Global test of Eltonian niche conservatism of nonnative freshwater fish species between their native and introduced ranges

Lise Comte, Julien Cucherousset and Julian D. Olden

L. Comte (lcomte@uw.edu) and J. D. Olden, School of Aquatic and Fishery Sciences, Univ. of Washington, Seattle, WA, USA. – J. Cucherousset, CNRS, Univ. Toulouse III Paul Sabatier, ENFA; UMR5174 EDB (Laboratoire Évolution & Diversité Biologique); 118 route de Narbonne, FR-31062 Toulouse, France.

Despite growing evidence that biotic interactions limit the distribution of species and their potential redistribution under climate change, the recent surge of interest in niche conservatism has predominantly focused on the Grinellian (abiotic) niche, whereas few studies have attempted to quantify potential lability in the Eltonian (biotic or trophic) niche. Here, we test for conservatism in the Eltonian niche of 32 freshwater fish species between their introduced and native ranges from 435 populations across the globe. We used stable isotope data to quantify niche shifts along the horizontal (δ^{13}C: indicating the origin of the resources consumed) and vertical (δ^{15}N: describing the trophic position) dimensions of the isotopic niche, as well as shifts in overall isotopic niche breadth. Using an assemblage centroid standardized isotope vector analysis and controlling for phylogenetic relatedness among species, we demonstrated that introduced freshwater fishes exhibited flexibility in both resource use and trophic position that was beyond levels of natural variability observed in their native ranges. By contrast, niche breadth showed variability only within the limits recorded in native populations and varied independently from shifts in mean isotopic niche positions. Across all species and introduction histories, we found a consistent shift towards more balanced acquisition of resources with mixed origins and at intermediate trophic positions, suggesting a general mechanism by which fish species successfully establish into recipient communities. The mechanisms that promote or inhibit species from shifting their Eltonian niche remains unknown, but trophic flexibility is likely to contribute to both the success and the ecological impacts of invasive species and range shifts of native species under future global change.

Understanding the tendency of species to retain their ecological niche through space and time, termed niche conservatism, has received renewed interest for predicting species responses to environmental change (Wiens and Graham 2005, Wiens et al. 2010, Lavergne et al. 2013). Most current modeling approaches assume stasis in species niches (both realized and fundamental) (Pearman et al. 2008); yet violation of this assumption is widely recognized to compromise the ecological inference garnered from such models (Davis et al. 1998, Larson and Olden 2012, Valladares et al. 2014). The basis of the niche conservatism hypothesis is that hard physiological tolerances constrain the evolution of many organismal traits (e.g. body size, feeding adaptations, thermal tolerances) (Blomberg et al. 2003). By contrast, mounting evidence that rapid ecological and evolutionary adaptations occur over relatively short time spans across diverse taxa (Bradshaw and Holzapfel 2006, Whitney and Gabler 2008) suggests that niche shifts might be more common than previously acknowledged. Whether such processes are of general significance in biodiversity modeling and conservation planning remains widely debated (Larson and Olden 2012, Lavergne et al. 2013, Valladares et al. 2014).

Present-day tests of the niche conservatism hypothesis are complicated, however, by the multidimensional nature of the niche concept. Hutchinson (1957) originally defined species' niche as the hyper-volume in the ecological space where a species can persist with permissive conditions and requisite resources as its axes (Colwell and Rangel 2009). Since then, literature has repeatedly emphasized the need to distinguish between these two articulations of species' niche, commonly referred to as the Grinellian (abiotic) niche and the Eltonian (biotic or trophic) niche (Soberón 2007, Devictor et al. 2010). While the distinction between Grinellian and Eltonian niches has set a meaningful heuristic basis to understand species spatial distributions, it is also relevant to better understanding the patterns of niche conservatism (Wiens et al. 2010). Indeed, the context in which niche evolution or conservatism occurs can depend upon different abiotic and biotic niche axes (Holt 2009). For instance, changes in abiotic conditions promote the selection and evolution of physiological characteristics through differential survival, reproduction and growth (Davis and Shaw 2001, Bradshaw and Holzapfel 2006). Similarly, trophic interactions, such as predation and competition,

are important agents of natural selection that can lead to shifts in trophic niche position or breadth through changes in foraging habitats or resource use (Robinson and Wilson 1994, Bolnick et al. 2010).

