratio $Log_{10}(N_0/N_1)$ indicates that the population has experienced a bottleneck.

N_0			N_1			T_a			$Log_{10}(N_0/ N_1)$		
Median	5% quartile	95% quartile	Median	5% quartile	95% quartile	Median	5% quartile	95% quartile	Median	5% quartile	95% quartile
18	0.26	257.93	5705	1563.72	19967.73	216	5	2828	-1.005	-2.739	-0.444
22	0.35	259.72	8449	2083.62	33151.99	260	6	3107	-0.999	-2.605	-0.500
20	0.38	168.39	5948	1734.11	19830.60	279	8	2375	-1.005	-2.479	-0.551
58	0.42	524.68	5499	1545.67	18950.53	419	5	5176	-0.705	-2.148	-0.342
7	0.09	77.55	9155	2506.26	32953.91	192	4	1792	-1.345	-3.182	-0.748
37	0.58	513.25	5286	1506.20	18441.77	307	7	4603	-0.810	-2.419	-0.332
63	1.06	401.75	5501	1426.57	20578.35	727	14	6349	-0.710	-1.968	-0.391
12	0.20	119.34	6541	1630.16	26012.09	333	8	3156	-1.135	-2.869	-0.628
15	0.27	142.15	6031	1652.18	20759.73	221	6	2008	-1.054	-2.810	-0.583

Table S7 Values for the Mann-Kendall's S statistic, variance in S (Var(S)), mean densities and *P* values obtained for the twelve time series with the modified Mann-Kendall trend test. Time series are identified by the three-letter code of their corresponding rivers. Negative S values denote decreasing trends, while positive values indicate increasing trends. * indicates that the trend is significant.

River	S	Var(S)	Mean density	P
HER	-25	125.0	5.9	**0.025***
VOL	-14	65.3	13.1	0.083
LOU	-18	268.7	1.8	0.272
ARI	10	65.3	1.8	0.216
VEN	-82	697.0	10.3	**<0.01***
GAR	-12	125.0	0.9	0.283
AUR	-37	268.7	3.8	**0.023***
ARR	-29	268.7	1.2	0.076
CEL	-29	165.0	4.0	**0.023***
VER	-49	589.3	2.3	**0.043***
BAR	-2	589.3	3.8	0.93
COU	23	33.8	7.4	**<0.01***

ANNEXE II (A_{II})



Conti L, **Comte L**, Hugueny B & Grenouillet G (Under Review) Drivers of freshwater fish colonisations and extirpations under climate change. Submitted to ***Ecography.***

Drivers of freshwater fish colonisations and extirpations under climate change

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ABSTRACT

Climate change is expected to determine profound rearrangement of ecological communities by affecting individual species distributions. The resulting communities arise from the idiosyncratic responses of species to future changes, which ultimately relate to both shrinking and expanding species' ranges. While spatial patterns of colonisation and extirpation events received great attention, the identification of specific drivers remains to date poorly explored. This study aims to investigate the relative contribution of species gain and loss to the turnover of fish assemblages in French rivers under future climate change, and to identify their principal drivers. Future projections of potential habitat suitability in 2080 derived from species distribution models for 40 fish species showed that colonisations and extirpations could play a comparable role in communities rearrangements. Simultaneously, these two processes exhibited patchy spatial patterns, and segregated along the altitudinal gradient, resulting in dramatic species turnover of ~60% of current species assemblages composition. Beyond the effect of topographic location, colonisations emerged to be driven by temperature seasonality while extirpations were affected by modifications in both thermal and precipitation regimes.

These results entail the possibility of developing ecosystem-based management tools, aiming at an early evaluation of needs and opportunities of climate-sensitive species. Disentangling the drivers of colonisation and extirpation processes provide a ready-to-use information to be integrated into conservation planning, aiming at identifying hotspots of potential species gain and loss and to compare them with actual accessibility of newly favourable areas, in order to facilitate future range shifts.

Keywords: species turnover, climate variability, stream fishes, spatial patterns

INTRODUCTION

Climate change is widely recognised as having a profound impact on species' distributions (Pearson & Dawson, 2003) and consequent modifications of biodiversity patterns are a key topic in recent published literature in terrestrial (Thuiller *et al.*, 2005*;* Levinsky *et al.*, 2007*;* Huntley *et al.*, 2008*;* La Sorte & Jetz, 2010), marine (Hiddink & ter Hofstede, 2008*;* Cheung *et al.*, 2009*;* Albouy *et al.*, 2012) and freshwater (Buisson *et al.*, 2008; Heino *et al.*, 2009; Comte *et al.*, 2013; Pace *et al.*, 2013; Tisseuil *et al.*, 2013) ecosystems. At ecological timescales, species assemblages are the result of the synergic interplay between colonisation and extirpation, two spatial and temporal-dependent processes acting under the pressure of regional and local drivers (He *et al.*, 2005; Korhonen *et al.*, 2010). At the continental scale, climate can be considered the dominant factor shaping species' distributions, whilst at more local scales factors including topography and land-cover type become increasingly important (Pearson & Dawson, 2003). For instance, a species might be buffered from the full magnitude of regional climate change by persisting in thermally sheltered microhabitats (Hof *et al.*, 2011), while anthropogenic drivers may act synergistically or antagonistically to climate change impacts (Le Roux & McGeoch, 2008; D'Andrea *et al.*, 2009; Hockey *et al.*, 2011). In this context, colonisations and extirpations ultimately relate to both shrinking and expanding species' ranges (Thomas, 2010) and result in the so-called niche tracking, the process by which species follow favourable environmental conditions through geographical space (e.g. Graham *et al.*, 1996; Tingley *et al.*, 2009).

In order to quantify modifications of species assemblages along geographical or environmental gradients (i.e. beta diversity), species turnover (ST) is among the most common metrics used, as well as its temporal equivalent to estimate compositional changes over time (Albouy *et al.*, 2012). Numerically, ST considers the number of colonisation (species gain) and extirpation (species loss) events within each spatio-temporal unit and compares them with the baseline species richness (Peterson *et al.*, 2002; Thuiller *et al.*, 2005).

