RESEARCH PAPER

Fish community comparisons along environmental gradients in lakes of France and north-east USA

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ABSTRACT

Aim To assess whether eight traits of fish communities (species richness, three reproductive traits and four trophic traits) respond similarly to environmental gradients, and consequently display convergence between the lakes of France and north-east USA (NEUSA).

Location 75 French and 168 north-east USA lakes.

Methods The data encompass fish surveys, the assignment of species into reproductive and trophic guilds, and environmental variables characterizing the lakes and their catchments. The analytical procedure was adapted from the recommendations of Schluter (1986) [*Ecology*, **67**, 1073–1085].

Results The comparison of the regional pools of lacustrine fishes indicated that NEUSA was about twice as speciose as France, mostly due to higher species turnover across lakes, although NEUSA lakes were consistently about 20% more speciose than French lakes for a given surface area. Warmer environments were consistently inhabited by a higher proportion of phytophilous and guarder species than were colder lakes. Hence there was convergence in community reproductive traits. Conversely, there was no evidence of convergence in the trophic structure of lacustrine fish communities between regions.

Main conclusions The influence of temperature on the availability and quality of spawning substrates appears to be a major constraint on present-day lacustrine fish communities. In parallel, phylogenetic constraints, past events such as the diversification of the North American fish fauna, and selective extinctions during Pleistocene glaciations and subsequent recolonizations contribute to explaining the dissimilarities between the communities of the two regions and differences in their relationship to the environment.

Keywords
Fish community, lake, community convergence, ecological guilds, species richness, environmental gradients, species–area relationship, intercontinental comparison.

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INTRODUCTION

Although the present-day organization of local communities results from a combination of local and regional processes, and is consequently bounded by limits set by historical and biogeographical contexts (Ricklefs & Schluter, 1993), several patterns in the response of freshwater fish communities to the environment have been consistently identified across continents. For example, the dependence of richness upon the area surveyed (species–area relationships; SARs) has been quantified for many ecological groups including fish (see Rosenzweig, 1995; Gaston & Spicer, 2004 for reviews), at a variety of scales and for various types of freshwater ecosystem (Barbour & Brown, 1974; Eadie *et al.*, 1986; Rahel, 1986; Angermeier & Schlosser, 1989; Oberdorff *et al.*, 1995; Griffiths, 1997; Matthews & Robison, 1998). Riverine fish communities on different continents also show consistent patterns of species additions and changes in trophic structure along longitudinal gradients at the basin scale (Schlosser, 1982; Oberdorff *et al.*, 1993). Such consistent patterns in different phylogenetic contexts suggest that present-day environmental conditions represent a

strong selective pressure towards some community properties. They suggest that communities experiencing similar habitat conditions become more similar than their ancestors (Orians & Paine, 1983), i.e. some community traits converge along environmental gradients (Winemiller, 1991; Losos *et al.*, 1998).

Freshwater fish communities present several advantages for addressing intercontinental ecological convergence. First, they encompass a large number of taxa — around 10,000 true freshwater fish species (Nelson, 1994). They have colonized all the freshwater bodies except those isolated by dispersal barriers, or those undergoing extremely stressful abiotic conditions such as periodic dry-outs or long-term ice cover inducing oxygen depletion. Second, and certainly contributing to them being widespread, fish have evolved a broad array of life-history strategies and ecological traits (Winemiller, 1992; Winemiller & Rose, 1992; Vila-Gispert *et al.*, 2002). Thus, there is sufficient variation in these traits for natural selection to act upon as a response to environmental conditions, including biotic interactions. Third, at least in temperate regions, their ecological requirements, habitat and other life-history features are reasonably well documented (Lamouroux *et al.*, 2002).

However, intercontinental comparisons of lake fish communities have seldom been carried out. The two studies we are aware of compared small forested lakes of Wisconsin and Finland (Tonn *et al.*, 1990; Magnuson *et al.*, 1998). Communities were described using species richness and species assemblages as community descriptors. Therefore, it appears that the guild structure (suites of species traits) of lacustrine fish communities has never been compared across continents.

Hence, the general objective of the present paper is to test whether the structure of the lacustrine fish communities from north-east USA (NEUSA) and France display convergence. We hypothesized that species richness and the proportions of trophic and reproductive guilds would: (1) respond to the same environmental gradients; (2) that these responses would be similarly oriented in NEUSA and French lentic systems; and (3) that these responses would be quantitatively equivalent between regions.

MATERIALS AND METHODS

Throughout this article we refer to lakes of natural origin as 'natural lakes' (although some might have been deepened by human actions) and to lentic systems created artificially by damming as 'reservoirs'; we use the generic term 'lakes' for both types. Although this study compares the structure of fish communities between lake sets in different continents, they are far from representative of all lakes of each continent. Therefore, the differences between these two lake sets are regional effects rather than true continental effects.

The data set

The data encompass the results of fish surveys, the assignment of species into reproductive and trophic guilds, and environmental variables characterizing the lakes and their catchments. For both French and NEUSA data, lakes with fewer than four species were omitted because they were unlikely to contribute meaningfully to community-level inferences. The data comprise 75 French and 168 NEUSA lakes, including 51 and 58 reservoirs, respectively.

Fish survey data

Fish data of French lakes and reservoirs originate from various sources (research institutes, universities, consultants and administrative authorities) and were collected between 1977 and 2005. These sites have not been specifically selected to be representative of the heterogeneity among French lakes. However, they represent a broad array of environmental conditions that we consider covers most of the variability observed in French natural lakes and reservoirs. The lakes were sampled using gillnets series with mesh sizes ranging from 10 to 60 mm, but there was no standardized sampling strategy. Only the most recent survey was considered for those lakes that had been sampled on several occasions because the sampling was more consistent. We also included data obtained by collecting fish during reservoir draining operations. Further information on data collection is available from Argillier *et al.* (2002b) and Irz *et al.* (2002, 2004a).

The NEUSA sites were chosen as a random draw from the census of NEUSA lentic systems (Larsen *et al.*, 1994). The fish surveys were carried out from 1991 to 1995 according to the EMAP-surface waters protocols (Baker *et al.*, 1997). The samples included catches from gillnets, fyke nets, beach seines and electrofishing. Because the French data did not include an equivalent set of fishing gear, and due to the low efficiency of gillnets above 10 mm mesh size on the young-of-the-year (YOY), we excluded the YOY from the NEUSA data. Restricting the analyses to the gillnet catches would have provided more comparable data between regions but the catches of the different gears had been pooled, preventing us from distinguishing those of gillnets. Consequently, it is clear that some of the between-region differences in community structure are due to the heterogeneity in sampling methods. Such problems are inherent to broad-scale studies (Blackburn & Gaston, 1998, 2004). Therefore, when carrying out such studies one must assume that the signal-to-noise ratio of the data is high enough to ensure that, by appropriate statistical analysis, the signal may be recovered and correct generalizations derived (Pielou, 1977). The few published intercontinental comparisons of lake fish community patterns also had to deal with sampling inconsistency (Tonn *et al.*, 1990; Magnuson *et al.*, 1998).

