

LETTER

Non-native species disrupt the worldwide patterns of freshwater fish body size: implications for Bergmann's rule

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Abstract

In this study, we test whether established non-native species induce functional changes in natural assemblages. We combined data on the body size of freshwater fish species and a worldwide data set of native and non-native fish species for 1058 river basins. We show that non-native fish species are significantly larger than their native counterparts and are a non-random subset of the worldwide set of fish species. We further show that the median body size of fish assemblages increases in the course of introductions. These changes are the opposite of those expected under several null models. Introductions shift body size patterns related to several abiotic factors (e.g. glacier coverage and temperature) in a way that modifies latitudinal patterns (i.e. Bergmann's rule), especially in the southern hemisphere. Together, these results show that over just the last two centuries human beings have induced changes in the global biogeography of freshwater fish body size, which could affect ecosystem properties.

Keywords

Bergmann's rule, communities, ecosystem function, freshwater ecosystems, invasion, invasive species, latitudinal gradients, macroecology, null model, species extinction.

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INTRODUCTION

In a lapse of time covering just two centuries, the introduction of non-native species has strongly increased worldwide (Ricciardi 2007). Established non-native species [i.e. introduced species that have established self-sustaining populations (ENNS)] have modified almost all ecosystems worldwide (Ricciardi 2007) and can alter spatial patterns of biodiversity (McKinney & Lockwood 1999).

To date, most research has focused on the taxonomic dimension of biodiversity and a further step would be to

consider non-native species within a multidimensional definition of biodiversity, including both the taxonomic and functional changes experienced through the introduction process. Although little attention has been devoted to this last aspect, it will undoubtedly give important insights (Purvis & Hector 2000; Gaston & Blackburn 2003). For instance, established non-native fish species are characterized by a high physiological tolerance and functional attributes differing from those of invaded communities (Moyle & Marchetti 2006). This parallels the work of Olden *et al.* (2006) on the Colorado River Basin,

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demonstrating that although native and non-native fish species share similar life histories, those occupying vacant niche positions in the life history space spread more rapidly than others. Furthermore, ENNS have been reported to affect functional diversity (i.e. the functional role species play in an ecosystem) of communities, and this can have strong cascading effects on the way the ecosystem functions (Hooper *et al.* 2005; Smart *et al.* 2006).

Potential functional changes induced by ENNS are expected to be non-random because ENNS are themselves not a random subset of the functional diversity observed within a taxonomic group (Cassey 2001; Rahel 2007). Non-randomness in the establishment of non-native species is partly a consequence of human selection of the species to be introduced (Jeschke & Strayer 2006). With regards to body size (a synthetic functional trait; Woodward *et al.* 2005), most vertebrate ENNS have been shown to be a non-random subset of the worldwide pool of species (Cassey 2001; Blackburn & Cassey 2007). All else considered equal, this non-random selection should lead the recipient communities to deviate away from their original states. Such directed selection could affect historically based spatial patterns of body size. For instance, Bergmann's rule stipulating that mean body size of most vertebrate communities tends to be smaller at low latitude (Bergmann 1847), may hence be disturbed by the establishment of non-native species.

In this study, we tested if ENNS are a major driver of functional changes (i.e. changes in body size distribution) in freshwater fish assemblages on a worldwide scale. Using information on the body size of most freshwater fish species, we first tested the hypothesis that fish ENNS are a non-random subset of the worldwide set of species. Fish are strongly associated with human diet and activities (e.g. aquaculture and angling), and large-bodied species are preferentially introduced in watersheds (Rahel 2007). We thus predicted that fish ENNS would be significantly larger than the worldwide set of species, and drive fish assemblages to a larger mean body size. We tested this prediction by comparing the median body size of the assemblage (BSA), of 1058 natural assemblages (i.e. 1058 river basins) distributed worldwide, before and after introduction. We further compared this result with the output of null-model simulations. In addition, we evaluated the relationships between several global scale factors (i.e. temperature, productivity and glacier coverage) and the latitudinal gradient of BSA (i.e. Bergmann's rule). Finally, we tested the hypotheses that these non-random choices imposed by human beings are strong enough to disrupt Bergmann's rule, and that non-native species establishment is an important process in explaining these new patterns.

MATERIAL AND METHODS

Databases

We used the worldwide database of freshwater fish occurrences per river basin described elsewhere (Leprieur *et al.* 2008). Briefly, we conducted an extensive literature survey of native and established non-native freshwater fish species check lists. Our database contains species occurrence data for the world's freshwater fish fauna on the river basin scale; i.e. 1058 river basins covering more than 80% of Earth's surface, and 9750 species corresponding to 80% of all freshwater species described. We considered as ENNS a species (1) that did not historically occur in a given basin and (2) that was successfully established, i.e. self-reproducing populations. By crosschecking the IUCN Red List (Baillie *et al.* 2004), FishBase (<http://www.fishbase.org>) and our own literature survey, we also indicated whether some native species have been extirpated (i.e. species extinctions from a given river basin that occurred in the two last centuries, whatever the cause). In total, we found 588 river basins containing at least one fish ENNS, and 53 river basins with at least one extirpated species. Fish species body size was based on maximum total body length from FishBase (89.5% of our whole set of data was informed, i.e. 8730 of 9750 species).