A vast number of studies and meta-analyses addressed the issue of spatial variability in species composition (see Heino, 2011; Leprieur *et al.*, 2011; Oberdoff *et al.*, 2011 for a review on freshwater realm), demonstrating that beta diversity could be driven by functional traits, geographical gradients and ecosystem properties (Soininen *et al.*, 2007). By contrast, assessing temporal turnover has been far less investigated, generally hindered by the lack of long-term data (Micheli *et al.*, 1999; Korhonen *et al.*, 2010). In particular, although the number of studies focusing on spatial and temporal patterns of species turnover (Buisson *et al.*, 2008; Buisson & Grenouillet, 2009; Villéger *et al.*, 2013) is progressively increasing, few attempts have been directed towards the identification of drivers and geographical patterns in the single processes shaping local richness, namely colonisations and extirpations.

At ecological timescales, climate change may influence the congruence between species' tolerance limits (i.e. species' niche) and their current distribution in three principal ways: (i) presently occupied sites may remain within the climatic niche of the species, (ii) the local environment may shift outside species' niche potentially leading to extirpation, or (iii) currently unoccupied sites may become favourable by shifting inside species' niche potentially leading to colonisation (i.e. niche tracking; Tingley *et al.*, 2009). When a new equilibrium is reached, the combined result of colonisation and extirpation events defines a new species' habitat suitability, although both processes may have not been equivalent in their extent, geographical location and, more importantly, in the drivers producing them (Hampe & Petit, 2005). Studies based on species distribution models (SDMs) often focused on the overlap between current and future favourable or unfavourable space units, in order to detect spatial patterns and local hotspots of potential increased or decreased species diversity. To date, the relative contribution of colonisations and extirpations to range shifts and local turnover of species have been investigated in a wide range of taxa and ecosystems (e.g. Bakkenes *et al.*, 2002; Erasmus *et al.*, 2002; Peterson *et al.*, 2002; Thuiller *et al.*, 2005; Cheung *et al.*, 2009). Nevertheless, few of these studies attempted to relate both shrinking and expanding ranges to specific drivers, while most of them focused on range contractions (i.e. increased extinction risk) (e.g. Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Brook *et al.*, 2009). Among them, Thuiller *et al.* (2005) showed that species loss may be positively correlated to accumulated warmth and decreased moisture availability across Europe.

Although disentangling the relative importance of synoptic (and often synergic) changes in environmental variables on geographical species responses is a major goal of current research (Brook *et al.*, 2009), the identification of specific environmental and climatic features affecting either colonisation or extirpation events remains to date poorly explored. Filling this gap may be particularly important for the development of well-advised conservation strategies of climate-sensitive species (Heller & Zavaleta, 2009). From a management perspective, colonisations and extirpations do not represent simple antinomies, but imply different adapting approaches deriving from the underlying responses of species coping with a changing climate (Hoegh-Guldberg *et al.*, 2008). Under a warming climate, species at their upper thermal limit may disappear rapidly after the loss of suitable habitat, while colonisation of new climatic favourable patches may not be straightforward (Jackson & Sax, 2009). Range shifts may be hindered by species dispersal abilities, landscape fragmentation, physical barriers and population survival in the new colonised patches which all contribute to delay the expansion at the leading edge (Warren *et al.*, 2001). This colonisation credit (i.e. the number of species committed to eventual immigration, Jackson & Sax, 2009) represents a great challenge for conservation, which may be cashed more rapidly by enhancing population survival (e.g. enlarging patch size and number of dispersing individuals) and facilitating range expansions through increased landscape-scale connectivity (e.g. corridors or matrix management, Lawson *et al.*, 2012).

In the present study, we used SDMs to model climate-induced changes in freshwater fish distributions in French rivers by 2080s in order to investigate the different pressures acting on species persistence. Starting from the assessment of the relative contribution of shrinking and expanding ranges to the species turnover, the main objectives were (i) to investigate spatial patterns in colonisation and extirpation events along the hydrographical network and (ii) to relate both processes to topographic and climatic predictors, quantifying the effects of these different drivers of species' range expansion and contraction.

METHODS

Study area

This study was conducted at the scale of the French hydrographical network. Geo-referenced data for 103790 river segments within French borders were extracted from the Catchment Characterisation and Modelling [CCM2, Version 2.0 (Vogt *et al.*, 2007)] database, a coding system for European continental waters (i.e. coastlines, rivers, river branches, watersheds and islands).

Biotic and abiotic data

Fish data

Fish data were provided by the French National Agency for Water and Aquatic Environment (Onema), which is the national fisheries organization in charge of the protection and conservation of freshwater ecosystems in France. Sampling records collected between 2000-2010 were pooled into a single dataset to avoid pseudo-replication and current distributions of fish species were based on a subset of 1038 well-sampled sites, for which at least 3 electro-fishing samplings were performed in the period 2000-2010. We used presence and absence records of the 40 most common species (i.e. occurring in at least 5% of the sites) (Appendix 1) belonging to 13 families, among which Cyprinidae represented by far the most abundant family, with 22 species.

Climate data

Six climatic variables were extracted from the WORLDCLIM Version 1.4 (Hijmans *et al.*, 2005) database, at a 30 arc-second resolution grid: temperature seasonality (Tsea), mean temperature of the warmest quarter (Twar), mean temperature of the coldest quarter (Tcol), precipitation seasonality (Psea), precipitation of the wettest quarter (Pwet) and precipitation of the driest quarter (Pdry).

Future climate predictions for each of the selected climatic descriptors were extracted for the time period 2051-80 (referred as the 2080s scenario) and derived from three General Circulation Models (GCMs): HadCM3 (Hadley Centre for Climate Prediction and Research's General Circulation Model), CGCM2

(Canadian Centre for Climate Modelling and Analysis), and CSIRO-MK2 (Australia's Commonwealth Scientific and Industrial Research Organization). For each GCM, two greenhouse emissions scenarios (GES) from the Special Report on Emission Scenarios of the Intergovernmental Panel on Climate Change (IPCC SRES) were used, namely the A2A (high energy requirements-emissions) and the B2A (low energy requirements-emissions), for a total of six coupled GCM-GES scenarios for 2080s.

A Principal Component Analysis (PCA) was performed on the six climatic variables, which were pooled into a single dataset encompassing current climate conditions and the six future scenarios. The first three axes of the PCA (PCA1, PCA2, PCA3) were then used as individual predictors.

