Research

Spatial synchrony in stream fish populations: influence of species traits

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Spatial synchrony in population dynamics has been identified in most taxonomic groups. Numerous studies have reported varying levels of spatial synchrony among closely-related species, suggesting that species' characteristics may play a role in determining the level of synchrony. However, few studies have attempted to relate this synchrony to the ecological characteristics and/or life-history traits of species. Yet, as to some extent the extinction risk may be related to synchrony patterns, identifying a link between species' characteristics and spatial synchrony is crucial, and would help us to define effective conservation planning. Here, we investigated whether species attributes and temperature synchrony (i.e. a proxy of the Moran effect) account for the differences in spatial population synchrony observed in 27 stream fish species in France. After measuring and testing the level of synchrony for each species, we performed a comparative analysis to detect the phylogenetic signal of these levels, and to construct various multi-predictor models with species traits and temperature synchrony as covariates, while taking phylogenetic relatedness into account. We then performed model averaging on selected models to take model uncertainty into account in our parameter estimates. Fifteen of the 27 species displayed a significant level of synchrony. Synchrony was weak, but highly variable between species, and was not conserved across the phylogeny. We found that some species' characteristics significantly influenced synchrony levels. Indeed, the average model indicated that species associated with greater dispersal abilities, lower thermal tolerance, and opportunistic strategy displayed a higher degree of synchrony. These findings indicate that phylogeny and spatial temperature synchrony do not provide information pertinent for explaining the variations in species' synchrony levels, whereas the dispersal abilities, the life-history strategies and the upper thermal tolerance limits of species do appear to be quite reliable predictors of synchrony levels.

Spatial synchrony in population dynamics (i.e. the degree to which spatially distant populations rise and fall together through time) has been identified in most taxa, ranging from plants (Koenig 1999), parasites (Cattadori et al. 2005), insects (Sutcliffe et al. 1996), fish (Grenouillet et al. 2001), amphibians (Aubry et al. 2012), and birds (Paradis et al. 1999) to mammals (Moran 1953). Studies focusing on synchrony patterns are closely related to the debate about the relative importance of intrinsic versus extrinsic environmental factors in determining fluctuations in population size (Grenfell et al. 1998, Forchhammer et al. 2002). It is generally considered that population dispersal and synchronous stochastic effects of density-independent factors (known as the Moran effect) are the two main mechanisms involved in spatial synchrony (Liebhold et al. 2004). These are not mutually exclusive, and their relative importance has been shown to be scale-dependent (Paradis et al. 2000): while population dispersal prevails at the local scale, environmental stochasticity prevails at larger scales (Ranta et al. 1998). In addition, trophic interactions involving species that are

themselves synchronized or mobile, could influence population synchrony (Liebhold et al. 2004).

In recent years, several studies have reported varying degrees of population synchrony among closely-related species (Sutcliffe et al. 1996, Koenig and Knops 1998, Paradis et al. 2000). These variations have generally been attributed to differences in parameters determining the dynamics of the populations, such as the strength and shape of density dependence (Kendall et al. 2000, Engen and Saether 2005) or differences in the spatial autocorrelation of environmental noise (Engen et al. 2005). Indeed, empirical analyses of population dynamics of many species have shown that the parameters describing population dynamics (e.g. density-dependent structure, carrying capacity) may show large spatial variations (Myers et al. 1997, Engen et al. 2005), thus reducing population synchrony (Engen and Saether 2005) and consequently species synchrony. Likewise, spatial variation in the effect of environmental covariates on population dynamics has been shown to influence species synchrony patterns (Engen and Saether 2005). Therefore, depending

on the spatial variability of 1) the parameters describing population dynamics and/or 2) the influence of environmental covariates on these dynamics, varying levels of species synchrony can emerge. However, such variations could also depend on species characteristics, because the influences of both density dependence (shape and strength) and environmental stochasticity have been shown to be dependent upon species characteristics (Lande et al. 2002, Sæther et al. 2013). For instance, several studies have shown that most density-dependent changes occur close to the carrying capacity for K-strategist species (long life-span, small clutches, large egg size), whereas the opposite is true for r-strategist species (Fowler 1981). Likewise, species with a short generation time have been found to be more sensitive to environmental stochasticity, and so also to the Moran effect (Sæther et al. 2013).

Despite these findings, very few studies have attempted to relate the level of spatial synchrony to ecological characteristics and/or the life-history traits of species, and most of the studies performed have failed to explain the observed differences in synchrony levels between species. However, it is crucial to identify a link between species characteristics and spatial synchrony, since this would help us to understand population dynamics and could also provide useful insights for management purposes; this is because to some extent the extinction risk may be related to synchrony patterns (Hanski and Woiwod 1993, Heino et al. 1997).