Environmental parameters

Numerous environmental parameters were available to characterize local habitat (Fig. 1). We obtained mean annual air temperature (Tm; average of mean monthly values) and the minimum (Tmin) and maximum (Tmax) mean monthly air temperature at the lake centroid from a 10′ latitude/longitude data set of mean monthly surface climate over global land areas (New *et al.*, 2002). Elevation (Elev), catchment area (AreaWS), shoreline development (Shore) and lake area (Lkha) were determined by digitizing topographical maps, while mean depth was obtained during the surveys (Argillier *et al.*, 2002b; Irz *et al.*, 2002, 2004a; Whittier *et al.*,
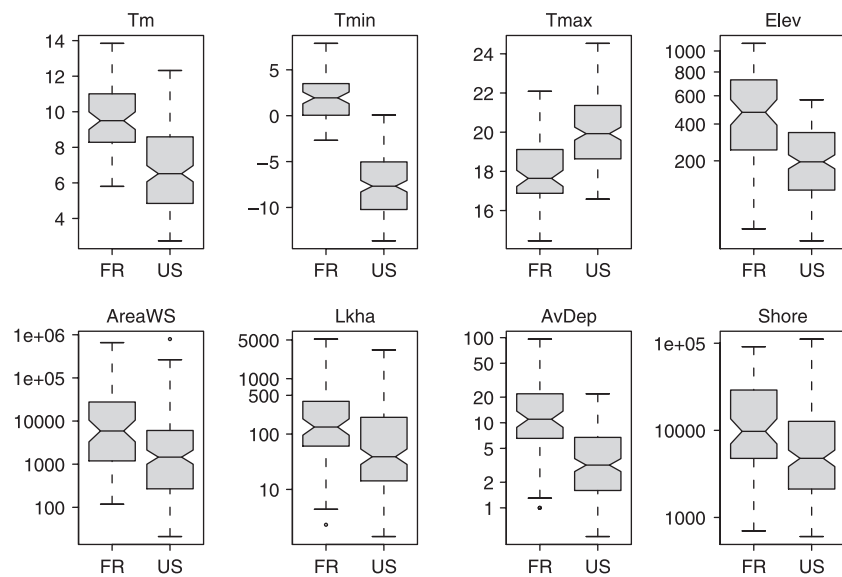
Figure 1 Box plots of features of the lakes of France (FR) and NEUSA (US): Tm = mean annual air temperature (°C); Tmin = minimum monthly air temperature (°C); Tmax = maximum monthly air temperature (°C); Elev = altitude a.s.l. (m); AreaWS = catchment area (ha); Lkha = lake area (ha); AvDep = mean depth (m); Shore = shoreline length (m).

Table 1 Pearson correlation coefficients between environmental variables for lakes of NEUSA (above the diagonal) and France (below the diagonal). Values over 0.4 are in bold and are highly significant ($P < 0.001$): Tm = mean annual air temperature (°C); Tmin = minimum monthly air temperature (°C); Tmax = maximum monthly air temperature (°C); sqrt(Elev) = square root[altitude a.s.l. (m)]; log(AreaWS) = log[catchment area (ha)]; log(Lkha) = log[lake area (ha)]; log(Shore) = log[shoreline length (m)]; log(AvDep) = log[mean depth (m)]

	Tm	Tmin	Tmax	sqrt(Elev)	log(AreaWS)	log(Lkha)	log(Shore)	log(AvDep)
Tm		**0.992**	**0.978**	**−0.672**	−0.137	−0.344	−0.231	−0.214
Tmin	**0.956**		**0.946**	**−0.631**	−0.127	−0.329	−0.211	−0.201
Tmax	**0.925**	**0.819**		**−0.737**	−0.142	−0.342	−0.241	−0.227
sqrt(Elev)	**−0.790**	**−0.759**	**−0.633**		−0.102	0.098	0.026	0.127
log(AreaWS)	0.138	0.164	0.149	−0.012		**0.697**	**0.729**	**0.441**
log(Lkha)	0.000	0.006	0.036	0.090	**0.716**		**0.948**	**0.681**
log(Shore)	0.059	0.091	0.091	0.092	**0.851**	**0.909**		**0.604**
log(AvDep)	−0.243	−0.220	−0.123	**0.456**	**0.485**	**0.633**	**0.588**	

2002). For graphical display and analyses, temperature data were not transformed, elevation was square-root transformed and the other variables were log-transformed.

Strong correlations appeared among the environmental parameters (Table 1). Two groups of variables could be distinguished: the first was related to air temperature, including elevation, while the second encompassed the attributes of lake size (shoreline length, mean depth, area of the catchment, lake volume). Hence, we chose Tm and log(Lkha) as weakly correlated habitat descriptors to represent these two groups.

These environmental parameters are likely to influence the composition of the communities in two distinct ways. Temperature is known to strongly affect patterns of fish communities (Rathert *et al.*, 1999) because it is one of the major dimensions of the ecophysiological requirements of fish species (Matthews, 1998), and is thereby related to the geographical distribution of individual species (Shuter *et al.*, 1980; Lelek, 1987; Shuter & Post, 1990). This parameter is also related to a broad range of other environmental parameters such as the water oxygen content (Matthews, 1998), and reflects an important aspect of the energy

availability within ecosystems (Lennon *et al.*, 2000; Evans *et al.*, 2004, 2005). Lake area had to be considered because the area of the sampled system is one of the most commonly recognized determinants of species richness in general (SARs; see Magurran, 1988; Rosenzweig, 1995 for reviews) and in lakes in particular (Barbour & Brown, 1974; Griffiths, 1997; Irz *et al.*, 2002, 2004a). Furthermore, lake area is tied to several other local (habitat diversity, stability) and connectivity features (catchment area) as shown in Table 1.

Species biological traits

Species were assigned to reproductive guilds according to Balon (1975) for French species and to Simon (1999b) for NEUSA ones (Table 2). The latter study extended the scope of the former to a larger array of North American species and in some cases updated the original classification according to more recent findings on the ecology of species. These classifications were based on the early development stages, spawning substrates and reproductive behaviour of species.

Table 2 List of the reproductive and trophic guilds used to derive community traits

	Trait code	Description
Reproductive guilds	LithPsam	Lithopsammophilous: can reproduce on mineral substrates
	LithPsam_strict	Strictly lithopsammophilous: need mineral substrates to reproduce
	Phyto	Phytophilous: can reproduce on vegetal substrates
	Phyto_strict	Strictly phytophilous: need vegetal substrates to reproduce
	Guarder	Guarders: exhibit parental care of the nests
Trophic guilds	Pisc	Piscivorous: feed on fish at least partially when adults
	Pisc_strict	Strictly piscivorous: feed exclusively on fish when adults
	Inv	Invertivorous: feed at least partially on invertebrates
	Inv_strict	Strictly invertivorous: feed exclusively on invertebrates
	Herb	Herbivorous: feed on vegetal items
	Herb_strict	Strictly herbivorous: feed exclusively on vegetal items
	Omn	Omnivorous: feed on both animal and vegetal items
	Benth	Benthophagous: feed mainly on benthic items
	Benth_strict	Strictly benthophagous: feed exclusively on benthic items

Trophic guild classifications were based on Bruslé and Quignard (2001) and Keith and Allardi (2001) for France and on a literature survey for NEUSA (Whittier, 1999). *Noturus insignis* was considered a benthic invertivore like the other *Noturus* species listed in Simon (1999a).

Community traits

Although analysis of density or abundance data would have been highly valuable, the French census data were too heterogeneous to allow assessment of such quantitative variables. Therefore, we limited our investigations to community traits that could be derived from species presence/absence data.

The first of these traits was species richness (SR). Then, fish survey data and species guilds were combined to obtain variables corresponding to community reproductive traits (CRTs) and community trophic traits (CTTs) in terms of proportions of the total species richness belonging to functional guilds (see Table 2; e.g. the trait 'Phyto' was calculated for each lake as the ratio of the number of phytophilous species to the species richness). As many species can spawn on various substrates and feed on several items, we initially considered two ways of deriving the traits (Table 2). The first was a strict encoding (e.g. Phyto_strict is the proportion of species that need macrophytes to spawn) and the second corresponded to the species ability (e.g. Phyto is the proportion of species that are able to spawn on macrophytes). However, the two sets of traits were strongly correlated (Table 3), so we removed those derived from the strict encoding. For example, Inv and Pisc_strict were almost complementary because few species feed exclusively on items including neither fish nor macro-invertebrates. Thus, interpreting variations for Inv is similar to interpreting those for Pisc_strict.

The trait Herb (Herbivores) was also removed because it was redundant with Omn (Omnivores). Despite these deletions, some correlations remained among community traits, reflecting the limited number of combinations in ecological traits among species and the non-independence of reproductive and trophic guilds. In the final data sets, Pisc and Guarder and Pisc and Benth for both lake types, and Benth and Guarder in reservoirs, had r values $> | 0.5 |$ (Table 3).

Analytical procedure

The analytical procedure was designed to assess whether lacustrine fish communities on the two continents displayed convergence in terms of species richness, CRT and CTT composition. An indirect methodology has been proposed to detect community convergence if data are available from local communities in contrasted habitats (Schluter, 1986). This methodology relies upon partitioning the variance in community traits into a habitat component (common between regions), a regional component (differences between regional groups that persist regardless of habitat), to which an interaction component, habitat × region, was added as an indicator of between-region quantitative difference in responses to habitat conditions (Lamouroux *et al.*, 2002).