Environmental data

For each river basin we extracted the mean longitude and latitude from a Global Information System (Vörösmarty *et al.* 2000a,b). As the underlying mechanisms explaining interspecific spatial variation of BSA remain to be tested for fish (Belk & Houston 2002; Knouft 2004; Kozłowski *et al.* 2004), we crosschecked the literature for relevant hypotheses. We collected four environmental variables to test the hypotheses we propose (see below) to explain Bergmann's rule (Blackburn *et al.* 1999; Olalla-Tarraga *et al.* 2006; Meiri & Thomas 2007). The first hypothesis (temperature hypothesis) states that fish raised at low temperature mature at larger sizes. As size at maturity is a good proxy of maximum body size, the temperature decrease from the equator to the poles should produce a cline of increasing maximum body size with increasing latitude (Kozłowski *et al.* 2004). The mean annual air temperature was calculated for each river basin to test this hypothesis. Air temperatures were used as a substitute for water temperatures, as it has been demonstrated that air and river water temperatures are strongly correlated (Caissie 2006). The second hypothesis (the primary productivity hypothesis) states that energy availability could act positively on body size as it must be maintained by a sufficient food supply (Rosenzweig 1968; Olalla-Tarraga *et al.* 2006). The mean actual evapotranspi-

ration and the net primary productivity (NPP in kg carbon m⁻² year⁻¹) were used as measures of energy availability (Currie *et al.* 2004). Although NPP and evapotranspiration are terrestrial measures, they have already been shown to correlate strongly with the energy available in rivers and to influence patterns of freshwater fish species richness (Guégan *et al.* 1998). The third hypothesis (the migration ability hypothesis) states that small species will be under-represented at high latitudes because their limited dispersal abilities did not permit them to colonize these regions following the retreat of the glaciers at the end of the Pleistocene (Blackburn *et al.* 1999). To test this hypothesis, we used the percentage of maximum glacier coverage during the Quaternary glaciation periods for each river basin (Dürr *et al.* 2005). These environmental variables were extracted from 0.5 × 0.5 grid data available in the Center for International Earth Science Information Network (CIESIN; <http://www.sage.wisc.edu/>) and the Atlas of the Biosphere (<http://www.sage.wisc.edu/atlas/>) (see also New *et al.* 1999).

Statistical analysis

Hereafter, we will use maximum body length on a per-species basis to test if non-native fishes are a random subset of all fishes, while maximum body length is used on a per-basin basis (i.e. the median BSA) to test Bergmann's rule and related hypotheses. In both cases, maximum body length is ln-transformed. Because the distributions of body size are often highly right-skewed (even when ln-transformed), we computed our statistics using the median values rather than mean values. Confidence intervals (CI, 95%) around median values were calculated using a resampling test (10 000 iterations) in which we randomly selected 75% of the observed values without replacement.

Firstly, we tested for differences in maximum body size between the worldwide set of species ($n = 8730$) and the set of ENNS ($n = 435$) using a resampling test (Manly 1997). We tested if the maximum body size of the ENNS represents a random subsample of the worldwide set of species. To do so, we sampled at random and without replacement, 435 species from the 8730 species. We calculated median body size for each of 10 000 random samples (null expectation) and for the observed set of introduced species. If the observed median body size fell outside of the 95% CI (two-tailed) of the random samples, we concluded that body size of ENNS was non-random. The same framework was used to explore differences in maximum body size between the worldwide set of species and the set of extirpated species ($n = 93$). Species strongly associated with human activities (angling, aquaculture and fisheries) should be large fish species (Rahel 2007). We

conjointly tested this assertion by calculating an index of human affiliation. FishBase provides four categorical indexes of human use. They refer to the fisheries, aquaculture, game fish and ornamental importance of each species. Each index was divided into several modalities according to its magnitude of variation. We assumed that each categorical index has an equivalent importance, and we hence calculated the arithmetic average of the four indexes. This synthetic index varies between 0 (i.e. for species not used by human) and 4 (i.e. for species strongly used by human). We used Pearson correlation to test if this index was positively correlated to the body size of ENNS.