In this study, our goal was to identify the determinants of interspecies variations in synchrony levels for 27 stream fish species across France. To do this, we investigated whether 15 species characteristics (ecological and life-history traits) and/or the Moran effect explained the observed differences in the degree of spatial synchrony measured over the different species. Consequently, we first estimated the level of spatial synchrony for each species, and then carried out tests to find out whether these levels were ecologically relevant at the spatial scale considered. We then used a comparative analysis 1) to detect phylogenetic signals in the levels of synchrony in order to find out whether evolutionary relationships between species provide information pertinent to explaining interspecies differences in synchrony patterns, and 2) to compute various multi-predictor models in order to determine the extent to which species characteristics and/or the Moran effect play a role in determining species synchrony, while taking phylogenetic relatedness into account. Our first expectation was that species living in a highly synchronous environment would display higher levels of synchrony. For species characteristics, we hypothesized that dispersal abilities, thermal tolerance, life-history strategies, diet, and habitat requirements would explain interspecies differences in fish spatial synchrony. More specifically, we expected species with strong dispersal abilities to be synchronized to a greater extent than those with low dispersal abilities. For thermal tolerance, species with a low upper thermal limit were expected to display higher synchrony levels, because in a spatially-correlated global warming context, these species can be expected to exceed their upper limit more often than species with a high upper thermal limit, which could lead to spatially-correlated population decline. Furthermore, because short-lived species display more immediate responses to environmental stochasticity than long-lived species (Sæther et al. 2013), short-lived species can be expected to be more synchronous. Finally, the trophic position of the species along the food-web and the species habitat requirements were also expected to influence synchrony levels, as an influence of these characteristics on synchrony patterns has already been demonstrated for other species (Paradis et al. 2000, Liebhold et al. 2004).

Material and methods

Fish and temperature data sets

To calculate the level of spatial population synchrony for fish species, we used abundance time series data provided by the French National Agency for Water and Aquatic Environment (Onema; for more details see Poulet et al. 2011). These annual data were obtained between 1982 and 2010 by electrofishing during periods of low flow. Fish were identified to species level, counted, and then released back into the river. From this data set we conserved only the species for which at least ten population time series including at least eight years of non-null captures were available. This resulted in the selection of 27 fish species (Table 1). We chose to have at least ten population time series, because we wanted to have 1) populations that were representative of the different conditions experienced by the species in its geographic range and 2) enough populations to compute a reliable estimate of species synchrony levels. For the number of years within the

Table 1. Spatial synchrony for the 27 fish species. N is the number of time series (i.e. sites) for each species. Npairs is the number of zero-lag Spearman cross-correlation coefficients (CCCs), GRS (km²) is the estimated geographic range size. Mean CCCs is the mean of all zero-lag Spearman cross-correlation coefficients computed between all pairs of time series that had at least eight years in common. Statistically significant ($p < 0.05$) coefficients are shown in bold type.

Species name	Mean CCCs	N	Npairs	GRS (km²)
Abramis brama	−0.017	26	233	278589
Alburnoides bipunctatus	**0.048**	52	745	273135
Alburnus alburnus	0.003	110	2830	451797
Ameiurus melas	0.023	17	64	138562
Barbatula barbatula	**0.054**	245	21312	550434
Barbus barbus	**0.025**	131	5162	407407
Blicca bjoerkna	0.001	24	94	247209
Carassius carassius	−0.039	13	55	195257
Chondrostoma nasus	0.027	30	373	185169
Cottus gobio	**0.146**	25	160	118620
Cyprinus carpio	0.024	11	55	163528
Esox lucius	**0.030**	61	1037	399757
Gasterosteus aculeatus	**0.172**	16	76	233558
Gobio gobio	**0.045**	219	14354	411718
Gymnocephalus cernua	0.040	21	138	219214
Lepomis gibbosus	**0.014**	81	5404	382141
Leuciscus leuciscus	**0.071**	59	922	244492
Perca fluviatilis	**0.038**	154	1595	410109
Phoxinus phoxinus	**0.043**	249	22544	542819
Pungitius pungitius	0.038	19	134	109912
Rhodeus sericeus	0.036	33	218	170673
Rutilus rutilus	0.002	250	16034	523535
Salmo trutta fario	**0.038**	284	29225	634422
Scardinius erythrophthalmus	−0.012	28	134	298309
Squalius cephalus	**0.031**	313	28084	534373
Telestes souffia	**0.089**	23	179	90144
Tinca tinca	**0.069**	42	490	415053

time series, we chose the same number as that used in a study involving a previous version of our database (Poulet et al. 2011). All time series with more than three consecutive years missing were eliminated. In this way, little information was likely to be contained by the population change during the missing years (Engen et al. 2005). At the end of the selection process, the data set used was composed of 610 sites covering the whole of metropolitan France (Fig. 1), with 8–25 yr of sampling (mean: 12.5 yr; SD: 3.6 yr), corresponding to a total of 7634 sampling occasions. The number of time series (i.e. sites) varied from 11 to 313 depending on the species (Table 1).