We ran the analyses separately for natural lakes and reservoirs because there was no a priori reason to assume that their fish communities respond similarly to environmental gradients (Irz *et al.*, 2006). However, when the separate models for a given community trait exhibited similar trends, both lake types were pooled to obtain final models.

Considering that the presence of exotic species homogenizing the regional and local fish faunas could modify the likelihood of detecting convergence, the analytical procedure for convergence assessment has also been carried out on a data set excluding the exotics.

Comparison of regional species pools

The objective of this analysis was to interpret whether observed dissimilarities in community traits could be affected by differences in regional species pools. Hence, differences between the structures of the regional pools were assessed using chi-square tests between regions and species binary traits. Although this was

Table 3 Pearson correlation coefficients between fish community traits for lakes and reservoirs of NEUSA (above the diagonal) and France (below the diagonal). Values over 0.6 are in bold. See Table 2 for trait descriptions

	log(SR)	LithPsam	LithPsam_strict	Phyto	Phyto_strict	Guarder	Pisc	Pisc_strict	Inv	Inv_strict	Herb	Omn	Benth	Benth_strict
log(SR)		0.162	0.198	−0.214	−0.203	−0.119	−0.185	−0.047	0.042	0.213	−0.070	−0.077	0.128	0.140
LithPsam	0.125		0.223	−0.150	**−0.856**	−0.029	−0.019	−0.203	0.176	−0.065	0.132	0.109	0.012	−0.018
LithPsam_strict	0.127	0.377		**−0.908**	−0.209	−0.008	0.051	−0.278	0.240	0.082	0.068	0.040	−0.078	0.032
Phyto	−0.129	−0.310	**−0.905**		0.208	−0.014	−0.065	0.266	−0.232	−0.085	−0.028	0.000	0.096	−0.013
Phyto_strict	−0.163	**−0.829**	−0.343	0.345		0.006	0.007	0.200	−0.176	0.053	−0.098	−0.076	0.017	0.054
Guarder	0.079	−0.068	−0.242	0.236	0.039		**0.648**	−0.165	0.181	−0.449	0.034	0.047	**−0.637**	−0.598
Pisc	−0.093	−0.116	−0.099	0.072	0.073	0.475		−0.076	0.087	**−0.711**	0.135	0.148	**−0.716**	**−0.723**
Pisc_strict	−0.078	−0.221	−0.444	0.438	0.212	0.268	0.247		**−0.949**	−0.035	−0.074	−0.048	0.111	0.042
Inv	0.073	0.219	0.440	−0.435	−0.210	−0.270	−0.245	**−0.996**		0.024	0.066	0.074	−0.125	−0.066
Inv_strict	0.178	0.130	0.254	−0.231	−0.098	−0.361	**−0.817**	−0.371	0.366		−0.340	−0.350	**0.644**	**0.770**
Herb	−0.265	0.038	0.033	0.013	0.056	−0.150	0.037	−0.125	0.125	−0.139		**0.964**	−0.156	−0.241
Omn	−0.269	0.037	0.031	0.014	0.056	−0.150	0.039	−0.125	0.127	−0.141	**0.998**		−0.168	−0.258
Benth	0.184	0.191	0.026	−0.009	−0.170	−0.276	−0.539	−0.160	0.156	0.418	0.049	0.047		**0.846**
Benth_strict	0.236	0.135	0.090	−0.075	−0.103	−0.284	−0.551	−0.179	0.176	0.489	−0.062	−0.065	**0.871**	

not strictly rigorous since the species pools were not totally independent (11/111 species were present in both regions: *Carassius auratus*, *Cyprinus carpio*, *Esox lucius*, *Lepomis gibbosus*, *Lota lota*, *Micropterus salmoides*, *Oncorhynchus mykiss*, *Salmo trutta*, *Salvelinus alpinus*, *Salvelinus namaycush*, *Scardinius erythrophthalmus*), we used significant *P*-values as indicators of trait differences.

In order to assess whether differences in regional richness arose from differences in the numbers of sites between regions or indicated differences in patterns of distribution of diversity, we constructed species accumulation curves. Such curves are plots of the cumulative number of species, SR(*n*), within a defined area, as a function of some measure *n* of the effort needed to find them (Colwell & Coddington, 1994). In our case, *n* was the number of lakes sampled. We plotted the mean cumulative number of species found in 100 random draws of lakes as a function of the number of lakes using E STIMATE S software (Colwell, 1997).

Convergence assessment

The analytical procedure is summarized in Fig. 2. In the different steps, we modelled species richness and the other community traits differently. For species richness, we used linear models of the log-transformed species richness. For the other community traits we used generalized linear models (GLMs), with binomial error distributions and a logit link function. This kind of model presents the following advantages over linear models in analysing the response of proportionality data: (1) it does not assume constancy of variance, but instead models it as a function of the mean; (2) it weights proportions by the number of observations (1/2 is given less weight than 500/1000); and (3) it constrains the response variable between 0 and 1.

In order to quantify the variability accounted for by the models, we used the pseudo *R*-square (Crawley, 2005) calculated as:

$$R^2 = 1 - \text{(residual deviance)}/\text{(null deviance)}.$$

All the analyses were performed with the free software R 2.2.1 (R Development Core Team, 2005).

We followed a five-step hierarchical analytical procedure summarized in Fig. 2:

Step 1: To identify the community traits significantly influenced by environmental gradients, species richness, CTTs and CRTs were modelled, for each lake type and region, as a function of log(Lkha) and Tm. If the model slopes were significant for the same explanatory variable, we proceeded to step 2. If the slope was significant in only one region, there was no convergence (case 5, Fig. 2). If slopes were not significant for NEUSA and for French lakes, we simply tested whether the community traits differed on average between regions [analysis of variance (ANOVA) for species richness and analysis of deviance for the guild structure parameters]. If traits differed, we inferred between-region dissimilarity (case 7, Fig. 2) and similarity (case 6, Fig. 2) otherwise.

Step 2: To test whether the community traits responded in the same direction to a given explanatory variable in the two regions, we examined the signs of the significant slopes from step 1. Similar signs between continents indicated at least qualitative
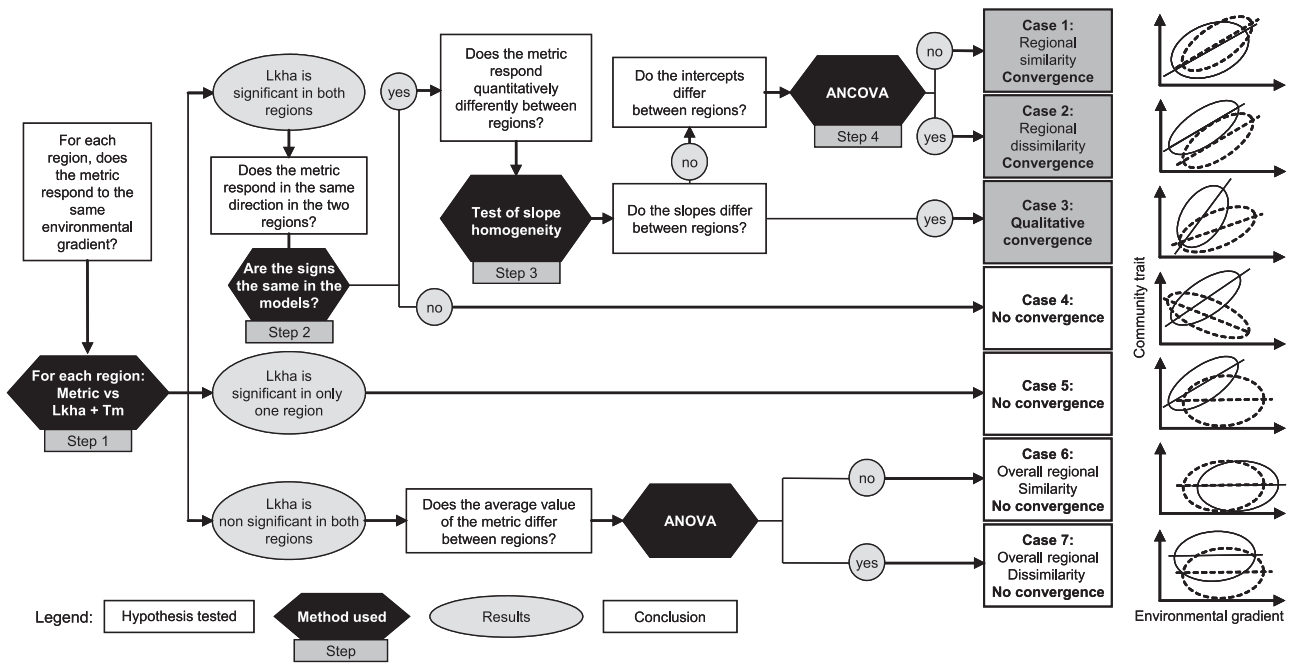
Figure 2 Summary of the conceptual framework and the analytical procedure implemented to test for between-region similarities in fish community traits along environmental gradients. Only lake area (Lkha) is shown here; similar procedures were followed for temperature (Tm). Conceptual representations for each case are shown on the right.

convergence (cases 1 to 3) and we proceeded to step 3. Conversely, opposite signs indicated an absence of convergence (case 4; never met in our data).