Topographic data

Four variables were used to describe the hydrographical network: surface area of the drainage basin above the sampling site (Sdb, km²), cumulated length of the upstream flow network (Clf, *m*), river slope (Slo, ‰), and altitude (Alt, *m*). Among these, two predictors were synthesized into an individual variable describing the longitudinal gradient (*G*), derived from the first axis of a PCA on Sdb and Clf. Generalized additive models (GAM) were then fitted between each of the three topographic (G, Alt, Slo) and climate (PCA1, PCA2, PCA3) variables in order to remove the strong correlations between them. Residuals of these three models were then used as individual predictors describing environmental variability, independent of climate (see Buisson *et al.*, 2008; 2010).

Ensemble forecasting of species distribution

The dataset of 1038 sites was split into a calibration set (2/3 of the original data) and a validation set (1/3 of the original data), preserving an homogeneous number of sites belonging to different river basins within the two datasets. This splitting procedure was repeated 50 times. For each iteration, seven statistical methods were used to infer the distribution of the 40 selected species: generalised linear models (GLM), generalised additive models (GAM), multivariate adaptive regression spines (MARS), mixture discriminant analysis (MDA), random forests (RF), generalised boosted trees (GBM), and artificial neural networks (ANN). Calibrated models were used to predict the current distribution of the 40 fish species at the scale of the French hydrographical network and to project future potential habitat suitability for the species under the six coupled GCM-GES scenarios (i.e. assuming an unconstrained dispersal). We used a consensus method based on the average value of the ensemble modelling predictions, an attractive modelling framework as it reduces the predictive uncertainty of single statistical models by combining their predictions (Araújo *et al.*, 2005; Grenouillet *et al.*, 2011). For each river segment, the current averaged probabilities of occurrence of the 40 species were then transformed into presence-absence data using a threshold maximising the sum of sensitivity (i.e. percentage of presence correctly predicted) and specificity (i.e. percentage of absence correctly predicted) (Fielding & Bell, 1997). Future probabilities of occurrence were also transformed into presence–absence values by using the same threshold value as for current predictions. The predictive accuracy of the seven single models and the 'consensus model' was tested using the area under the curve (AUC) of a receiver operating characteristic (ROC) plot. Paired *t*-tests with correction for multiple testing were performed on AUC values to rank model performances (Benjamini & Hochberg, 1995), showing that consensus models outperformed single models ($P < 0.001$), with the exception of RF providing comparable predictions (Appendix 2). Information about the performance measures of the consensus models are given in the supplementary data (Appendix 1).

Spatial patterns in species richness, turnover, colonisations and extirpations

Coefficient of variation (CV) of predictions across the six consensus models was computed to assess the congruence of spatial patterns obtained with the different scenarios, while variability in current species richness was quantified by the CV of the summed occurrences predicted in the 50 iterations, following a ‘predict first, assemble later’ strategy (Ferrier & Guisan 2006). Finally, for each river segment, species turnover rate was computed as following:

$$\text{turnover} = 100 \times (SG+SL)/(SR+SG)$$

where SR is the current species richness, SG is the species gain (number of colonising species) and SL is the species loss (number of extirpated species) (Peterson *et al.*, 2002; Broennimann *et al.*, 2006). Turnover values range from 0 (i.e. current and future assemblages are identical) to 100 (i.e. current and future assemblages are completely different).

Drivers of turnover, colonisation and extirpation

We performed RF to model species turnover (RFtur), colonisations (RFcol) and extirpations (RFext). Based on its mathematical formulation, species turnover was modelled from three input variables (SR, SG and SL), while RFcol and RFext were calibrated using the whole set of topographic (G, Alt, Slo) and climatic predictors, the latter being represented by climatic anomalies, i.e. the change between future and current conditions (ΔTsea, ΔTwar, ΔTcol, ΔPsea, ΔPwet, ΔPdry) (see Appendix 3 for climatic anomalies maps). Similarly to the SDM procedure described above, 2/3 of the dataset were used to calibrate the models, while the remaining 1/3 was used as the validation subset. The splitting procedure was repeated 10 times. The relative influence (i.e. importance) of individual predictor variables in the models was estimated by looking at the prediction error (mean squared error, MSE) on the out-of-bag (oob) portion of the data, after permuting the predictor variable while all other variables are left unchanged. The increase in oob error is proportional to the predictor variable importance (Peters *et al.,* 2007). Finally, partial dependence plots of responses to individual predictor variables, derived from the best RF model among the 10 iterations, were used to interpret the marginal effect of each variable in the model, after accounting for the average effects of other variables.

RESULTS

Spatial patterns in species richness, turnover, colonisations and extirpations

Current species richness was highest in the main channels of large rivers (e.g. Garonne, Rhone, Loire and Seine rivers) while lower richness was observed along the English Channel coast, Brittany and in all the French mountainous areas (e.g. Pyrenees, Massif Central, Alps and Vosges mountains) (Fig. 1a). Predictions were generally congruent (CVSR = 0.34 ± 0.19), and particularly for those river segments hosting a large number of species. High species turnover rates were observed over the whole hydrographical network (mean ~60%) (Fig. 1b), although lower values were observed in the Alps, along the Mediterranean coast, and in Brittany, as well as in high-order rivers. As for species richness, projections of taxonomic turnover were generally congruent (CVtur = 0.32 ± 0.34) with higher variability of projections in mountainous areas (e.g. the Massif Central, the Alps and the Pyrenees). Colonisation and extirpation events displayed clearer spatial patterns compared to turnover (Fig. 1c-d). Colonisations showed three main hotspots associated with the foot of Pyrenees in southern France, the Massif Central and the Vosges mountains in North-Eastern France, while extirpations showed higher values in Western and North-Western France plains. The degree of agreement among scenarios was also spatially heterogeneous (CVcol = 0.51 ± 0.35; CVext = 0.65 ± 0.71). As for species turnover, colonisations projections were less congruent in mountainous areas, while for extirpations, projections showed higher discrepancies at intermediate altitudes, lining the principal mountainous areas, and in two coastal areas, along the Mediterranean and at the extreme edge of Brittany.

Colonisation and extirpation events also involved a different number of species, with more species immigrating in newly favourable river segments (up to 31 among the 40 species analysed) compared to those extirpated from currently occupied segments (maximum 20 species) (Fig. 2). Nevertheless, extremely high numbers of colonisations and extirpations were predicted only for a reduced fraction of hydrographical network (i.e. only ~3% of river segments were predicted to be colonised by 20 or more species, or to be abandoned by 10 or more species).