Daily air temperature data from 1982 to 2010 were provided by Météo France. More precisely, we used the SAFRAN database (Le Moigne 2002), which is a regular eight kilometer grid, in which the daily air temperature was calculated for each cell by optimal interpolation of climatically-homogeneous zones (for further details, see Le Moigne 2002). Although we do not have the corresponding water temperature data, studies have shown that air temperature provides a reliable proxy for water temperature (Caissie 2006). From this data set, we calculated the average annual temperature at each site, and used this measure to estimate the degree of environmental correlation between the different sites.

Species and temperature synchrony

For each species, we computed zero-lag Spearman cross-correlation coefficient (CCC) for all pairs of raw abundance time series (Buonaccorsi et al. 2001). Species synchrony was then calculated as the average of these CCCs weighted by the number of overlapping years between pairs of time series. The same procedure was used to estimate the level of temperature synchrony (TEMP) between the subset of sites occupied by each species. This measure was considered to provide a proxy of the Moran effect, and was used in the model selection procedure (see below) to determine whether it influenced species synchrony levels. To determine whether species synchrony was significantly different from zero, we used a bootstrap procedure with resampling of timepoints within each time series, and then recalculated the mean between all the CCCs computed from the resampled time series (Lillegård et al. 2005). This procedure was repeated 1000 times to generate a distribution of mean species synchrony values under the hypothesis of no synchrony (Buonaccorsi et al. 2001). Species synchrony was considered significant if less than 5% of the simulated means (i.e. means calculated using the bootstrap algorithm) exceeded the observed mean.

As the distribution of the estimated spatial synchrony for the 27 fish species was skewed (Shapiro–Wilk normality test; $p < 0.01$), which could lead to violation of the assumption of residual normality for most of the multi-predictor models computed, this variable was normalized using a Box–Cox power transformation (lambda $= -7.05$; Box and Cox 1964).

Species traits

To test our hypotheses regarding the different morphological, physiological, life-history, and behavioral characteristics
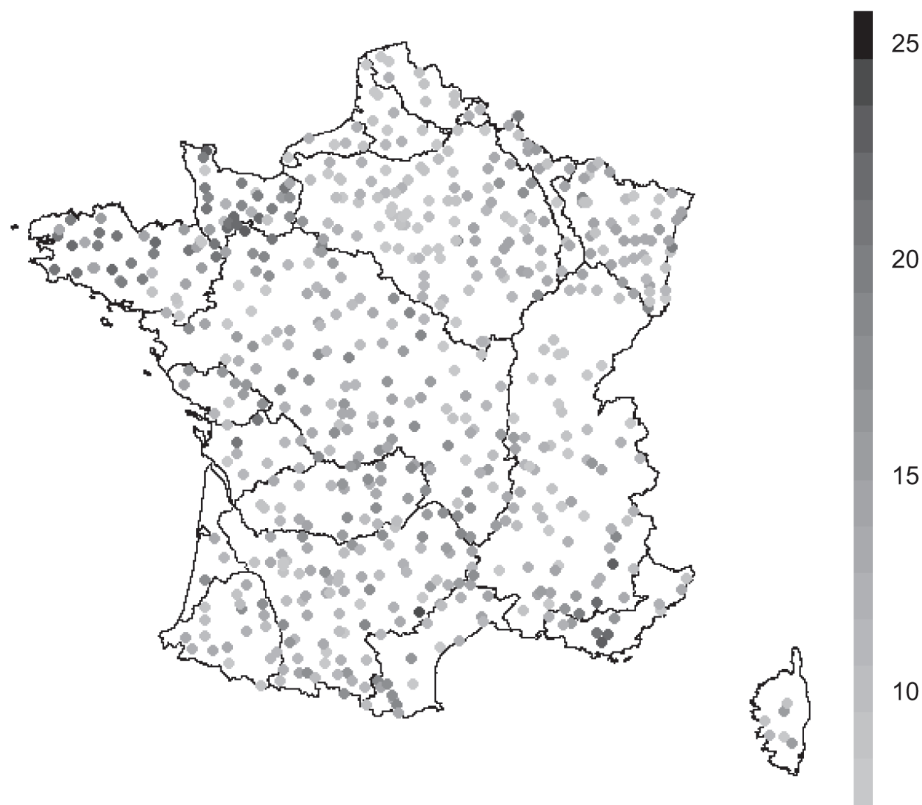