Secondly, we tested for differences in BSA in river basins before and after introduction. We calculated the BSA using (1) the data on occurrences of native and extirpated species (the assemblage before introduction) and (2) the data on occurrences of native and ENNS (the assemblage after introduction). We then compared the median of these two distributions using two-tailed resampling tests (Manly 1997). To do so we performed a resampling test (10 000 iterations) in which we randomly selected 75% of the river basins without replacement. For each iteration, we calculated the median value across all river basins and we compared the median values for the assemblages before and after introduction to obtain a P -value. This comparison was performed separately for the whole data set of river basins and for the river basins that have received at least one ENNS. Using the same approach, we then measured the changes (before vs. after introduction) in variance, skewness and kurtosis of the body size distribution of assemblages. Furthermore, to distinguish between the effect of introduction from that of extirpation, we used the same framework to explore the effect of extirpations on BSA (i.e. comparison of assemblages before and after extirpation occurred).

Thirdly, we used null-model simulations to explore the possibility that changes in the BSA observed after introductions can be due to a selective choice of ENNS by human beings. Three introduction strategies were simulated, ranging from low to high spatial and taxonomic conservatism in species selection. In null-model 1, we randomly replaced each ENNS by a species from the total worldwide fish fauna, so that the number of establishment events did not differ between real and simulated assemblages. That least conservative model simulated a totally random selection of exotic species. In null-model 2, we randomly replaced each ENNS by a species from the original distribution range of the species to be replaced. The original distribution range of each ENNS was defined as the set of river basins in which the species was recorded as native. This simulated an introduction process that keeps the main pathways of introduction realistic (i.e. spatial conservatism), and hence avoids over-sampling species-rich basins which are dominated by small-bodied species (Blanchet *et al.* 2009).

In null-model 3, we accounted for both spatial distribution and taxonomic identity of the ENNS, and this model is hence the most conservative. It checks for a greater-than-expected body size for ENNS that could result from the bias in the taxonomic composition of such species, if ENNS tend to come from families with larger than average body sizes (Blackburn & Cassey 2007). We replaced the body size of each ENNS with that of a species chosen at random from the same family and from the original distribution range of the species to be replaced. We reiterated this procedure 10 000 times for each river basin that has received at least one ENNS, and at each simulation calculated the difference between the BSA before and after introduction. For each river basin, we hence produced a distribution of 10 000 random simulated changes under the three null hypotheses that were compared (two-tailed test) to the observed changes.

Fourth, we tested if the interspecific variation of median body size follows Bergmann's rule and if this distribution is significantly affected by introductions. We built generalized linear mixed models (GLMM) in which the BSA before and after introduction was the dependent variable, the mean latitude of each river basin was the continuous predictor and the sampling period (before or after introduction) was the categorical predictor. Because each assemblage was sampled temporally (i.e. before and after introduction), the identity of the river basin was used as the random factor to account for pseudo-replication. We also included the quadratic term of the mean latitude to test for nonlinearity in the relationship between BSA and mean latitude as it is expected that the BSA will be lower at the equator and larger at the extremes. The two-term interactions between the sampling period and the latitude (single and quadratic terms) were tested to compare the slope of the relationship between latitude and BSA before and after introduction. This model was applied separately for the whole data set and for the restricted data set of river basins that had received at least one ENNS. In addition, we performed separate GLMM for river basins from the southern and northern hemispheres since it has been recently shown that the relationship between BSA and mean latitude can differ between the two hemispheres (Rodríguez *et al.* 2008).

Finally, we conjointly tested the three above cited hypotheses that are likely to explain interspecific spatial variation of body size. The whole data set of river basins was used in these analyses but we separated river basins from the southern and northern hemispheres to gain insight into mechanisms underlying the patterns observed (Rodríguez *et al.* 2008). In a first set of two models (southern and northern hemispheres), we used the BSA before introduction as the dependent variable and the four environmental variables (temperature, NPP, actual evapotranspiration and glacier coverage) as continuous predictor variables. In

addition the quadratic term of temperature was included to test for nonlinearity (Rodríguez *et al.* 2008), and the coefficient of variation of temperature (calculated from monthly data) as well as the native species richness per river basin were additional predictors (Meiri & Thomas 2007; Olson *et al.* 2009). To account for possible spatial autocorrelation in our data set, we imposed a Gaussian spatial correlation structure as random effects into the linear predictors. A second set of two models was built using the BSA after introduction as dependent variable. The same model structure was used but we added the ENNS richness per river basin as a continuous predictor, and we tested whether ENNS can drive the worldwide interspecific spatial variation of body size and thus be considered as a major hypothesis.