Step 3: To detect quantitative differences in the responses between regions, we tested whether the hypothesis of common slopes in both continents was rejected (i.e. if the interaction term habitat × region was significant). This step was carried out by means of analyses of covariance (ANCOVA) only for those community traits × lake type combinations for which the signs of the coefficients indicated a common direction of response between regions. A significant difference between slopes indicated that the convergence was only qualitative (case 3).

Step 4: When slopes did not differ significantly in step 3, the interaction term was removed from the model and an ANCOVA was performed to test for significant differences between intercepts. A significant difference indicated convergence in the intensity of the response to the environmental gradient, despite an overall regional dissimilarity (case 2). The non-significance of both indicated convergence and an absence of regional dissimilarity (case 1).

Step 5: If both lake types corresponded to the same case in Fig. 2, we pooled the data and rebuilt the model with lake type as a factor (with possible interactions with the other terms). Non-significant terms were removed step-by-step to obtain the final model. This allowed us to detect differences in response according to region, lake type or both.

In step 1, a hierarchical partitioning procedure (Chevan & Sutherland, 1991) was implemented to identify the environmental gradient that was most influential on local community traits using a modification of the hier.part R package (Mac Nally &

Walsh, 2004). This procedure allows the assessment of the independent contribution of each explanatory variable to the modelled variance by processing all the possible models that do not include the variable of interest, then adding it and calculating the mean improvement of the goodness-of-fit (pseudo R-square) attributable to this variable. Steps 2 to 5 were carried out separately for the responses to Tm and log(Lkha) because none of the community traits appeared to respond simultaneously to both variables in both regions.

RESULTS

Comparability of lakes between regions

On average, the French natural lakes and reservoirs were slightly warmer, but they clearly experienced a smaller annual temperature range and less harsh winter conditions than NEUSA lakes (Fig. 1). One of the difficulties in convergence studies is that the environment is never totally similar across regions (Orians & Paine, 1983). Our data were no exception. However, despite these differences, all the environmental variables overlapped across regions and their standard deviations had the same order of magnitude (apart from depth). Therefore, we considered that the two sets of lakes were similar enough to provide meaningful comparisons of the responses of fish communities to habitat conditions.

Overall comparison of regional lacustrine fish fauna

The number of species occurring in NEUSA lakes was 83 vs. 39 in French lakes (Table 4). NEUSA natural lakes were about twice as

Table 4 Distribution of the fish species sampled from NEUSA (US) and France (FR) across families and functional guilds (see Table 2 for trait codes)

		Region	
		FR	US
Family	Amiidae		1
	Anguillidae	1	1
	Aphredoderidae		1
	Atherinidae		1
	Balitoridae	1	
	Blenniidae	1	
	Catostomidae		6
	Centrarchidae	2*	13
	Clupeidae		2
	Cobitidae	1	1
	Cyprinidae	19	24
	Cyprinodontidae		2
	Esocidae	1	2
	Gasterosteidae		3
	Ictaluridae	1*	6
	Lepisosteidae		1
	Lotidae	1	1
	Mugilidae	1	
	Osmeridae		1
	Percichthyidae		1
	Percidae	3	5
	Percopsidae		1
	Poecilidae	1*	
	Salmonidae	5	8
	Sciaenidae		1
	Siluridae	1	
	Umbridae		1
Functional guild	Lithopsammophiles	29	63
	Phytophiles	20	38
	Guarders	8	30
	Piscivores	15	42
	Invertivores	36	74
	Omnivores	10	18
	Benthivores	17	19

*exclusively composed of exotic species.

speciose as French natural lakes, regardless of the differences in number of sites sampled (Fig. 3). This difference was slightly lower in reservoirs, but a random draw of 51 NEUSA reservoirs on average contained 51.6 species as compared with 36 observed in French reservoirs.

The distribution of species across families (Table 4) revealed that 13 families were found exclusively in NEUSA while four were only found in France. The Cyprinidae was by far the most speciose family in both regions, encompassing half the total species in France. The Centrarchidae was the second most speciose family in NEUSA. In France, 10/14 families were represented by a single species. This ratio was 12/22 in NEUSA. The numbers of lithopsammophiles, phytophiles, invertivores and omnivores in NEUSA were about twice those in France (Table 4), therefore
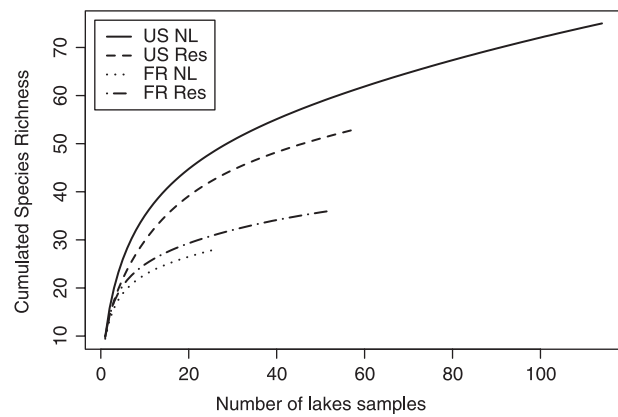
Figure 3 Rarefaction curves indicating the cumulative number of species found in random draws of lakes differing in number for the natural lakes (NL) and reservoirs (Res) of NEUSA (US) and France (FR).

their proportional importance did not differ across regions (chi-square test, $P > 0.7$). Conversely, NEUSA lakes had a low proportion of benthic feeders ($P = 0.01$) and a high proportion of guarders and piscivores ($P = 0.12$ and 0.29, respectively) compared with French lakes.

Response of community traits to habitat variables within a region

Fifteen of 16 community trait × lake type combinations were significantly explained by at least one habitat variable in the NEUSA data, but only 6/16 were significant in the French data (Table 5).

Species richness

Species richness was positively related to the lake surface area regardless of the type of lake or region (Table 5). The independent contribution of log(Lkha) in explaining the variation in log(SR) (p_Lkha) ranged from 30 to around 50% and was strongest in NEUSA. Species richness also increased significantly with mean annual air temperature (Tm) in the NEUSA natural lakes and reservoirs.

Community traits

Nine out of 12 CRT models were significant. The proportion of lithopsammophilous species (LithPsam) was not significantly related to the environment except in NEUSA natural lakes where it decreased with Tm and increased with log(Lkha). Phyto increased with Tm regardless of the type of lake or region and decreased with log(Lkha) in French reservoirs and NEUSA natural lakes. In both regions Guarder responded (negatively) to log(Lkha) in reservoirs (despite a Tm effect in NEUSA) and exclusively (positively) to Tm in natural lakes. Altogether, Tm significantly entered eight models and log(Lkha) entered five.