Figure 1. Study area showing the distribution of the sampling sites. The gray scale indicates the number of years available for each site. Sites shown in light gray are those for which we have the fewest years, while sites shown in dark gray are those for which we have greatest number of years.

of the 27 fish species studied, we used values for 15 different traits (Supplementary material Appendix 1, Table A1) taken from the literature (Buisson and Grenouillet 2009, Keith et al. 2011, Tissot and Souchon 2011), from FishBase (Froese and Pauly 2002), and from expert knowledge. We chose these traits for their diversity, the fact they could be expressed numerically or ordered hierarchically, and the likelihood that values would be obtained for most of the species. Among these, six were quantitative variables and the others were all ordinal variables (Supplementary material Appendix 1, Table A2). We chose to express the categorical variables as ordinal variables, because this allowed us to reduce the number of parameters that had to be estimated when computing the multi-predictor models.

To describe the dispersal abilities of the 27 fish species, we used morphological characteristics known to be representative of this parameter (Poff and Allan 1995). We therefore included two traits related to body size (body length and larval length), and two ratios describing the hydrodynamic profile of the fish (shape factor; i.e. the ratio of total body length to maximum body depth), and the fish's swimming ability (swimming factor; i.e. the ratio of minimum depth of the caudal peduncle to the maximum depth of the caudal fin). Large species with a low swimming factor and a high shape factor were expected to display high dispersal abilities (Olden et al. 2008). To reflect the physiological characteristics of species, we used the upper thermal tolerance limit (UTT). We used seven traits to describe the different life-history strategies of the 27 fish species: life span, parental care, incubation period, sexual maturity, spawning time, absolute fecundity, and egg diameter. The diet was ordered to describe the trophic position along the food-web as follows: omnivorous, invertivorous, invertivorous-carnivorous, and piscivorous. Finally, for fish habitat requirements, we included two habitat variables that reflect the position of the fish in the water column during feeding (feeding habitat) and resting (resting habitat).

To describe species dispersal abilities, life-history strategies, and habitat requirements, we used various traits (four,

seven and two, respectively) that could be correlated with one another. For each of these trait categories, colinearity was reduced by carrying out a principal coordinate analysis (PCoA, Gower 1966), and then using the axes of each analysis as synthetic variables of species' characteristics. Like principal component analysis, PCoA is a metric multidimensional scaling method based on projection, which uses spectral decomposition to approximate a matrix of distances from the distances between a set of points in a few dimensions. We chose this method instead of principal component analysis, because the matrix of distances can be computed from mixed type variables (i.e. both ordinal and quantitative) by using the dissimilarity coefficient proposed by Gower (1971). Once PCoA has been performed for each trait category, species dispersal abilities and species life-history strategies were described by two variables (MPC1, MPC2 and LPC1, LPC2, respectively), whereas species habitat requirements were described by one variable (HPC1) (Table 2).

Phylogeny and the phylogenetic comparative approach

One of the problems encountered in carrying out a comparative analysis is phylogenetic non-independence, i.e. the fact that closely-related species tend to be more similar than more distantly-related ones (Felsenstein 1985).

To take into account the phylogenetic relatedness between the species, we first built the phylogeny of the 27 species (Fig. 2A) using 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 ribosomal 16S sub-unit, respectively. We used the Lamprey as an outgroup to root the tree, and we reconstructed phylogenetic relationships among species using the Bayesian method under the TVM + I + G substitution model. The phylogeny estimation was implemented with MrBayes and PAUP softwares.

We then used the phylogenetic generalized least squares (PGLS) comparative method described in Freckleton et al. (2002), first to detect phylogenetic signals in the levels of species synchrony and species traits, and second to construct multi-predictor models with species synchrony levels as the dependent variable and species traits and temperature synchrony as independent variables. This approach allows for the non-independence of data by adjusting a variance/covariance matrix based on the phylogenetic relatedness among species. Unlike phylogenetic independent contrasts (Felsenstein 1985), PGLS makes it possible to introduce some degree of trait liability, relative to a strict Brownian model of evolution, by multiplying the off-diagonal elements of the variance/covariance matrix (i.e. the covariances) by a measure of phylogenetic correlation. Here, we used Pagel's λ (Pagel 1999), which varies from 0 to 1, as a measure of phylogenetic correlation, because it has been shown to be a statistically-powerful index for measuring whether data exhibit phylogenetic dependence or not (Freckleton et al. 2002). $\lambda = 0$ means that all species are independent (star phylogeny), $\lambda = 1$ corresponds to a Brownian model of evolution, and $0 < \lambda < 1$ corresponds to some degree of trait lability.

Table 2. Pearson's correlations between the species traits and PCoA axes. Three PCoAs were performed, each summarizing different species characteristics. The percentage of variance explained by each axis is shown in parentheses.