RESULTS

As predicted, the median body size of the 435 ENNS [32.5 cm (30.0–39.5), median (resampling 95% CI)] was significantly larger than that of the whole available set of species [12.0 cm (10.0–13.0)] (resampling test, $P < 0.001$; Fig. 1). This result shows that ENNS are not a random subset of the whole set of species. Furthermore, we detected

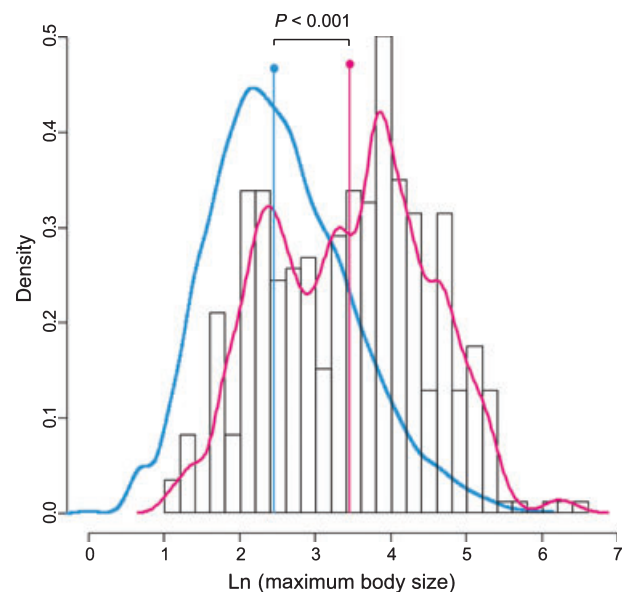


Figure 1 Density curves of size distribution [(Ln maximum body size), i.e. measured as the body length] of native (blue line) and established non-native freshwater fish (red line). Raw data for the 435 established non-native species is shown as a histogram. Raw data for the 8730 native species are not shown for clarity. Median value of native and established non-native distributions are indicated on the graph and size distributions of native and established non-native species were compared using a resampling test.

a significant bimodal distribution of the body size of ENNS [Dip statistic = 0.0256, $n = 435$, $P = 0.02$ (Hartigan & Hartigan 1985)]. The first mode paralleled the distribution peak of the whole set of species whereas the second peaked in strikingly larger body sizes (Fig. 1). In addition, we found a highly significant correlation between the body size of ENNS and the index of human affiliation ($r = 0.651$, $n = 432$, $P < 0.001$; see the Fig. S1). As already shown in fish (Olden *et al.* 2007), locally extirpated species were larger than the worldwide set of species [28 cm (21.5–35.5)] (resampling test, $P < 0.001$).

Considering all the river basins, the BSA was significantly larger after, than before introduction [$n = 1058$ river basins; before introduction, 34.63 cm (33.72–35.51); after introduction 36.85 cm (35.91–37.75); resampling test, $P = 0.002$]. This trend was even clearer when considering only the river basins that had received at least one ENNS [$n = 588$ river basins; before introduction, 34.79 cm (32.93–36.69); after introduction 38.77 cm (36.85–40.65); resampling test, $P = 0.001$]. We further found that after introduction, the distribution of BSA was significantly more variable, less skewed to the left and less peaked (Table S1).

The three null-model formulations provided significantly lower changes in BSA than those actually observed. The observed changes [$n = 588$; +3.97 cm (2.86–5.06), median change (bootstrap 95% CI)] were significantly larger than

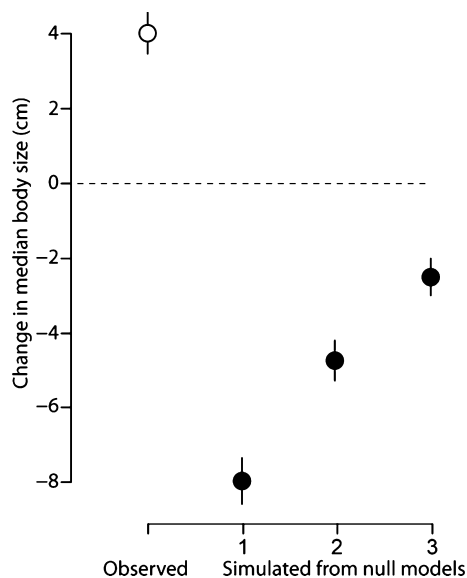


Figure 2 Change in median body size of assemblages (cm; mean \pm bootstrap 95% confidence interval) after non-native species establishment for observed and simulated assemblages from three null-models simulating three introduction strategies from low (i.e. null-model 1) to high (i.e. null-model 3) spatial and taxonomic conservatism in species selection. See Material and methods for details.

the changes simulated under the null hypotheses (Fig. 2), and even the most conservative model (which accounts for both family membership and geographical location of ENNS) provided a lower-than-observed increase in BSA [–2.54 cm (–2.97 to –2.03); resampling test $P < 0.001$, Fig. 2]. Indeed, ENNS do not result from a random sample of species, even within particular geographical localities or fish families, which would have led to a significant decrease of the BSA due to the preponderance of small species (Fig. 2). It is noteworthy that local extirpation had no significant effect on the BSA, even when we considered only river basins with at least one recorded extirpation [$n = 53$; before extirpation, 35.59 cm (30.34–40.82); after extirpation 33.24 cm (28.65–37.71); resampling test, $P = 0.744$].