All the CTTs responded to habitat variables in NEUSA but none did in France (Table 5). In NEUSA, Pisc decreased with log(Lkha) in reservoirs and increased with Tm in natural lakes; Inv decreased

Table 5 Summary of models of community traits in reservoirs (Res) and natural lakes (NL) in France (FR) and in north-east USA (US) vs. mean annual air temperature (Tm) and log-transformed lake area [log(Lkha)]. Species richness (SR) models are multiple regressions. The other community trait models are generalized linear models with binomial distribution errors (link function: logit). Table entries are model coefficients, independent contributions of explanatory variables to the adjusted *R*-square (p_Tm and p_Lkha), residual deviance (Dev.), and model significance (Sig.). See Table 2 for trait descriptions

Lake type	Trait	Region	Intercept	Tm	log(Lkha)	p_Tm	p_Lkha	Dev.	Sig.
Reservoirs									
FR: *n* = 51	log(SR)	FR	1.561***	0.000	**0.124***	0.007	0.293	—	***
US: *n* = 58		US	1.221***	0.045*	**0.160***	0.028	0.490	—	***
	LithPsam	FR	0.669	0.003	0.096	0.002	0.072	19.296	
		US	1.678**	−0.085	0.073	0.093	0.065	27.596	
	Phyto	FR	0.242	**0.190**	−0.172*	0.127	0.088	57.275	***
		US	−0.233	**0.136**	−0.077	0.152	0.058	47.894	**
	Guarder	FR	−1.727	0.117	**−0.273**	0.054	0.147	48.581	**
		US	−0.998*	0.173***	**−0.112***	0.295	0.136	31.489	***
	Pisc	FR	0.388	−0.013	−0.021	0.002	0.003	24.008	
		US	4.079***	−0.094	−0.296***	0.010	0.168	73.914	***
	Inv	FR	2.610*	−0.073	0.001	0.033	0.001	24.212	
		US	2.458**	0.076	−0.211**	0.038	0.165	36.700	**
	Omn	FR	−1.119	0.003	0.118	0.004	0.124	20.316	
		US	0.473	−0.035	−0.198***	0.008	0.396	21.627	***
	Benth	FR	−0.983	0.034	−0.002	0.012	0.001	28.406	
		US	−2.089*	−0.219*	0.235*	0.088	0.092	52.513	**
Natural lakes									
FR: *n* = 24	log(SR)	FR	1.548***	−0.004	**0.123**	0.006	0.329	—	**
US: *n* = 110		US	1.042***	0.059***	**0.189***	0.056	0.503	—	***
	LithPsam	FR	0.469	0.142	−0.062	0.202	0.012	12.058	
		US	1.423***	−0.131***	0.112*	0.178	0.102	59.825	***
	Phyto	FR	−0.395	**0.211**	−0.095	0.222	0.014	27.987	*
		US	−1.041***	**0.290***	−0.102*	0.452	0.077	86.381	***
	Guarder	FR	−7.921***	**0.393***	0.224	0.463	0.175	11.061	***
		US	−2.062***	**0.256***	−0.018	0.352	0.015	105.580	***
	Pisc	FR	−0.115	0.043	−0.043	0.054	0.026	7.995	
		US	1.249**	0.141**	−0.094	0.074	0.031	150.965	***
	Inv	FR	2.432**	−0.028	−0.027	0.019	0.012	6.578	
		US	3.473***	−0.213***	0.002	0.147	0.004	99.561	***
	Omn	FR	−0.424	0.078	−0.120	0.195	0.287	3.548	
		US	0.362	−0.062	−0.149***	0.027	0.152	64.658	***
	Benth	FR	−1.905**	0.047	0.121	0.079	0.202	9.541	
		US	−2.886***	−0.154*	0.192*	0.054	0.059	105.615	***

*P < 0.05, **P < 0.01, ***P < 0.001.

with log(Lkha) in reservoirs and with Tm in natural lakes; and regardless of the lake type, Omn decreased with log(Lkha) while Benth decreased with Tm and increased with log(Lkha). Consequently, lake area was the main explanatory variable explaining CTTs (significant in 6/8 NEUSA models), particularly in reservoirs.

In NEUSA lakes, the models were consistent among lake types for Omn and Benth. The models that were not significant in French reservoirs (LithPsam and all the CTTs) were also not significant in natural lakes. For the other community traits, some differences appeared between lake types; however, there was no case of an opposite significant response to an environmental gradient between lake types.

When averaged over lake types and continents, the respective contributions of Tm (p_Tm) and log(Lkha) (p_Lkha) to CRTs

were 21% and 8%, respectively, while the contributions to CTTs were 5% and 11%, respectively.

When averaged over lake types and community traits, the respective contributions of Tm and log(Lkha) to community traits in French lakes were 11% and 8%, respectively, while the contributions were 15% and 10%, respectively, in NEUSA lakes.

When averaged over continents and community traits, Tm and log(Lkha), respectively, explained 7% and 11% of the variation in reservoir community traits compared to 20% and 8% in natural lakes.

Between-regions comparison

The analysis of deviance comparing the proportions of LithPsam in reservoirs (the only trait that displayed no relationship to habitat
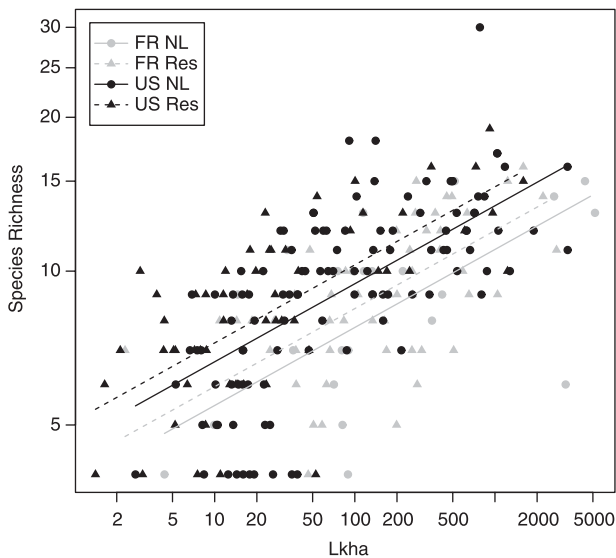
Figure 4 Log–log scatterplot of species richness vs. lake area (Lkha) for the natural lakes (NL) and reservoirs (Res) of NEUSA (US) and France (FR) with models fitted by the ANCOVA analysis (assumption of similar slopes not rejected).

variables) versus regions showed that the proportions of species belonging to this reproductive guild did not differ between regions ($P = 0.995$). The hypothesis of similar proportions in the two regions was not rejected and this pattern corresponds to case 6 in Fig. 2. The community traits that were significantly related to the same habitat variables in both regions were the same for natural lakes and reservoirs and displayed the same direction of response between continents (Table 5). Consequently, these effects were compared.

For species richness, slopes did not differ significantly between lake types or between regions in the pooled data set (natural lakes and reservoirs of both regions) (Fig. 4 and Table 6). However, the ANCOVAs revealed that intercepts differed significantly, indicating that, for a given area, NEUSA lakes were more speciose than French lakes ($P < 0.001$) and that reservoirs were more speciose than natural lakes ($P = 0.029$). Hence, the observed SARs indicated both convergence and regional dissimilarities

(case 2 in Fig. 2). Analyses omitting the exotic species led to similar results, except that the difference between natural lakes and reservoirs was no longer significant ($P = 0.33$).

The other two traits submitted to ANCOVA were Phyto and Guarder (Table 6). A single model could be fitted for Phyto (Fig. 5a), with no differences either in slopes or in intercepts across regions or lake types ($R^2 = 0.45$, case 1). This trait was therefore the only one displaying convergence and regional similarity. Guarder only differed in intercepts between regions in its response to Tm in natural lakes (Fig. 5b) and log(Lkha) in reservoirs, thereby indicating convergence despite overall regional dissimilarities (case 2 in Fig. 2). Excluding exotics did not change the nature of the relationships for natural lakes ($R^2 = 0.50$ for Phyto and 0.61 for Guarder). Conversely, the increase in Phyto and Guarder with Tm was no longer significant for French reservoirs (case 5 in Fig. 2).

DISCUSSION

The aim of the present study was to assess whether eight traits of fish communities (species richness, three reproductive traits and four trophic traits) responded similarly to environmental gradients, and thus displayed convergence, between the lentic systems of NEUSA and France. Only Phyto conformed to case 1 (convergence with no significant regional dissimilarity), regardless of the lake type (Fig. 2, Table 7). Species richness and Guarder corresponded to case 2 (convergence despite regional dissimilarity), in both lake types. Thus, convergence was detected in six out of 16 community trait × lake type combinations and was restricted to SR and CRTs. Variability in species richness was mainly due to lake size, whereas CRTs exhibited a clear response to mean annual air temperature.