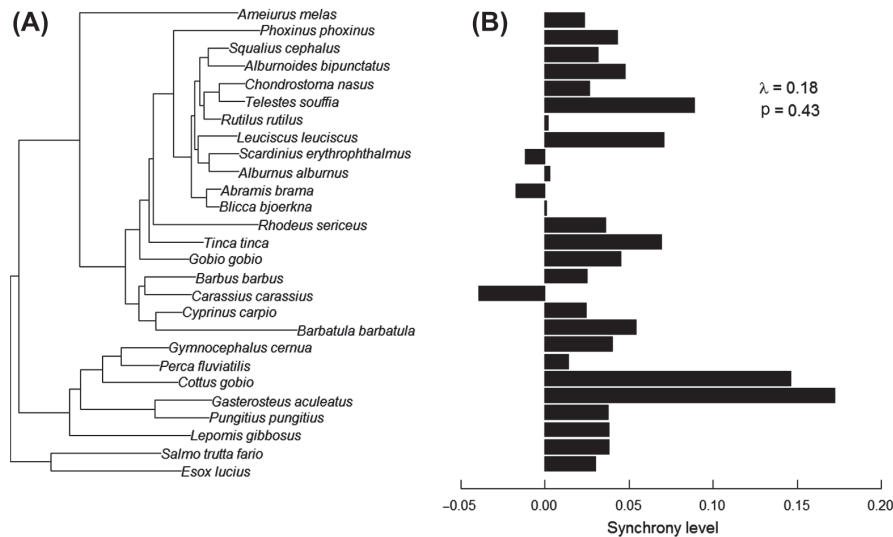| Trait	Correlation	
	PC 1	PC 2
Dispersal ability	(26.8%)	(16.4%)
Body length	–0.41	0.31
Larval length	–0.94	–0.25
Shape factor	0.32	–0.81
Swimming factor	0.002	0.42
Life-history strategy	(24.3%)	(22.7%)
Fecundity	0.49	–0.46
Spawn time	0.91	0.32
Egg diameter	–0.6	–0.11
Life span	–0.09	–0.9
Female maturity	–0.01	–0.9
Incubation period	–0.66	0.32
Parental care	–0.35	0.62
Habitat preference	(31.4%)	
Resting habitat	–0.80	–
Feeding habitat	–0.82	–

Figure 2. Phylogenetic tree (A) and synchrony level (B) of the 27 stream fish species. λ is the value of the phylogenetic signal in the synchrony level, and p its associated p-value.

Multi-predictor models and model averaging

Because the distance over which the species were sampled could influence the levels of population synchrony (Bjørnstad et al. 1999), and consequently the subsequent analyses (i.e. the estimations of the levels of species synchrony and so the inferences drawn from the multi-predictor models), we first performed a linear regression between the levels of synchrony estimated for each species and the geographic range size (GRS; Table 1) occupied by the species. For each species, GRS was measured as the area (km²) of the smallest convex set of the subset of sites occupied by the species (i.e. the convex hull; Barber et al. 1996). The residuals of this model were then extracted and used as the dependent variable in the PGLS models we used to test the influence of species traits and the Moran effect on the level of spatial synchrony among species.

In order to compare the relative strength of the eight predictors on the level of spatial synchrony among species, the predictors were transformed to z-scores to standardize their slope coefficients (β). We then considered all possible multi-predictor models that included three terms or fewer. We chose to not include more than three terms in these models so as to limit the number of estimated parameters (i.e. four), regarding the number of data points at our disposal (i.e. 27). We also considered models that included interaction terms between independent variables. Interactions were tested only in models that included two variables. Once all the models had been computed, we used the Akaike information criterion adjusted for small sample size (AICc) to assess the information content of each model (Burnham and Anderson 2002). For each model, we calculated pseudo-R^2 following Nagelkerke (1991). To take model uncertainty into account, and obtain robust estimates of the slope coefficients associated with each predictor, we performed model averaging (Johnson and Omland 2004). Specifically, we summed the Akaike weights of each model (wi) from the largest to the smallest until the sum reached 0.95. The corresponding subset of models was then used to calculate a weighted average of the slope coefficients using the wi of each model (Burnham and Anderson 2002). For each weighted

average coefficient, we calculated confidence intervals from the variance of the estimated coefficient among the selected models (Johnson and Omland 2004). As the predictors could be correlated with one another, we assessed the variance inflation factor; colinearity was considered to pose a problem if it had a value of more than five (Kutner 2005). For all models, we tested the residual normality using the Shapiro–Wilk normality test. All calculations were performed using R environment software ver. 2.15.3 (R Core Team).