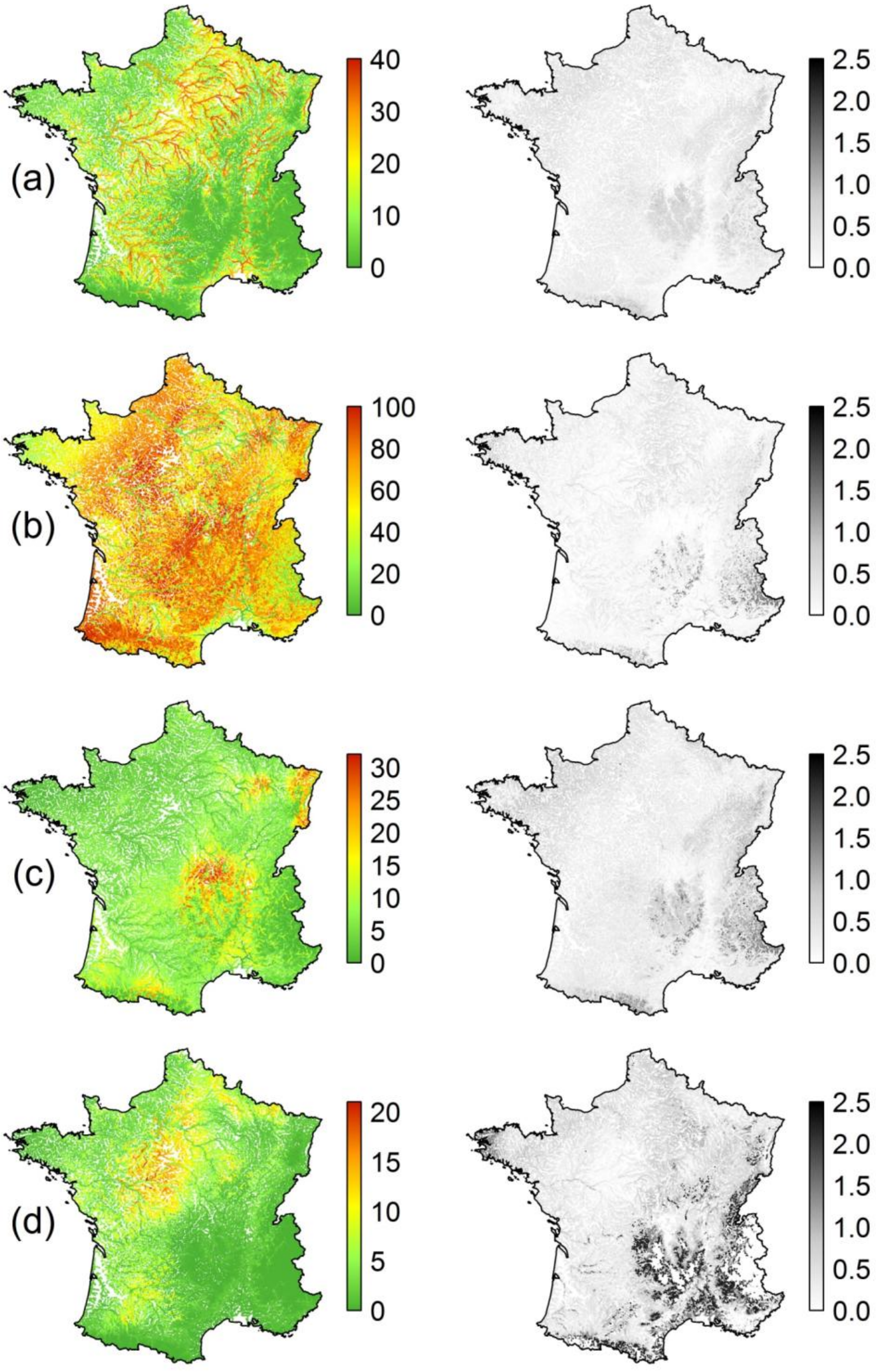

Figure 1 Maps of the average model outputs for the French hydrographic network (left) and relative spatial congruence among the projections (right). Spatial congruence is represented by the coefficient of variation (CV) computed among the 50 iterations outputs (for current projections) or among the 6 GCM-CES scenarios outputs (for 2080s projections). (a) current species richness; (b) species turnover (%); (c) number of colonisation events and (d) number of extirpation events by 2080s.

Drivers of turnover, colonisations and extirpations

Performances of RF models predicting species Performances of RF models predicting species turnover were good (R^2_{tur}= 0.96 ± 0.001). Current species richness emerged as the most influencing factor (Fig. 3a), showing a linear negative relationship with species turnover, with the highest taxonomic variation expected for the originally poorest communities (Fig. 3b). Colonisation and extirpation events showed similar effects on species turnover (Fig. 3a), with both species loss and gain determining an increased turnover (Fig. 3b).

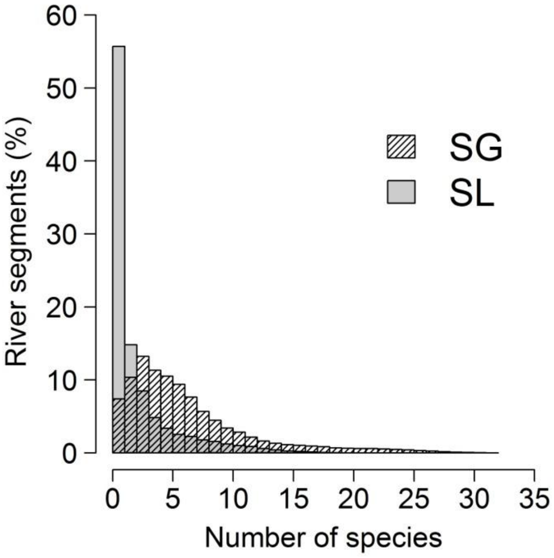

Figure 2 Frequency of colonisation (species gain, SG) and extirpation (species loss, SL) events in the French hydrographic network.