Among the 10 traits that did not display convergence, only LithPsam in reservoirs indicated no overall regional dissimilarity (case 6). The nine other community trait × lake type combinations (LithPsam in natural lakes and all CTTs for both lake types) responded to the environmental gradients in NEUSA only, corresponding to case 5. Cases 3, 4 and 7 were never observed. In sum, there was no sign of convergence in the trophic structure of lacustrine fish communities across regions.

Table 6 Summary of final models of species richness (SR, linear models) and proportions of species (generalized linear models; distribution error, binomial; link function, logit) belonging to reproductive guilds vs. log-transformed lake area log(Lkha) or temperature (Tm). Lake type: natural lake (NL) or reservoir (Res). Dev: residual deviance of the model. d.f.: residual degree of freedom. R^2: pseudo R-square. See Table 2 for trait descriptions

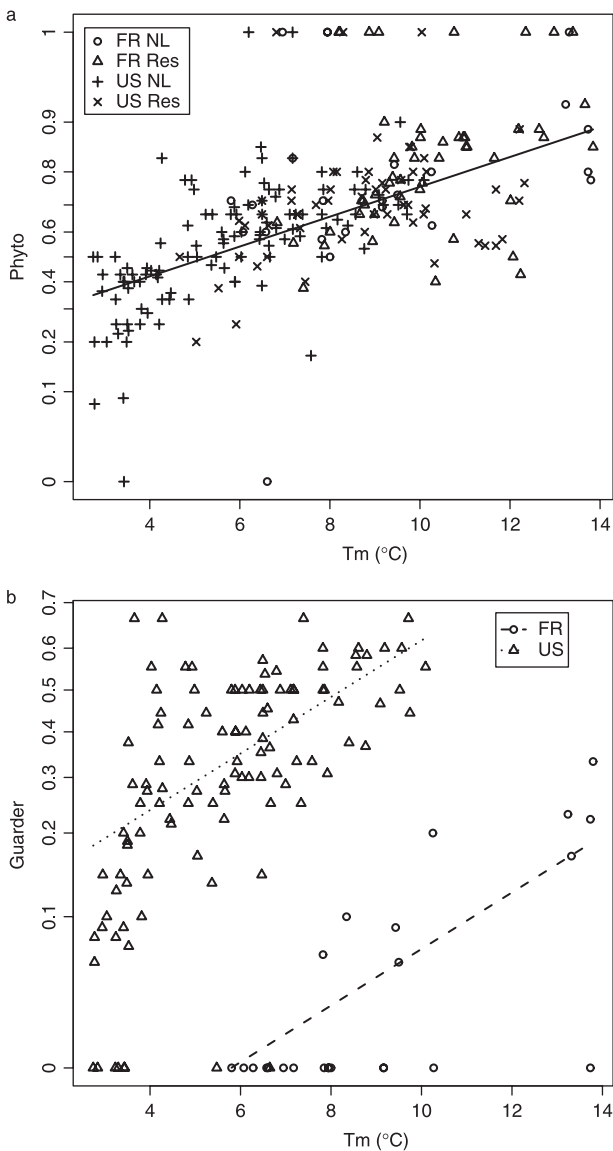| Trait	Lake type	Intercept	Difference in intercept (compared to USA)	Difference in intercept (compared to reservoirs)	log(Lkha)	Tm	Deviance	d.f.	R^2
log(SR)	Res + NL	1.346***	0.197***	0.085 *	0.153***	—		239	0.436
Guarder	NL	−5.251***	2.991***	—	—	0.274***	121.9	131	0.555
Guarder	Res	−0.971***	1.736***	—	−0.181***	—	98.1	106	0.673
Phyto	Res + NL	−1.291***	—	—	—	0.243***	245.6	241	0.454

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Figure 5 Examples of relationships between community reproductive traits and mean annual temperature (Tm). (a) Phyto (percentage of phytophiles, logit scale) with a single model fitted for NEUSA (US) and France (FR) and natural lakes (NL) and reservoirs (Res). (b) Guarder (percentage of the species that spawn in a nest and guard it, logit scale) with different trend curves fitted for natural lakes and reservoirs of NEUSA and France. Trends assessed using GLM with binomial error distribution and logit link function.

Regional species pools

The regional pool of lacustrine fishes in NEUSA was about twice as speciose as in France, comparable to the differences between lake fish communities of Wisconsin and Finland (Tonn *et al.*, 1990) and the rivers of Poland and Ontario (Mahon, 1984). Indeed, the stream fish faunas of western Europe and of North America west from the Rocky mountains are more similar to each other than communities from north-eastern America, both

in terms of richness and ecological features (Moyle & Herbold, 1987). The main taxonomic differences between regions are the presence of Centrarchidae, Catostomidae and Ictaluridae and the diversification of small Percidae (darters) and Cyprinidae (minnows) in North America, which explains its higher species richness. These taxonomic differences also contribute to overall differences in the structure of the regional fauna such as the higher proportions of piscivores and guarders in NEUSA lakes than in French lakes. The differences in climatic conditions between the two study regions during glacial periods (harsher in Europe) as well as in the layout of their hydrographic networks explain most of the differences between the regional faunas (Mahon, 1984).

Species–area relationships

The slope of the log–log SAR obtained from our data (0.153) is less than that observed on small forested lakes in Wisconsin (0.32) and in Finland (0.34) (Tonn *et al.*, 1990). That study, however, included much smaller lakes than ours and the slope of the SAR may differ between small and large lakes (Griffiths, 1997) due to higher extinction rates in small biogeographical units (Reyjol *et al.*, 2007).

Our results revealed convergence in SR between the lacustrine fish communities of NEUSA and France. Despite a significant increase in SR with temperature detected in NEUSA natural lakes, lake area appears to be a major determinant of local richness, with consistent quantitative effects across lake types and regions. Earlier studies comparing lake fish communities of Wisconsin and Finland also identified convergence in SARs (Tonn *et al.*, 1990; Magnuson *et al.*, 1998).

At least four hypotheses have been proposed to account for the SARs in lake systems. (1) Larger lakes could be more speciose because they contain more individuals than small ones. It has been shown that, for a set of individuals belonging to species following the classical log-normal species abundance distribution and distributed randomly across a given surface, the individuals contained in successively larger areas tended to belong to a higher number of species (Coleman, 1981; Coleman *et al.*, 1982). (2) This relationship could be a consequence of the reduced environmental (physico-chemical) stability of small lakes as compared with large ones. Such temporal fluctuations in habitat conditions could increase local extinction risks (Jackson *et al.*, 2001). (3) The habitat diversity hypothesis (Williams, 1943; MacArthur & Wilson, 1967; Diamond, 1975) suggests that the heterogeneity of the habitat (and consequently the diversity of food resources) increases with the size of the area, thus offering a larger number of niches and favouring the coexistence of a larger number of species (Williamson, 1988). (4) The SAR could reflect the outcome of an equilibrium between stochastic extinction and colonization events (MacArthur & Wilson, 1967). The island biogeography theory states that the rates of colonization depend on the degree of isolation of the islands (i.e. distance to the mainland), while the rates of extinction are size dependent. Thus, the equilibrium richness increases with island area and decreases with island isolation. Lake ecosystems share a number of

Table 7 Summary of the convergence tests referring to the cases displayed in Fig. 2 for natural lakes (NL) and reservoirs (Res). The environmental gradients used to assess convergence are indicated (Lkha, lake area; Tm, mean annual air temperature). See Discussion for an explanation of the table. See Table 2 for community trait abbreviations

Cases	log(SR) NL	log(SR) Res	LithPsam NL	LithPsam Res	Phyto NL	Phyto Res	Guarder NL	Guarder Res	Pisc NL	Pisc Res	Inv NL	Inv Res	Omn NL	Omn Res	Benth NL	Benth Res
1					Tm	Tm										
2	Lkha	Lkha					Tm	Lkha								
5			×						×	×	×	×	×	×	×	×
6				×												

×= no convergence; when the variable name is given = convergence was detected.