By comparing the spatial patterns in BSA before and after introduction, we showed that the non-random changes reported above significantly affected the latitudinal BSA gradient. Before introduction, on the worldwide scale, we found a geographical pattern that fits Bergmann's rule, with assemblages tending to have larger body size as latitude increases (Table S1, Figs 3a and 4a). Although this global tendency was similar after introduction, the relationship between latitude and BSA before and after introduction significantly differed (see the interaction terms in Table S1, see also Fig. 3a). This was true when analysing all the river basins as well as when considering only the river basins that had received at least one ENNS (Table S1). These changes mainly occurred in the southern hemisphere, with assemblages tending to have larger species at high latitudes than observed before introduction (Table S1, Figs 3 and 4b). It is worth noting that when each hemisphere was analysed separately, we in fact showed that, before introduction, Bergmann's rule holds for the northern but not for the southern hemisphere (GLM; northern hemisphere, effect of the latitude on BSA: $F(1,784) = 810.00$, $P < 0.001$; southern hemisphere, effect of the latitude on BSA: $F(1,260) = 1.36$, $P = 0.243$). On the contrary, after introductions, Bergmann's rule holds for both the northern and the southern hemisphere (GLM; northern hemisphere, effect of the latitude on BSA: $F(1,784) = 903.66$, $P < 0.001$; southern hemisphere, effect of the latitude on BSA: $F(1,260) = 4.65$, $P = 0.032$). This latter result confirms the role of ENNS as a major driver of spatial patterns of BSA.

We finally showed that the establishment of non-native species provides a new hypothesis by which the current spatial variation in BSA can be explained. Indeed, we highlighted, for each hemisphere, several environmental variables that correlated strongly to geographical patterns in BSA before introduction (Table 1a; Fig. 3b,c). Some variables were common to the two hemispheres and had similar relationships (i.e. negatively related to native species richness, Table 1a) or opposite relationships (i.e. average annual temperature and its coefficient of variation; Table 1;

Table 1 Results of the generalized linear mixed models (GLMM) used to test the relationship between several predictors on the median body size of freshwater fish assemblages before [(a) native and extirpated species only] and after species introductions [(b) native and non-native species only]

	Northern hemisphere			Southern hemisphere		
	Estimate	<i>t</i> -Value	<i>P</i> -value	Estimate	<i>t</i> -Value	<i>P</i> -value
(a) Body length distribution before invasion						
Basin area	0.010	0.464	0.643	0.011	0.716	0.475
Native species richness	-0.044	-2.270	0.024	-0.034	-2.379	0.019
Non-native species richness	NI	NI	NI	NI	NI	NI
Evapotranspiration	0.000	0.011	0.991	0.008	0.536	0.593
Net primary productivity	-0.093	-3.384	0.001	0.016	0.888	0.376
Average annual temperature	-0.815	-14.770	<0.001	0.034	2.004	0.047
(Average annual temperature) ²	-0.109	-6.349	<0.001	0.054	3.817	<0.001
CV annual temperature	-0.389	-8.393	0.000	0.045	2.827	0.005
Maximum percentage of glacier coverage	0.073	2.499	0.013	-0.003	-0.166	0.869
(b) Body length distribution after invasion						
Basin area	0.024	1.156	0.248	0.004	0.396	0.693
Native species richness	-0.057	-3.022	0.003	-0.037	-3.843	<0.001
Non-native species richness	0.093	4.717	<0.001	0.052	5.630	<0.001
Evapotranspiration	0.003	0.130	0.897	-0.021	-2.175	0.031
Net primary productivity	-0.076	-2.880	0.004	0.012	0.947	0.345
Average annual temperature	-0.784	-14.650	<0.001	-0.005	-0.455	0.650
(Average annual temperature) ²	-0.111	-6.027	<0.001	0.058	6.016	<0.001
CV annual temperature	-0.346	-7.816	<0.001	0.032	3.045	0.003
Maximum percentage of glacier coverage	0.075	2.666	0.008	-0.017	-1.591	0.114

Gamma error distribution was assumed. We tested each hemisphere (southern hemisphere, $n = 148$; northern hemisphere, $n = 626$) separately. Bold *P*-values are significant ($P < 0.05$).

NI, predictor that was not included in the model; CV, coefficient of variation.