Results

Fifteen of the 27 fish species displayed a significant ($p < 0.05$) level of synchrony (Table 1). The synchrony level was weak, but varied considerably in all species, ranging from –0.04 (*Carassius carassius*) to + 0.17 (*Gasterosteus aculeatus*). Furthermore, these levels were not conserved across the phylogeny (λ = 0.08; p = 0.69) (Fig. 2B) suggesting that variations occurred even amongst closely-related species. Similarly, among the seven traits considered, we found that only two of them, MPC1 and diet, displayed a significant ($p < 0.001$) phylogenetic signal (λ = 0.98 and λ = 0.88, respectively; Table 3).

Eight of the 120 multi-predictor models computed were sufficient to provide a sum of wi of more than 0.95 (Table 3). Consequently these models were used to perform model averaging. The amount of variance explained by the selected models varied from 0.70 to 0.76 (Table 3). Colinearity did not appear to be a problem for any of the models selected (the variance inflation factor was always less than two), and their residuals were normally distributed (Shapiro–Wilk normality test; p > 0.05). Taken together, these models encompassed all the predictors considered. Six out of the eight models included UTT as a significant predictor of synchrony levels. Likewise, MPC2 and LPC2 both appeared in four models, and were always significant. Diet appeared in three models, but was significant in only one model. Although included in the subset of models, none

Table 3. Phylogenetic conservatism of each traits and results from the models selected among the 120 multi-predictor PGLS models. LPC1 and LPC2: first and second axes extracted from the PCoA performed on the seven life-history traits; MPC1 and MPC2: first and second axes extracted from the PCoA performed on the four morphological variables; TEMP: temperature synchrony; UTT: upper thermal tolerance limit; HPC1: first axis extracted from the PCoA performed on the two habitat variables. The slope coefficients (β) of each predictor and their levels of significance are shown for each model. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. – indicate that the variables were not retained in the model. AICc, the weight of each model (*wi*), and R² are also shown.

Trait	Phylogenetic conservatism λ	Selected models							
		M1	M2	M3	M4	M5	M6	M7	M8
LPC1	0.65	–	–	–	–0.004	–	–0.002	–	–
LPC2	0.37	0.018**	–	0.015**	0.016**	–	0.012**	–	–
MPC1	0.99***	–0.003	–	–	–	–	–	–0.01	–
MPC2	0	–	–0.021***	–	–	–0.018***	–	–0.022***	–0.019***
Diet	0.88	–	–	–	–	–0.001	0.001	–0.004*	–
UTT	0.88	–0.011*	–0.012*	–0.010*	–0.010*	–0.011*	–	–	–0.011*
HPC1	0.67	–	–	–	–	–	–	–	–0.001
TEMP	–	–	–	–0.005	–	–	–	–	–
AICc	–	–140.25	–137.73	–137.16	–136.22	–135.97	–134.67	–134.58	–134.36
wi	–	0.5	0.14	0.11	0.07	0.06	0.03	0.03	0.03
R²	–	0.76	0.7	0.73	0.72	0.72	0.7	0.7	0.7

of the other predictors emerged as significant. MPC1 and LPC1 appeared in two models, while TEMP and HPC1 appeared in only one model. No interaction terms appeared in the models selected.

After averaging the slope coefficients for the eight models, we found a significant negative relationship between MPC2 and the level of spatial synchrony (Fig. 3), reflecting the fact that species associated with a low swimming factor, a high shape factor, a small body length, and a large larval length displayed higher levels of synchrony. We also found a significant positive relationship between LPC2 and the level of species synchrony (Fig. 3). Thus, species with a low age at maturity that produce small clutches several times per year were more synchronous than species with the opposite characteristics. Finally, we found a significant negative relationship between UTT and the level of species synchrony (Fig. 3) suggesting that species with a low UTT were more synchronized than species with a high UTT. Once the slope coefficients were averaged, we found no significant relationship between the level of species synchrony and diet, LPC1, HPC1, MPC1, or TEMP.