Performances of RF models predicting colonisation and extirpation were also good (R^2_{col}= 0.95 ± 0.001; R^2_{ext}= 0.93 ± 0.001). Topographic variables emerged as the most important predictors for modelling both species gain and loss (Fig. 4). In particular, longitudinal gradient outperformed any other input variable in predicting both colonisation and extirpation events, followed by altitude, while slope played a stronger role in driving colonisations compared to extirpations (Fig. 4a). Although colonisation events occurred along the whole range of altitudes (0-2600m), the peaks in species gain and loss were segregated along longitudinal and altitudinal gradients, with colonisations occurring mainly upstream (lower *G* values) and at higher altitudes compared with extirpations (Fig. 5). In fact, colonisation showed a peak around 460 m above the sea level (Fig. 5a), while the number of extirpation events sharply decreased at mid altitudes, with the highest number of species disappearing from lowland river segments (< 80 m) (Fig. 5b).

Overall, climatic variables played a minor role compared to topographic variables (Fig. 4). Among them, changes in temperature seasonality showed the highest contribution to colonisation events, with strong increase in variability favouring species gain (Fig. 4a and 5a). In contrast, the number of extirpation events depended both on changes in temperature and precipitation (Fig. 4b). In particular, increase in average temperature in the coldest quarter and stable precipitation in the driest quarter contributed to species loss (Fig. 5b).

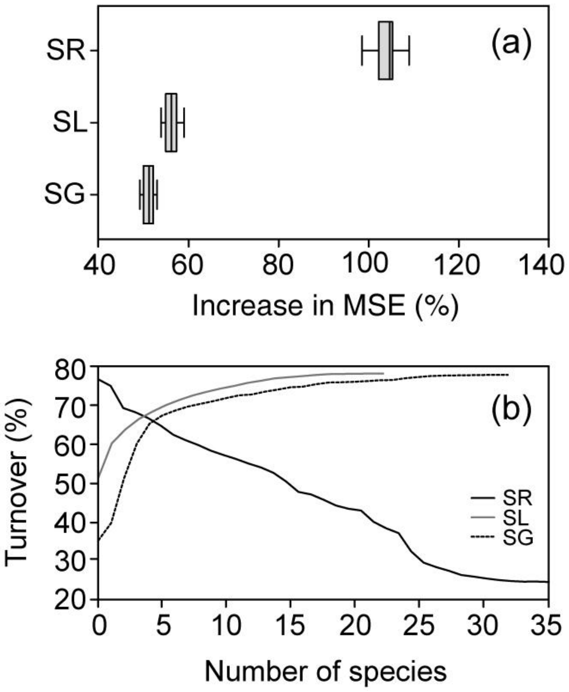

Figure 3 (a) Box-and-whiskers plot of the percentage variation of mean squared error (MSE) of RFtur output after permutations, among the 10 iterations. The input variables are ranked according to their importance in predicting turnover of species assemblages. (b) Partial dependence plot of the input variables: original species richness (SR, black solid line), average number of extirpation events (SL, grey solid line) and average number of colonisation events (SG, black dashed line). Partial dependence is the dependence of the probability of presence on one predictor variable after averaging out the effects of the other predictor variables in the model (Cutler *et al.*, 2007).

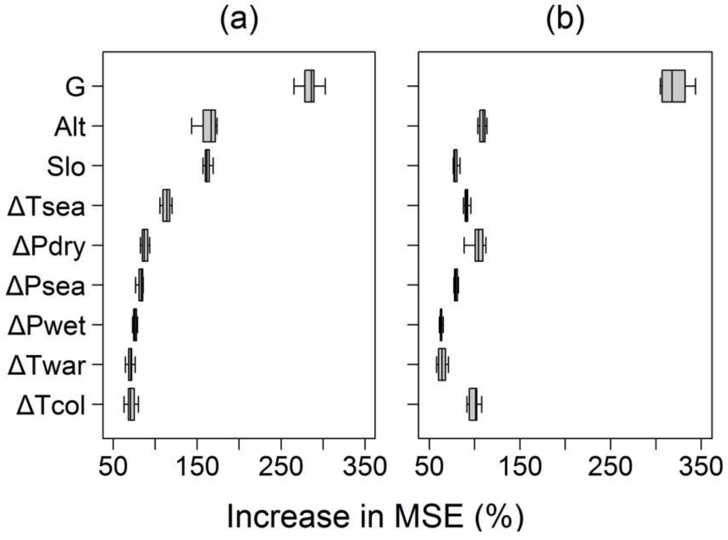

Figure 4 Box-and-whiskers plot of the percentage variation of mean squared error (MSE) of (a) RF_{col} and (b) RF_{ext} outputs after permutations, among the 10 iterations. The input variables are ranked according to their importance in predicting colonisation events.