Table 8 Pearson correlation coefficients between the log-transformed lake area log(Lkha), number of individuals sampled log(NIS) and species richness log(SR) obtained for north-east USA natural lakes and reservoirs

	log(Lkha) vs. log(NIS)	log(NIS) vs. log(SR)	log(SR) vs. log(Lkha)
Natural lakes	0.382***	0.291***	0.656***
Reservoirs	0.536***	0.341**	0.59***

$*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

common features with islands (Barbour & Brown, 1974; Magnuson, 1976; Browne, 1981; Eadie *et al.*, 1986; Magnuson *et al.*, 1998). They are isolated from each other and colonization events are rare because connections between lakes are mainly through flowing waters that limit dispersal for limnophilous fishes.

In the first hypothesis, lake size would determine the number of individuals in the lake, that would in turn determine the number of species. Hence, if we assume that the fish survey samples are representative of the distribution of the individuals across species at the lake scale, this hypothesis should lead to stronger correlations between log(Lkha) and the log-transformed number of individuals in the samples log(NIS), and between log(NIS) and log(SR), than directly between log(Lkha) and log(SR) (Angermeier & Schlosser, 1989). This is not the case in NEUSA lakes (Table 8), so this hypothesis is not likely to explain the observed SAR in this region (NIS was not available for French lakes, and thus not used in our study).

The three other hypotheses are not mutually exclusive. Except for the great lakes (e.g. Baikal, Victoria), lakes are generally not speciation sites due to their geologically ephemeral nature (Matthews, 1998). So, the number of species they shelter is the outcome of colonization and local extinctions. The last three hypotheses represent different processes influencing species richness through their action on the rates of colonization or extinction. Therefore, they can be represented in the framework proposed in Fig. 6. Assessing the relative importance of the different pathways through which lake area influences species richness would require data on the level of isolation and an assessment of the within-lakes habitat diversity as well as the monitoring of the physico-chemical properties of waters. Such data are not currently available.

Scale and species richness

Different spatial scales can be considered when analysing patterns of species richness (Whittaker, 1972). The regional richness (gamma diversity) can be estimated by several methods, but if we consider it as the cumulated species occurring in the localities in the regions compared, NEUSA natural lakes are about twice as speciose as French ones.

In a given region, gamma diversity can be expressed as the sum of the mean local (alpha) diversity and the turnover (beta) diversity (Loreau, 2000). So, the higher gamma diversity in NEUSA lakes compared with French lakes could be due to higher mean alpha diversity, higher beta diversity or both. In the model corresponding to Fig. 4, the intercept difference between NEUSA and France is 0.197 (Table 6) on a log–log scale. This means that for a given surface area, the local species richness in a NEUSA lake is $e^{0.197} =$ 1.22 times that of a French lake. Hence, the higher alpha diversity in NEUSA lakes explains only a small portion of the two-fold difference in gamma diversity and therefore beta diversity is higher in NEUSA. A comparison of the small forested lakes of Finland and Wisconsin (Tonn *et al.*, 1990) also identified higher beta diversity in North American lakes. The relationship between alpha, beta and gamma diversity has been used to infer saturation of local communities (Cornell, 1985a,b; Hugueny & Paugy, 1995; Oberdorff *et al.*, 1998) with proportionality among the three considered to be indicative of unsaturated communities. Conversely, the independence of alpha over gamma diversity or the tendency of the ceiling of alpha diversity to be equivalent to high values of gamma diversity would indicate that local conditions tend to set a limit to the number of species that can coexist within local communities. However, great care is needed in interpreting such patterns (Lawton, 1999; Srivastava, 1999; Hillebrand & Blenckner, 2002; Mouquet *et al.*, 2003; He *et al.*, 2005; Hillebrand, 2005; Shurin & Srivastava, 2005).

Although comparing two regions has limited power to determine the shape of a local–regional species richness plot, we found that individual NEUSA lakes are only 20% more speciose than French lakes despite a species pool that is twice as speciose.
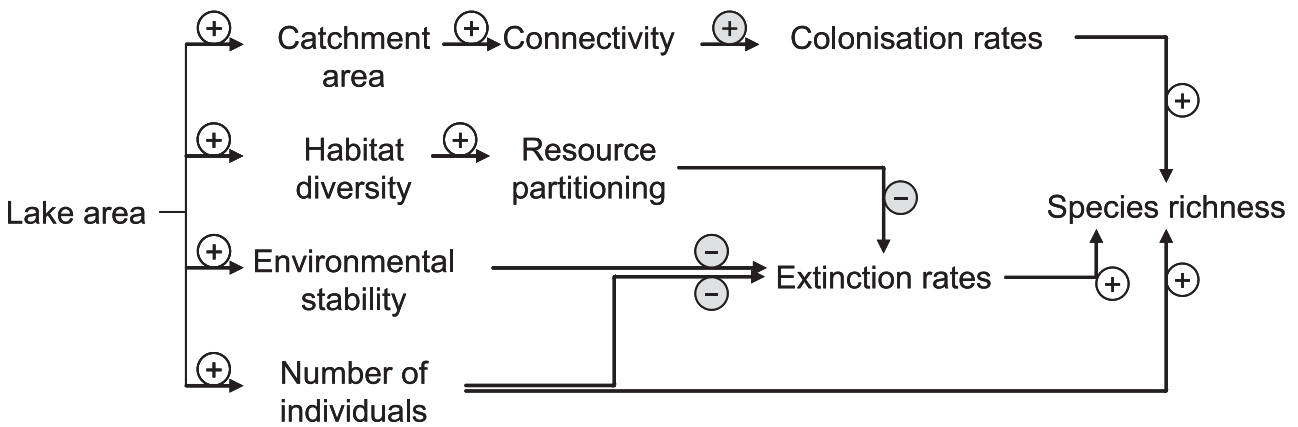
Figure 6 Synoptic representation of various processes potentially contributing to the increase in fish species richness with lake size. The signs indicate the direction of the effects. The shaded signs are those influenced by the regional species pool.

That is, the regional differences in local and regional richness are not proportional. However, for such analytical approaches to allow meaningful inferences about the relative importance of local versus regional processes in determining local species richness, it is important that the regional species be precisely assessed as the pool of potential colonizers of individual lakes (Srivastava, 1999). In our study, this regional pool is clearly overestimated because both the NEUSA and the French regions encompass several basins. This may explain why our results seem to partially contradict earlier studies in France on almost the same set of lakes (Irz *et al.*, 2004a) and in North America on different data (Griffiths, 1997), both indicating proportionality between local and regional species richness for the native fishes, a result that is blurred when introduced species were included in the analyses. Consequently, an important part of the beta diversity may be attributed to the between-basin turnover in species. The basin is an intermediate spatial scale that should be considered to obtain more comprehensive inferences on the patterns of distribution of fish diversity relating broad regions and local biota (Tonn, 1990).

Reproductive traits of lake fish communities

Most reproductive traits of fish communities appeared to be very consistent in their responses to the environment across regions and lake types. Although the development of Indices of Biotic Integrity (IBIs) (Karr & Chu, 2000), generally including CRTs, in a broad array of regions and ecosystem types suggested some kind of generality in the response of these traits to environmental gradients and anthropogenic stressors, convergence in CRTs as identified here has never, to our knowledge, been shown. A comparative study of the fish communities of the Rhône river catchment (France) and of Virginia (USA) showed some convergence in the response of life-history traits to hydraulic conditions (e.g. body length, longevity and fecundity; Lamouroux *et al.*, 2002), but these conclusions did not take into account reproductive habitat requirements.

The convergence in the response of reproductive habitat requirements to temperature shows that warmer lakes are consist-

ently inhabited by a higher proportion of phytophiles (and therefore less strictly lithopsammophilous species) than colder lakes. This indicates a turnover in species reproductive substrates along a temperature gradient and consequently suggests that some of the correlates of temperature are related to the availability of spawning substrates. For example, it can be hypothesized that warmer waters allow more primary productivity both by macrophytes (thereby providing adequate substrates for phytophiles) and by phytoplankton. Strong productivity could lead to the accumulation of organic matter and consequently the clogging of the mineral substrates required for lithopsammophiles to reproduce.

Our results show that, in natural lakes, the increase in the proportion of guarder species with temperature is a pattern that is consistent across regions. Three primary life-history strategies, representing the endpoints of a trilateral continuum, have been identified in North American fishes (Winemiller & Rose, 1992) and could be applied in a variety of regions and ecosystem types (Vila-Gispert *et al.*, 2002). In this framework, parental care is associated with a suite of traits classically considered indicative of a *K* strategy (Pianka, 1970) and called the equilibrium strategy (Winemiller & Rose, 1992). This strategy is likely to be an adaptation to stable, resource-limited and competitive environments (Pianka, 1972).