Discussion

Few studies have attempted to relate the levels of synchrony to species characteristics, and most of them have failed to identify any clear link between synchrony and any species characteristics other than dispersal (Koenig 1998, Paradis et al. 1999, Burrows et al. 2002). For instance, Paradis et al. (1999) studied 53 bird species and found no significant relationship between the degree of spatial synchrony and several life-history traits (clutch size, age at first breeding, juvenile and adult survival rates, migration status, and body size). Likewise, diet, clutch size and body size failed to explain the different levels of synchrony in 79 Californian land bird species (Koenig 1998). In a study involving 26 species of rocky shore communities, Burrows et al. (2002) found no influence
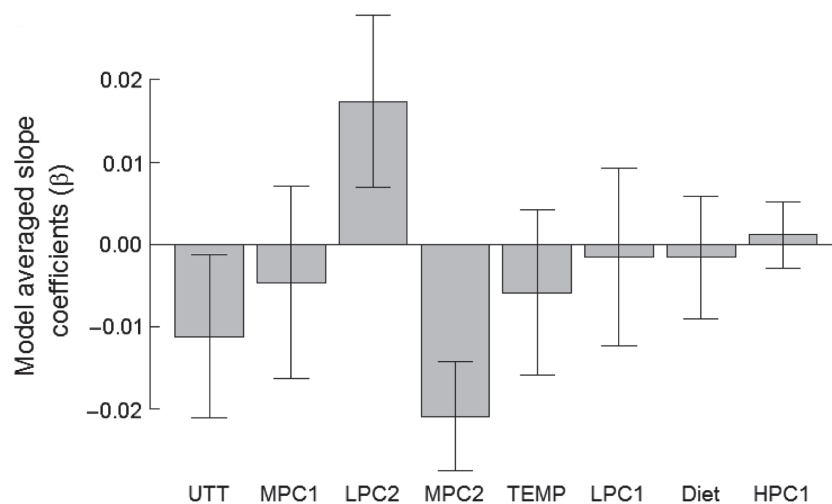

Figure 3. Weighted average slope coefficients (β) calculated for the eight selected models. LPC1 and LPC2: first and second axes extracted from the PCoA performed on the seven life-history traits; MPC1 and MPC2: first and second axes extracted from the PCoA performed on the four morphological variables; UTT: upper thermal tolerance limit; HPC1: first axis extracted from the PCoA performed on the two habitat variables; TEMP: temperature synchrony.

of reproductive biology or ecology on the levels of synchrony in the different species. Thus, although the dispersal abilities of species appear to be a reliable predictor of population synchrony in different taxa (Liebhold et al. 2004), this did not seem to be the case for other traits (but see Tedesco and Hugueny 2006, Franzén et al. 2013).

In this study, although the level of spatial synchrony was low for all species, it was highly variable and we found that some species characteristics could explain the observed differences in synchrony levels. Morphological attributes related to the dispersal abilities of species were significantly related to interspecies differences in the synchrony pattern, species with high dispersal abilities (i.e. species with a low swimming factor, a large larval length, and a high shape factor) being more synchronized than those with low dispersal abilities. This finding was consistent with previous studies. For instance, analyses of breeding bird population time series (Koenig 1998, Paradis et al. 1999) have indicated that species with greater dispersal capabilities were more highly synchronized, implying that dispersal was a major cause of the synchronous dynamics observed. However, dispersal is a scale-dependent phenomenon, and other studies have shown that this relationship vanishes at larger scales. This is borne out by Sutcliffe et al. (1996), who found that butterfly dispersal had a significant effect on the level of synchrony at the local scale, but not at the regional scale. Likewise, Peltonen et al. (2002) found that spatial synchrony was not directly associated with the dispersal capabilities of six forest insect species at the regional scale. Altogether, these findings have led to the general conclusion that dispersal can have the effect of synchronizing populations only at the local scale, whereas stochastic environmental correlation (i.e. the Moran effect) prevails at larger scales (Ranta et al. 1998). However, a study on mussels has demonstrated that dispersal between neighboring populations could interact with local demographic processes to generate patterns of spatial synchrony over quite large scales (Gouhier et al. 2010). In our study, although the spatial scale considered (i.e. France) was large, we found that environmental stochasticity (i.e. temperature synchrony) failed to explain differences in synchrony levels among species, whereas dispersal capabilities did, thus providing further confirmation of the findings of Gouhier et al. (2010). Therefore, although large-scale synchrony was usually attributable to the Moran effect, in some cases, it could also be the result of dispersion. It is noteworthy that we used the spatial correlation of the average annual temperature as a proxy for the Moran effect. However, other environmental factors, such as river discharge, could influence fish population synchrony (Cattanéo et al. 2003) and further studies are needed to determine the extent to which it influences our conclusions.

We found that species with a low thermal maximum were more synchronous than those with a high thermal maximum. However, as temperatures are increasing (Moisselin et al. 2002) and are spatially correlated (Koenig 2002), populations of species with a low thermal maximum can be expected to exceed their upper limit more often than those of species with a high thermal maximum, leading to population declines correlated over large distances. This hypothesis is supported by a study of 110 European bird species that revealed that species with the lowest thermal maximum showed the sharpest declines between 1980 and 2005 (Jiguet

et al. 2007). Similar conclusions have been reached for ectothermic species in freshwater ecosystems. For instance, several studies have reported that warm-water species (which are characterized by a high thermal maximum) are globally increasing in abundance in response to increasing temperatures, whereas the abundances of cold-water species (which are characterized by a low thermal maximum) are decreasing (Daufresne and Boët 2007, Poulet et al. 2011).