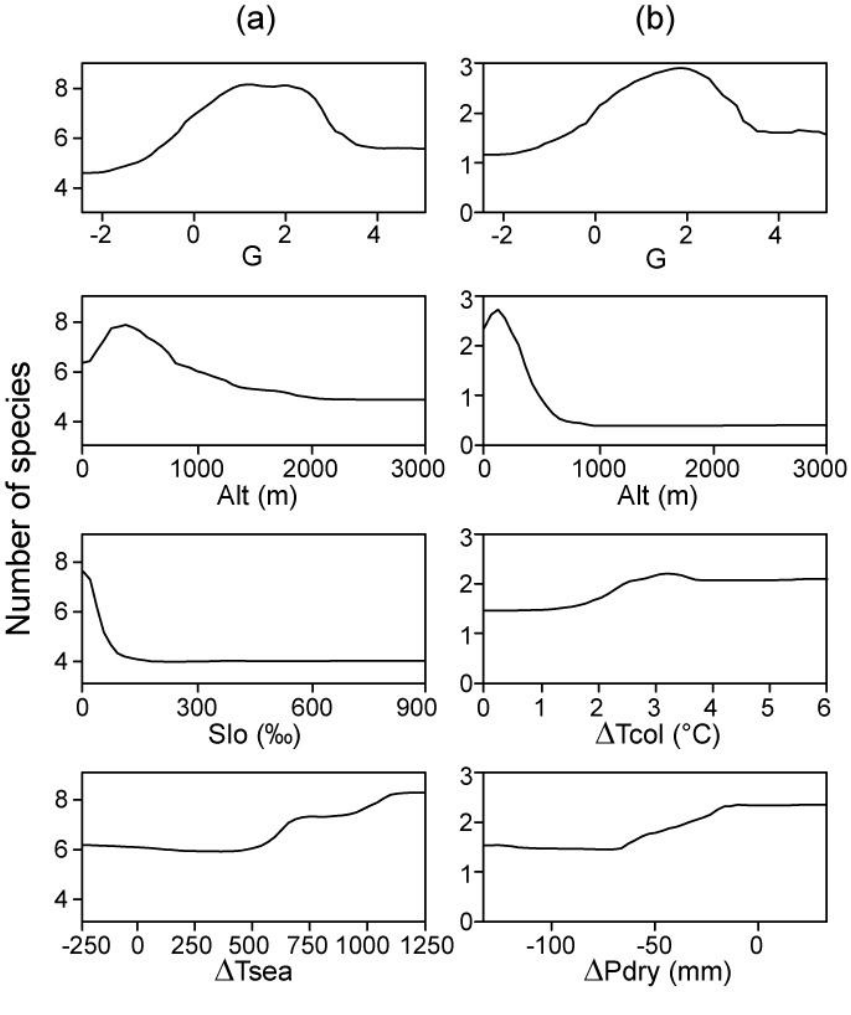

Figure 5 Partial dependence plot of the four most important input variables driving (a) colonisation and (b) extirpation. Species gain was mainly affected by the three topographical variables [longitudinal gradient (*G*), altitude (*Alt*) and slope (*Slo*)] and by changes in temperature seasonality (*ΔTsea*), while species loss was driven by elevational gradient, changes in average temperature in the coldest quarter (*ΔTcol*) and in average precipitation in the driest quarter (*ΔPdry*).

DISCUSSION

With this study we showed that future climate change might induce severe reorganisation of freshwater biodiversity patterns, resulting from spatially non-random species loss and gain, driven by both topography and climatic predictors. By decomposing the mechanisms driving changes in turnover of species assemblages, we observed that beside current species richness, both extirpation and colonisation events similarly influenced the taxonomic rearrangement of communities. This finding contrasts with the overriding influence of colonisation on turnover patterns described in other studies (Buisson & Grenouillet, 2009; Cheung *et al.,* 2009). Species turnover rates indicated that more than half of the current pool of species may be changed over the whole hydrographical network. Nevertheless, the greatest number of colonisation events suggested that range expansion may be more common that range contraction, a pattern commonly observed as a result of ongoing climate change (Parmesan *et al.,* 2005; Cheung *et al.,* 2009).

Species gain and loss displayed spatially structured (i.e. patchy) patterns, with colonisations concentrating along the major mountainous systems, while extirpations were principally predicted in Western France plains. Species loss was also predicted to be higher in lowland rivers, which generally host more diverse fish assemblages compared to upstream stretches (Horwitz, 1978). Spatial segregation of colonisation and extirpation events along altitudinal gradient has already been observed across a wide range of taxonomic groups (Peterson *et al.,* 2002; Chen *et al.,* 2011), including stream fishes (Comte & Grenouillet, 2013). An exception to this general pattern was represented by the low occurrence of colonisations in the Alps. This discrepancy may be linked to a combination of different temperature and precipitation scenarios predicted for Eastern France compared with the other mountainous systems. Shifts in precipitation regimes may be expected to have an even greater impact on ecosystem dynamics than temperature (Weltzin *et al.,* 2003), especially in freshwater ecosystems, where precipitations determine the hydrological regimes having direct and indirect effects on the biota (Poff, 1992). Thus, although an upward shift of communities along spatial gradients is expected as a consequence of climate tracking (Tingley *et al.,* 2009), the interaction with complex patterns of regional climate change may ultimately determine the magnitude and direction of species responses (Dowbroski *et al.,* 2012; Tingley *et al.,* 2012; VanDerWal *et al.,* 2013).

Topographic variables emerged as the strongest drivers of both species gain and loss. Nevertheless, colonisation and extirpation appeared to be affected by different facets of climate change, with expanding ranges being influenced by changes in temperature seasonality while shrinking ranges were related to changes in both temperature and precipitation patterns. These findings could have important implications for ecosystem monitoring and conservation planning, while the effects of different drivers on single-species responses need further studies, exploring the additional influence of species characteristics on their vulnerability to future climate change (Thuiller *et al.,* 2005).

In this study, climate change was taken as the principal driving force of species distribution, although at more local scales strong species interactions may override regional processes (He *et al.,* 2005). However, previous studies on freshwater ecosystems support the idea that stream fish communities are not fully saturated, suggesting that biotic interactions are unlikely to prevent colonisation and biotic homogenization at some spatial scale (Oberdorff *et al.,* 1998; Olden & Rooney, 2006). In addition, our models assuming unconstrained species' dispersal, the range of future suitable habitat might not be entirely available for the species (Peterson, 2003). Indeed, compared to other terrestrial or marine vagile species, the constrained dendritic structure of river networks strongly reduce the range of geographical responses that may derive from niche tracking of complex hydrological changes. Further barriers to dispersal originate from the high levels of natural and anthropogenic fragmentation of favourable habitats (Fagan, 2002). For instance, lack of elevational refugia imposed by low connectivity or steep slopes may preclude upstream movements of warm- or cold-water fish, which may result in an overestimation of the number of predicted colonisation events (Hein *et al.,* 2011). Finally, other aspects of anthropogenic disturbances (e.g. urbanisation and water development) may add to global warming trends, magnifying thermal threats on already affected populations, especially in lowland river stretches (Isaak & Rieman, 2013).

Disentangling the drivers of colonisation and extirpation processes overcome the challenge of considering idiosyncratic responses of species to changed climate conditions which represent a major issue for ecosystem management plans (Ackerly *et al.,* 2010). By contrast, the identification of focal areas of greater expected changes, driving either species gain and loss, could represent a ready-to-use information to be integrated into conservation planning. Maps of future scenarios of those climate facets driving colonisation may support an early evaluation of the extrinsic limitations on species ability to reach newly favourable habitat, and therefore help to immediately incorporate land use constraints to species movement into dynamic planning (Early & Sax, 2011; Lawler *et al.,* 2013).