These results deserve to be considered within the context of current global change. The predicted increase in average global air temperature is about 4 °C within the coming half century (Boer *et al.*, 1992). The models fitted here suggest that the community reproductive traits could strongly respond to such warming (Fig. 7). The communities of the coldest lakes could be those most affected in such a scenario.

Trophic traits of fish communities in lakes

Unrelated fish species happen to evolve similar morphological adaptations to their main food resources or feeding habitats (Winemiller *et al.*, 1995; Hugueny & Pouilly, 1999). However, the trophic models obtained here were only statistically significant for NEUSA lakes, even though the models obtained for French
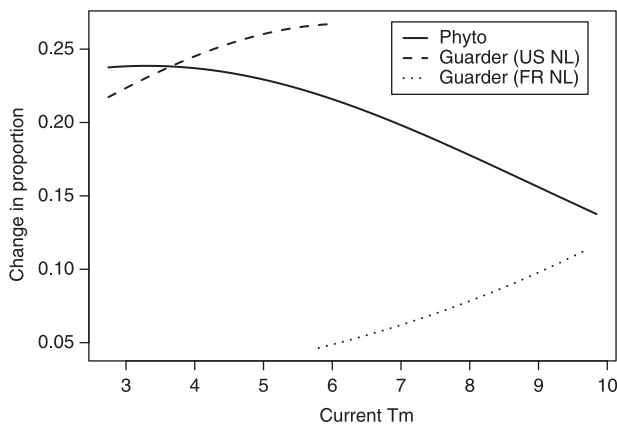
Figure 7 Modelled response of Phyto (in both lake types and regions) and Guarder in natural lakes (NL, natural lakes; FR, France; US, United States) to a 4 °C increase in mean annual air temperature as a function of current mean annual air temperature.

lacustrine water bodies generally displayed similar tendencies (Table 5). In NEUSA, log(Lkha) was the main variable explaining the variability of CTTs in reservoirs while both Tm and log(Lkha) were significant in natural lakes. Tm is likely to be related to the amount of food resource available within each lake (although primary productivity might be better explained by nutrients), while lake area could, to some extent, reflect the diversity of the food items.

These results suggest that the constraints driving convergent morphological evolution at the species level do not transfer to the community level for lacustrine fishes in the temperate regions of the Northern Hemisphere. At least three non-exclusive factors could explain this lack of convergence.

First, the temperate lakes in our study are new systems on an evolutionary time-scale and have undergone severe temporal environmental fluctuations related to the Pleistocene climatic changes. Such conditions limit the ability to specialize among species because specialization hastens the extinction of populations by increasing their sensitivity to environmental conditions (Leigh, 1990). Thus, lake-dwelling species are mostly generalists. This is also true for reservoirs due to the temporal fluctuations induced by hydraulic management practices (Fernando & Holcik, 1991). Indeed, most of these species are rather opportunistic feeders and our CTT, based on their classification into trophic guilds, may not accurately reflect the actual trophic structure of the fish communities. Furthermore, the assignment of species into trophic guilds precludes taking into account the frequent diet shifts fish species undergo along their ontogenic development.

Second, trophic structure does not appear to respond to environmental gradients in French lakes. Strong trophic constraints on communities may lead to guild proportionality, i.e. a proportional representation of the different guilds that is constant among communities (Cohen, 1977; Jeffries & Lawton, 1985; Schluter, 1990). If that was the case, convergence as we considered it here was not to be expected.

Third, the absence of convergence may reflect the strong constraints that historical and biogeographical processes have set upon present-day local fish communities in Western Europe. It has been shown for mammals that trophic guilds of species in a given region were strongly influenced by regional and phylogenetic history, and largely by the traits of species that initially colonized these regions (Kelt *et al.*, 1996). The extinctions of the Pleistocene (Moyle & Herbold, 1987; Banarescu, 1989) were not only massive, but certainly also selective upon species traits. Western Europe underwent the most severe climatic conditions during the glaciations and had few catchments that could serve as refuges for freshwater species (Reyjol *et al.*, 2007). Thus, the filtering of the ancestral taxocenes has certainly been even more constraining in Europe and those species that are found at present in this temperate region are strongly selected subsets of the species pools prior to the glaciations in which generalists are overrepresented.

Phylogeny

Although the pool of species in NEUSA and French lakes are clearly distinct with only 10% of fish species occurring in both regions, they cannot be considered independent in that they share nine families. Such non-independence may have important consequences in community ecology (Webb *et al.*, 2002) due to niche conservatism (Wiens & Graham, 2005). Indeed, depending on the level of phylogenetic homogeneity across regions, similarity in ecological requirements between closely related species may explain most of the patterns identified in our study. For example, if families were restricted to a single region, we could expect any of the cases displayed in Fig. 2 due to idiosyncratic family-level niche requirements. If similar families were present in both regions, we could expect case 6 if the environmental gradient did not correspond to a niche dimension influencing species distribution, or case 1 due to the equivalent sorting of families along environmental gradients across regions. Such sorting is well documented for river Salmonids that occur in cold waters both in France (Huet, 1949; Illies & Botosaneanu, 1963) and in the USA (Rahel & Hubert, 1991; Torgersen *et al.*, 2006). This family is both very homogeneous in terms of reproductive requirements (lithophilous and nest spawners) and clearly distinct from the others. Therefore, the response of CRTs to temperature may be strongly related to the distribution of Salmonids along the temperature gradient. However, the response of Phyto and Guarder to temperature remains highly significant on the subset of lakes lacking Salmonid species ($P = 4.19 \times 10^{-10}$ and 1.61×10^{-7}, respectively). This shows the robustness of the relationship that cannot be explained solely by the distribution of this family. However, the slope of the relationship is steeper in lakes with Salmonids. Therefore, the overall response of CRTs to temperature is likely to be attributable to the combined effects of niche conservatism within families that are shared between regions and of community processes.

While some families with holarctic distributions may contribute to explaining the convergence, those that are restricted to a single region can explain some of the differences in the traits of species

pools. For example, in North America, the Centrarchidae and Ictaluridae are two families of freshwater fishes of which most species inhabit still waters. They are predators with advanced styles of reproduction (nesting and guarding) that are uncommon in the European fish fauna (Mahon, 1984).

Potential developments

Throughout this paper, lake habitat conditions have been summarized using only two variables: lake surface area and mean annual air temperature. The choice of environmental parameters constraining community features is essential in the search of convergence. The absence of response in CTTs in French lakes may result from inappropriate environmental gradients. For example, water quality variables directly related to primary productivity, but unavailable on the French lakes, may have revealed different patterns. In a context of increasing anthropogenic stress exerted on freshwater ecosystems, measurements of several types of such stresses may also be useful for assessment of convergence and for the development of the scientific knowledge necessary to design efficient bioassessment tools using lake fish communities. Our results further indicate some consistent responses of community traits to environmental gradients, which highlight the need to account for the effects of natural variability when developing broad-scale bioassessment tools.

The widespread introduction of fish species in lakes frequently leads to the establishment of new species in both study regions (Whittier & Kincaid, 1999; Argillier *et al.*, 2002a; Irz *et al.*, 2004a,b). This constitutes a disturbance in community composition that could eventually perturb the patterns of both species richness and community functional traits. This was apparently not the case in our study, as excluding exotics from analyses did not strongly change the nature of the relationships found using the all data set.

This study revealed some degree of convergence across regions. However, phylogenetic constraints, past events such as the diversification of the North American fish fauna, the selective extinctions during the Pleistocene glaciations and the subsequent recolonizations, by their influences on the regional species pools, also contribute to the current patterns of fish communities in north temperate regions.

Whether due to community-level processes or to the similar sorting of families along a temperature gradient, the distributional patterns observed here suggest that the reproductive traits of lake fish communities are likely to be altered in the event of global warming.

ACKNOWLEDGEMENTS

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BIOSKETCHES

Pascal Irz has research interests in the patterns of fish species richness and community structure in relation to the environment and anthropogenic stressors. He recently finished a PhD on the macroecology of lacustrine fish communities.

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