To the best of our knowledge, only Tedesco and Hugueny (2006) have reported a significant relationship between species life-history traits and synchrony. Indeed, they showed that species associated with high fecundity, small egg size, and a high gonado-somatic index (what is known as the 'periodic' strategy, sensu Winemiller (1992)) were more synchronous than species associated with the opposite traits (what is known as the 'equilibrium' strategy). However, they excluded from their analyses any species that were characterized by early maturation, continuous reproduction, and low fecundity (known as the 'opportunistic strategy'), because of a low capture efficiency. Yet, these were exactly the species that we found displayed the highest levels of spatial synchrony. However, our results are difficult to compare to those of Tedesco and Hugueny (2006) as their study was based on tropical species that were sampled at only two sites between which dispersion of individuals was impossible as they were located in different catchments. Thus, any synchrony observed could only be due to the Moran effect, whereas in our study the synchrony observed could be attributable to dispersal and/or to the Moran effect.

We did not found any influence of the trophic position on synchrony levels which is in contradiction with some studies (Satake et al. 2004) but in accordance with others (Koenig 1998). One possible explanation would be that the effect of biotic interactions on synchrony levels is more likely to be detected on local spatial scale or simple trophic networks. In large scale studies such as ours and the one of Koenig (1998), we can expect large spatial variations in the complexity of trophic interactions, thus masking their effects on synchrony patterns. Likewise, we found that fish habitat requirements failed to explain interspecies differences in synchrony levels whereas Paradis et al. (2000) found an influence of habitat on spatial population synchrony for birds; populations located in farmland sites being more synchronized than those located in woodland sites. However, this result was not a test of the influence of species habitat requirements on the level of spatial synchrony but rather of whether the synchronizing factors were habitat dependent or not. That being said, our findings still suggest that habitat requirements have an influence on synchrony levels, and further studies are needed to find out whether this is true for other taxa or biogeographic regions.

In this study, we used a phylogenetic comparative framework that revealed that the level of synchrony was not conserved across the phylogeny. This suggests that the phylogenetic distance between species does not provide information that is pertinent for explaining spatial synchrony. Similarly, Raimondo et al. (2004) failed to detect any influence of the phylogeny on the levels of spatial synchrony measured on 10 Lepidopteran species. Even though their analysis was just a test of whether species within a family displayed higher synchrony relative to species between families, this result, coupled with ours, do not provide encouraging

support for an influence of the phylogeny. A possible explanation for our findings could be that the traits mainly involved in determining population synchrony (i.e. the dispersal ability, the upper thermal tolerance, and the life-history strategies) were themselves not conserved across the phylogeny. Such an interpretation has already been proposed, for instance in primates, to explain the low phylogenetic signal found for the 'total group size' variable (Kamilar and Cooper 2013). Another possible explanation is that closely-related species often experience different habitat-specific conditions that could lead to differing levels of population synchrony, and therefore to a low phylogenetic signal. It should also be noted that phylogenetic signals cannot account for within-species variations, even though many species do in fact have numerous traits (e.g. ecological, behavioral, morphological) that display considerable intra-species differences (Kamilar et al. 2012). This could also contribute to explain the low phylogenetic signal observed in the level of synchrony.

Spatial population synchrony may be related to the risk of species extinction, as it increases the likelihood of a correlated population decline across large areas (Hanski and Woiwod 1993, Heino et al. 1997). However, many studies have shown that the extinction risk is conserved across the phylogeny (Purvis et al. 2000, Cardillo et al. 2005), and it may be influenced by species traits linked to the common evolutionary history of species (Willis et al. 2008). Our data do not reveal any phylogenetic pattern in the level of synchrony among species, and suggest that species traits that promote spatial synchrony are not necessarily shared by close relatives. Thus, although the upper thermal tolerance limit, the life-history strategies, and the dispersal abilities can be useful for identifying the species most at risk (i.e. most synchronized), the phylogeny, and the spatial synchrony in average annual temperature do not seem to be pertinent. This highlights the fact that we still know little about the causes of population synchrony, and further studies are clearly needed to determine the extent to which species characteristics can provide insights into the causes of population synchrony. So far, any such studies have focused on just a few taxa even though synchrony has been demonstrated in nearly all taxa. It would be very interesting to find out whether ecological, behavioral, or physiological characteristics are related to the level of synchrony in other taxa. Moreover, although it has already been demonstrated that the dispersal abilities of a species are related to population synchrony (Sutcliffe et al. 1996, Paradis et al. 1999), we have shown that the upper thermal tolerance limit as well as the life-history strategies can also be reliable predictors of this pattern. In a context of global change, it is of the utmost importance to find out whether this is a general pattern found in the various different taxa. If it is, this pattern could be helpful for elucidating the mechanisms underlying spatial synchrony, and identifying the species that should be priority targets for conservation.

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