Our findings reveal that topographical and climatic predictors both triggered species range shifts, driving potential modifications of species geographical distribution. Nevertheless, species climatic paths tracking favourable conditions pass through a human dominated world, where ecosystems are highly fragmented and modified (Opdam & Wascher, 2004; Lawler *et al.*, 2013). In this context, we argue that large scale climate projections should be linked to local landscape, in order to develop new tools for early identification of needs and opportunities of climate-sensitive species and to reduce the potential delay for cashing the immigration credit.

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SUPPORTING INFORMATION

Table S1 List of the 40 fish species used in the study. Percentage of occurrence in the calibration dataset and consensus model performances are given. See also Figure S1 for a comparison between single statistical model performances and the consensus model.

Family	Scientific name	Occurrence	AUC	PCC	Sensitivity	Specificity
Anguillidae	*Anguilla anguilla*	52%	0.92	0.84	0.82	0.86
Centrarchidae	*Lepomis gibbosus*	35%	0.86	0.82	0.79	0.81
	Micropterus salmoides	7%	0.89	0.80	0.89	0.80
Cobitidae	*Cobitis taenia*	7%	0.88	0.84	0.86	0.84
Cottidae	*Cottus gobio*	56%	0.82	0.76	0.73	0.80
Cyprinidae	*Abramis brama*	30%	0.91	0.82	0.86	0.80
	Alburnoides bipunctatus	21%	0.87	0.79	0.84	0.78
	Alburnus alburnus	37%	0.92	0.85	0.87	0.84
	Barbus barbus	37%	0.93	0.87	0.89	0.85
	Barbus meridionalis	7%	0.94	0.82	0.96	0.82
	Blicca bjoerkna	27%	0.90	0.82	0.84	0.81
	Carassius auratus auratus	6%	0.73	0.66	0.76	0.65
	Carassius carassius	22%	0.84	0.77	0.82	0.75
	Chondrostoma nasus	21%	0.95	0.86	0.95	0.84
	Cyprinus carpio	28%	0.85	0.77	0.81	0.75
	Gobio gobio	65%	0.88	0.80	0.74	0.89
	Leucaspius delineatus	10%	0.82	0.72	0.83	0.71
	Leuciscus leuciscus	44%	0.90	0.83	0.88	0.79
	Phoxinus phoxinus	66%	0.78	0.72	0.71	0.75
	Parachondrostoma toxostoma	10%	0.85	0.76	0.83	0.76
	Pseudorasbora parva	10%	0.87	0.78	0.83	0.78
	Rhodeus amarus	21%	0.90	0.81	0.90	0.79
	Rutilus rutilus	56%	0.90	0.82	0.79	0.86
	Scardinius erythrophthalmus	35%	0.85	0.78	0.79	0.78
	Squalius cephalus	63%	0.90	0.82	0.77	0.90
	Telestes souffia	11%	0.92	0.81	0.95	0.80
	Tinca tinca	36%	0.86	0.78	0.83	0.76
Esocidae	*Esox lucius*	38%	0.90	0.82	0.84	0.82
Gasterosteidae	*Gasterosteus aculeatus*	20%	0.81	0.69	0.87	0.66
	Pungitius pungitius	15%	0.89	0.78	0.83	0.78
Ictaluridae	*Ameiurus melas*	17%	0.86	0.77	0.84	0.76
Lotidae	*Lota lota*	8%	0.90	0.80	0.94	0.79
Nemacheilidae	*Barbatula barbatula*	67%	0.82	0.77	0.76	0.78
Percidae	*Gymnocephalus cernua*	23%	0.92	0.86	0.86	0.87
	Perca fluviatilis	47%	0.89	0.82	0.82	0.82
	Sander lucioperca	19%	0.89	0.83	0.81	0.83
Salmonidae	*Salmo salar*	12%	0.90	0.86	0.83	0.87
	Salmo trutta	78%	0.85	0.76	0.75	0.80
	Thymallus thymallus	8%	0.85	0.76	0.86	0.75
Siluridae	*Silurus glanis*	14%	0.95	0.90	0.90	0.90

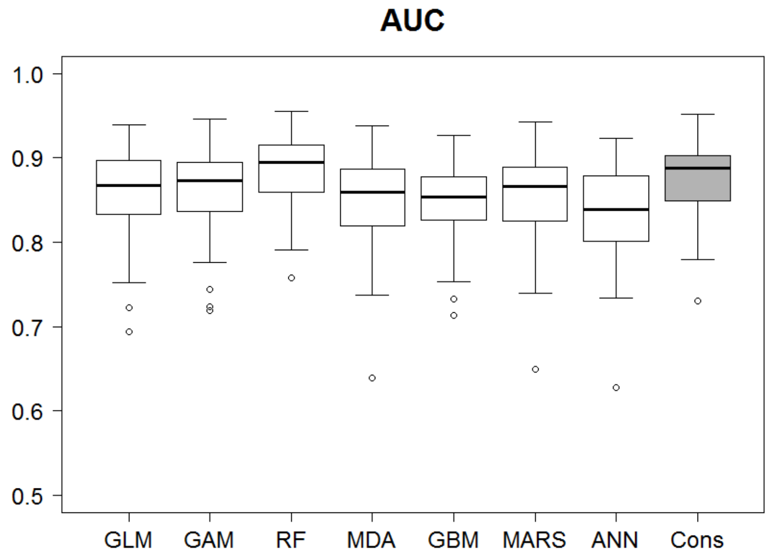

Figure S1 Box-and-whiskers plot of model performances (AUC) for the 40 fish species analysed. From left to right, generalised linear models (GLM), generalised additive models (GAM), random forests (RF), mixture discriminant analysis (MDA), general boosted trees (GBM), multivariate adaptive regression spines (MARS) and artificial neural networks (ANN). The last box (grey) refers to the 'consensus model' (Cons).