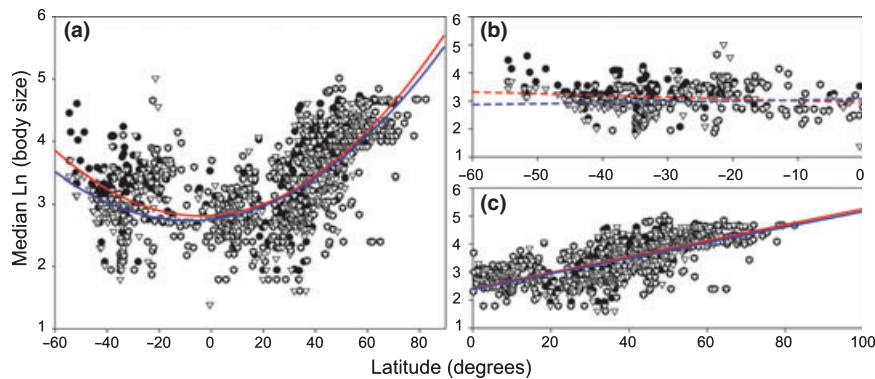


Figure 3 Latitudinal variation of the median body size (measured as ln-transformed body length in cm) of freshwater fish assemblages (BSA). Black dots represent assemblages before introduction (i.e. native species + extirpated species). White triangles represent the assemblages after introduction (i.e. current assemblages: native species + established non-native species - extirpated species). The latitudinal trends of BSA are shown for before introduction (blue line) and after introduction (red line) states and compared using resampling tests. Latitudinal variation was shown worldwide (a), and for the southern (b) and northern (c) hemispheres separately, to test for the effect of established non-native species on Bergman's rule on the worldwide and the hemisphere scales.

Fig. S2). On the contrary, other variables were specific to one hemisphere (e.g. positive correlation of BSA with glacier coverage and negative correlation of BSA with NPP

in the northern hemisphere, Table 1a). Although the variables listed above were still significantly correlated to BSA after introduction, the number of ENNS in a given

river basin became a significant predictor of the BSA in both hemispheres (Table 1b). This last result supports our conclusion that the establishment of non-native species is a major process explaining current geographical patterns of BSA. It should also be noted that, after introduction, one predictor (i.e. evapotranspiration in the southern hemisphere) became slightly significant, and the form of the relationship between average temperature and BSA changed. These two latter results might be indirect consequences of species establishment.

DISCUSSION

Here, we show that ENNS are not a random subset of the worldwide fish fauna, as non-native fish body size is significantly larger than expected by random. This confirms and extends previous studies on exotic birds (Cassey 2001; Blackburn & Cassey 2007). This pattern can be attributed to the strong association of ENNS with human activity rather than their own biological performance, spatial colonization pressure (i.e. the number of river basins in which a species has been released) being one of the main determinants of non-native species establishment (Jeschke & Strayer 2006; Lockwood *et al.* 2009). In addition, our analysis revealed that the distribution of body size of fish ENNS was bimodal, which probably underlies two types of introductions: i) random species sampling (the left-hand peak of the curve), that probably accounts for unintentional introduction (Smith *et al.* 2004); and ii) non-random choice (the right-hand peak of the curve) probably due to large species strongly associated with human activities. This was confirmed when we found a highly significant correlation between the body size of ENNS and the index of human affiliation. The successful establishment of non-native species might therefore result from high spatial colonization pressure due to random and non-random species introductions.

This non-random pattern of ENNS body size increases the BSA worldwide. This increase represents up to 10% of the initial BSA, which is remarkable given that most species introductions are recent (i.e. < 150 years). Using null-model simulations, we further demonstrated that this change in median body size was significantly different and even opposite to the change expected if ENNS were a random subset of the freshwater fish fauna (i.e. null-model 1). This result might reflect the fact that small fish species are more numerous than bigger ones and that fish are not evenly distributed across the World (according to their body size). This implies that randomly selecting species to be introduced from particular localities or particular taxonomic groups might contribute to producing the observed pattern (Blackburn & Cassey 2007). This was tested here by accounting for the geographical location and family mem-

bership of the ENNS (null-models 2 and 3). Even for these conservative simulations, the observed trend still holds, testifying for a strongly directed human choice towards the introduction of large species. Indeed, all null models demonstrate that introducing randomness in the selection of species to be introduced would have induced a decrease in the BSA. In addition, the observed pattern might – in part – be due to the fact that invaded river basins have native BSA that are larger than the BSA of non-invaded basins (ANOVA, $F(1, 1045) = 5.041$, $P = 0.025$). Despite this possibility, our results suggest that changes in median BSA induced by species introductions are non-random because ENNS are themselves not a random subset of the worldwide set of species. Such a pattern probably arises from a strong interaction between the functional characteristics of established species and the location where they established *per se*. Distinguishing between the relative effects of the functional identity of established species and the location of species establishment is one of the main challenges for future large spatial scale researches. Furthermore, we showed that extirpated species were on average larger than the worldwide set of species (see also Olden *et al.* 2007), but that extirpations had no significant effect on the change in BSA. However, extirpations of small-bodied species are often less detectable (Olden *et al.* 2007), meaning that our data on extirpation might be biased towards large-bodied species. If true, losses of small-bodied fishes would tend to shift BSA towards larger BSA.