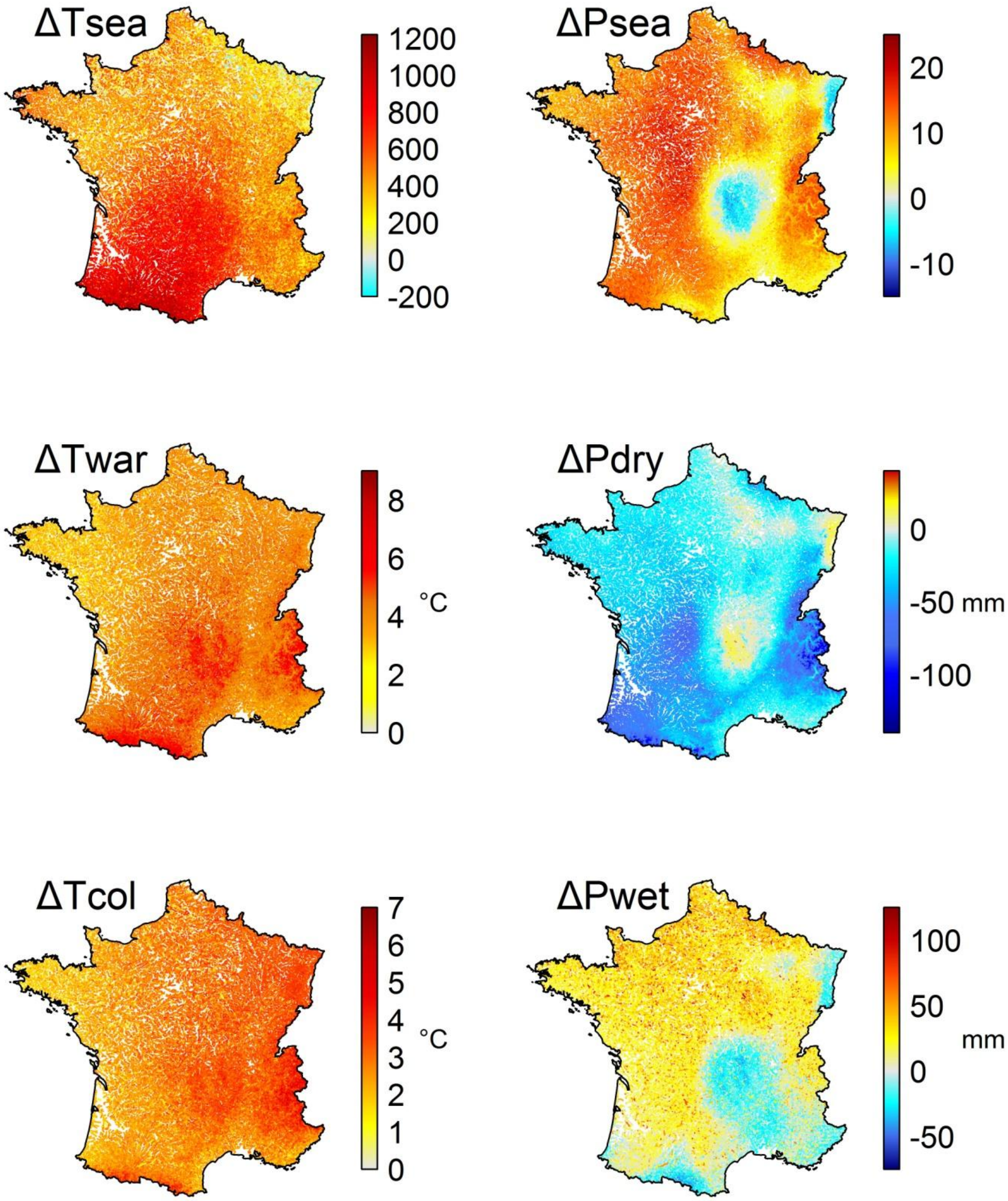

Figure S2 Anomalies of the six climatic variables used to calibrate the models temperature seasonality (*Tsea*), mean temperature of the warmest quarter (*Twar*), mean temperature of the coldest quarter (*Tcol*), precipitation seasonality (*Psea*), precipitation of the wettest quarter (*Pwet*) and precipitation of the driest quarter (*Pdry*). Values go from strong decrease (blue) to strong increase (red) between current and 2080s scenario.

GLOBAL CHANGE AND SPATIAL DISTRIBUTION OF FRESHWATER FISH: RECENT TRENDS AND FUTURE PREDICTIONS

ABSTRACT

Despite increasing recognition that recent climate changes are influencing biodiversity, the specific impacts of those changes are still largely unknown. This thesis highlights systematic stream fish species shifts towards higher elevation and upstream habitats, consistent with the geographic variation associated with climate change. The results demonstrated, however, that patterns in climate-driven range shifts were less marked than those attributed to non-climatic drivers, suggesting more severe longer-term effects of climate warming on stream fish and profound consequences on the ability of species to cope with future climate modifications. Nevertheless, the results also provide evidence that several mechanisms are linked to species' evolutionary history and some key biological and ecological traits, allowing species to persist *in situ* or to track their climatic niche through space. These research findings improve our ability to anticipate future climate change-induced impacts and will assist with initiating effective conservation and management strategies, which can no longer be effectively designed without taking into account climate change.

AUTEUR : Lise COMTE

TITRE : CHANGEMENTS GLOBAUX ET DISTRIBUTION SPATIALE DES ESPECES DE POISSONS D'EAU DOUCE : OBERVATIONS RECENTES ET PREDICTIONS FUTURES

DIRECTEUR DE THESE : Gaël GRENOUILLET

LIEU ET DATE DE SOUTENANCE : Université Paul Sabatier le 13 Décembre 2013

RESUME

Les changements climatiques actuels reçoivent une attention grandissante mais leurs impacts sur la biodiversité restent mal appréhendés. Cette thèse a permis de mettre en évidence une réponse cohérente des poissons d'eau douce au réchauffement climatique des dernières décennies se traduisant par des remontées en altitudes et vers les sources. Il est cependant apparu que des facteurs non-climatiques avaient majoritairement contribué aux changements observés, ce qui pourrait indiquer l'existence de délais importants dans la réponse des espèces et avoir des conséquences importantes pour leur capacité à faire face aux changements climatiques à venir. Néanmoins, certains mécanismes en lien avec des caractéristiques clés des espèces et leur histoire évolutive semblent conditionner leur capacité à persister *in situ* ou à suivre leur niche climatique. Ces résultats pourraient avoir des implications importantes quant à notre capacité à anticiper les changements à venir et à initier des politiques de gestion adaptées, dont les missions futures ne peuvent désormais plus être conçues sans tenir compte de l'évolution du climat.

MOTS-CLES : Changements de distribution; Changements climatiques; Poissons de rivière; Limites de distribution; Vulnérabilité; Colonisation; Extinction

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DISCIPLINE ADMINISTRATIVE : ECOLOGIE

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