Our results show that human beings are affecting the body size structure of most freshwater fish assemblages worldwide towards an increase in the median BSA. The changes concerned the whole BSA distribution as reflected by a variance increase as well as a decrease in the skewness and kurtosis of BSA after species establishment. The greatest changes in median BSA strikingly matched several invasion hotspots previously identified for freshwater fish (Leprieur *et al.* 2008). This result has important implications because there is clear empirical evidence that changing the body size structure of assemblages affects the way ecosystems function (Long & Morin 2005; Woodward *et al.* 2005). Notably, large-bodied fish often share biological attributes that can affect the function of recipient ecosystems either through predation, carbon storage, nutrient recycling or bioturbation (Taylor *et al.* 2006; Bruno & Cardinale 2008). For instance, non-native species introductions have substantially increased the median BSA in high latitude river basins of the southern hemisphere (Fig. 4b). This mainly results from the successful establishment of large predatory salmonid species, particularly in rivers and lakes of Patagonia and New Zealand (Townsend 2003; Pascual *et al.* 2009). In these regions, there is now ample evidence that these non-native fish have reshaped both food webs and historical fish assemblages (Townsend 2003; Pascual *et al.* 2009).

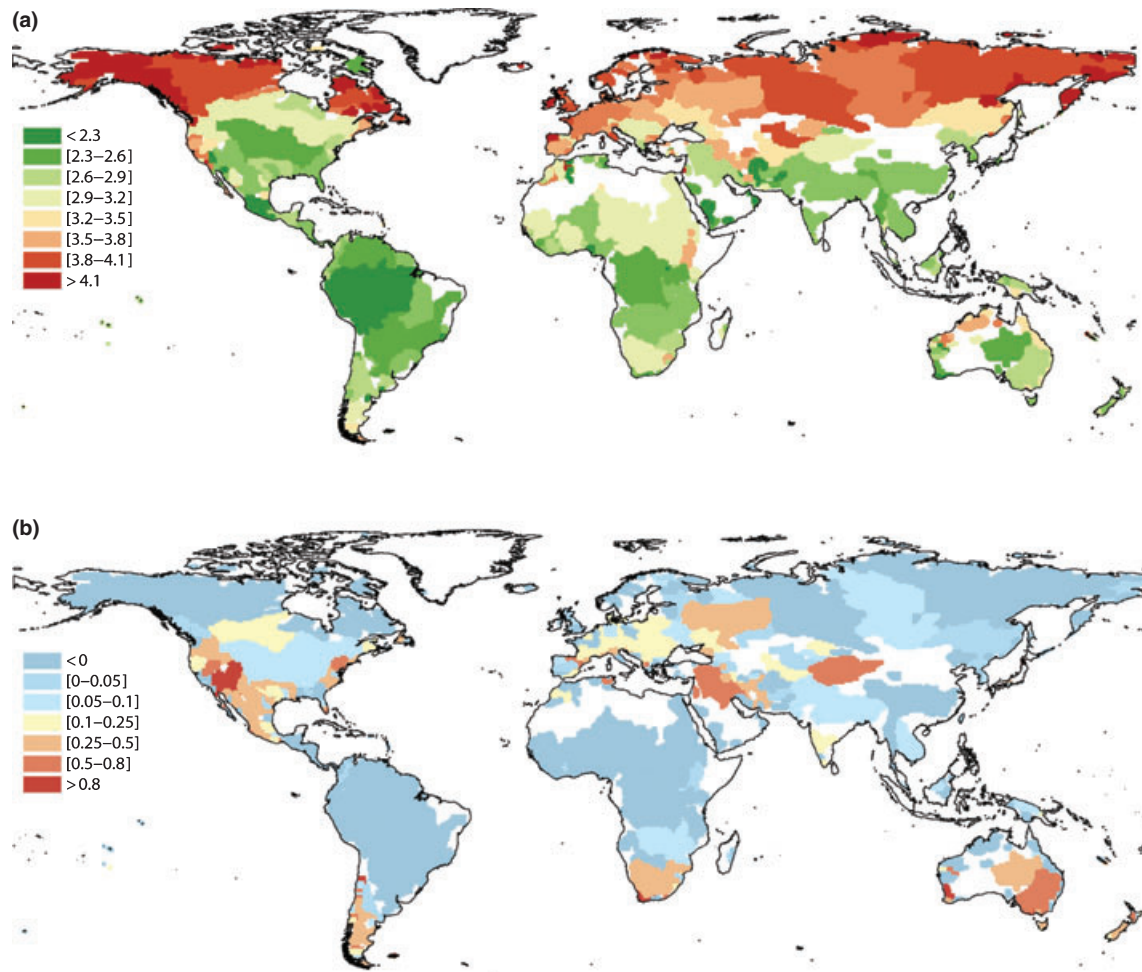


Figure 4 (a) Worldwide patterns of the median body of size (measured as the body length) of freshwater fish assemblages. Only native species were considered. (b) Worldwide patterns of the difference between the median body size of freshwater fish assemblages after and before species introductions. The median body size of each assemblage was ln-transformed prior to calculations. Each assemblage (i.e. river basin) was delimited by a GIS using $0.58 \times 0.58^\circ$ grids. The maps were drawn using species occurrence data for 9968 species in 1058 river basins covering more than 80% of continental areas worldwide.

Here we provide new insights for understanding latitudinal variations of the BSA. In its interspecific version, Bergmann's rule has been tested for both ectotherms and endotherms on the continental scale (Roy *et al.* 2000; Knouft 2004; Rodriguez *et al.* 2008). However, our study is, to our knowledge, one of the first attempts to test Bergmann's rule on the worldwide scale (Olson *et al.* 2009). Considering native species, we showed that the BSA of freshwater fish followed Bergmann's rule in the northern hemisphere but not in the southern hemisphere. Our result must be considered with caution because (i) Knouft (2004) demonstrated that Bergmann's rule does not hold for all fish families on the continental scale and (ii) this rule does not necessarily hold at the intraspecific level in freshwater fish (Belk & Houston 2002). The contradiction between the

northern and southern hemispheres parallels a previous study on mammal body size (Rodriguez *et al.* 2008), and shows that an eco-geographical rule cannot be generalized until it has been verified worldwide.

Furthermore, this is the first attempt to highlight the processes underlying the worldwide variation of fish BSA. For both hemispheres, the strongest factors significantly associated to BSA were temperature-related (average annual temperature and thermal amplitudes). In contrast to recent findings in birds (Olson *et al.* 2009), the effects of average annual temperature and thermal amplitudes were related in the same direction to BSA, indicating that these two forces might influence BSA synergistically. However, the relationships between average annual temperature, annual temperature variation and BSA vary between the two hemispheres.

Particularly, in the northern hemisphere, BSA was larger in river basins where annual temperature and thermal amplitudes are low while the reverse holds true in the southern hemisphere. This suggests that the physiological effect of temperature on BSA might be highly context-dependent (Rodríguez *et al.* 2008). Contrary to expectations (Olalla-Tarraga *et al.* 2006), we also found that BSA in the northern hemisphere were larger in low-productivity river basins. It is possible that small-bodied species, that often need to reproduce rapidly, are not able to become mature quickly in low-productivity areas, and are hence counter-selected. Finally, in the northern hemisphere, dispersal ability probably limited post-glacial colonization of high latitude regions by small-bodied species. Indeed, there was a highly significant positive relationship between the glacier coverage and BSA. This result differs from previous studies in other taxa (Olalla-Tarraga *et al.* 2006; Rodríguez *et al.* 2008), probably because freshwater fish have a much lower dispersal ability than other animals (Tedesco *et al.* 2005; Griffiths 2006). It is possible that such a pattern was not found in the southern hemisphere because only rivers flowing in the extreme southern part of the hemisphere were affected by ice cover (Wright *et al.* 1993).

Interestingly, we found that these worldwide latitudinal patterns were significantly affected by ENNS. This was especially true in the southern hemisphere where we showed significant changes (1) in the relationship between body size and latitude and (2) in relationships between some environmental predictors and BSA (average annual temperature and evapotranspiration). As already stated, the high latitude regions of the southern hemisphere are among the most affected by non-native freshwater fish (Leprieur *et al.* 2008), which probably explains the strong impact of non-native fish on median BSA in this part of the world. It is furthermore noteworthy that in both hemispheres the ENNS richness in a river basin is a major predictor of the worldwide BSA distribution. Such results suggest that the establishment of non-native species is an ongoing driver of the worldwide geography of body size for freshwater fish.

To conclude, our study participates in showing that the establishment of non-native species is a process affecting most biomes. This is remarkable as human beings have facilitated the establishment of a few selected species (*c.* 0.04% of the worldwide species pool) in a very narrow lapse of time (*i.e.* hundreds of years). In regards to body size, this selection has been so intense and directed that most recipient assemblages have rapidly deviated away from their historical states, and hence have begun to reshape the eco-geographical patterns of body size. Although quantifying the ecological and evolutionary impacts of the functional change induced by non-native species is currently an irresolvable task on the worldwide scale, there is evidence that body size structure of communities affects ecosystem

functioning (Long & Morin 2005; Woodward *et al.* 2005). Given that human-assisted species introduction is an ongoing process, and that body size evolution is affected by other components of global change (Millien *et al.* 2006; Bruno & Cardinale 2008), we can expect further changes in the near future.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Relationship between the index of human affiliation (see calculation above) and the body size (measured as the logarithm of the total body length) of established non-native fish.

Figure S2 Median body size (measured as the body length) of freshwater fish assemblages (BSA; ln-transformed) as a function of mean annual temperature (degrees Kelvin).

Table S1 Results of generalized linear mixed models (GLMMs) used to test the effect of latitude (and its quadratic term) and sampling period (before and after species introductions) on the median body size of freshwater fish assemblages [(a) assemblages from both the Northern and Southern hemispheres; (b) assemblages from the Southern hemisphere only and (c) assemblages from the Northern hemisphere only].

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