Contemporary biological invasions provide valuable replicated experiments to assess the degree of niche conservatism across a broad range of environmental conditions (Hierro et al. 2005, Sax et al. 2007). To date, the literature has demonstrated the propensity of some nonnative species to shift their Grinnellian niche during the colonization process (Broennimann et al. 2007, Early and Sax 2014, Parravicini et al. 2015), however, little research has focused on similar questions involving the Eltonian niche. Limited evidence suggests that species can rapidly shift their trophic niche once established into new environments. Previous investigations have documented a decrease in trophic position (Gido and Franssen 2007, Tillberg et al. 2007, Jackson and Britton 2014), whereas others have reported an increase in trophic position (Correa et al. 2012), a reduction in trophic niche breadth (Tran et al. 2015), and conservatism in both trophic niche position and breadth (Larson et al. 2010). These studies have been conducted predominantly on single species and often at small spatial extents, thus necessitating a more robust evaluation across diverse phylogenies and ecologies.

This unbalanced focus compared to the Grinellian niche may have important implications as the consequences of altered biotic interactions are expected to be superimposed on the effects of abiotic changes in setting the overall response of species to changing environmental conditions (Van der Putten et al. 2010). This may be particularly important in the context of biological invasion, where biotic filters (e.g. prey availability, predation, competition, parasites) are likely to constraint the successful establishment of nonnative species into new communities (Moyle and Light 1996). Evaluating the prevalence of Eltonian niche conservatism in nature and identifying the occurrence of niche shifts would therefore represent a step forward to predict community reorganization under global changes.

Trophic niche conservatism may depend on both intrinsic traits of species and extrinsic characteristics of the environment. For example, the degree of niche conservatism may vary across species according to differences in morphology (e.g. body size), physiology (e.g. digestive enzymes) or trophic ecology (e.g. herbivores, omnivores, carnivores) (Chubaty et al. 2014). Similarly, we might expect that environmental conditions (e.g. productivity) that differ between native and introduced ranges would differentially influence species trophic niches via effects on competition and resource availability. To what extent species characteristics and the environment interact to promote or inhibit conservatism in trophic niches remains unknown, yet is crucial when evaluating the intrinsic capacity of species to adapt to changing conditions.

Here, we provide a global assessment of trophic niche conservatism for 32 freshwater fish species that represent a wide spectrum of trophic ecologies in their native range. We evaluated changes using stable isotope values of carbon and nitrogen (δ^{13}C and δ^{15}N) between introduced and native populations on different continents, thus serving as a proxy for potential shifts in trophic niche. More specifically, we considered shifts in isotopic niche positions along two dimensions (the horizontal dimension indicating the relative dependence on resources with different origins and the vertical dimension describing the trophic position) as well as shifts in isotopic niche breadth. Our main goals were to 1) quantify the consistency in niche shifts of species between their introduced and native ranges, 2) assess the magnitude of these shifts with respect to observed variability within their native range or with co-occurring species, and 3) determine whether niche shifts were related to broad-scale ecological and environmental factors. Specifically, we tested whether the interaction between the isotopic attributes of species in their native range, changing community structure, changing resource availability, or introduction histories could predict the degree of trophic niche conservatism.

Material and methods

Stable isotope data and species selection

Stable isotope data of tissues were compiled from both published and unpublished studies using online search engines (ISIWeb of Knowledge® and Google Scholar™) reporting mean and variability in δ^{13}C and δ^{15}N values for freshwater fish communities. Local communities were considered as the set of species for which stable isotope values were quantified at a given location as reported in the original publications (four species was set as a threshold criterion to avoid studies targeted on specific species). When more than one value was reported for each species (e.g. different life-stages or size-classes), we averaged the data to get one value per species using a weighted average procedure according to the sample sizes. Population status and estimated time of initial introduction for introduced populations were collected from the publications (if available) or using FishBase (Froese and Pauly 2015) and the USGS Nonindigenous Aquatic Species database (<http://nas.er.usgs.gov>). Due to the lack of information regarding the local ecological impacts of nonnative species on native organisms and recipient ecosystems, introduced populations were classified as nonnative when sampled outside of their native range without distinction between 'invasive' and 'nonnative' status.

From this database, we selected species for which stable isotopes were quantified for at least two populations in both the native and introduced ranges for either lentic (i.e. lakes, reservoirs, backwaters) or lotic (i.e. rivers, streams) freshwater habitats. To account for the potential influence of phylogenetic relatedness among species in their degree of niche conservatism, we excluded species for which comprehensive phylogenetic information was not available according to Rabosky et al. (2013). This resulted in a selection of 32 fish species in 184 localities across the world, resulting in a database of 435 localities × species (Table 1 and Supplementary material Appendix 1, Fig. A1). The mean number of sampled individuals per population was 13.0 ± 15.8 SD within native ranges and 13.0 ± 16.8 SD within introduced ranges. Among the selected species, four species (*Cyprinus carpio*, *Micropterus salmoides*, *Oncorhynchus mykiss*, *Salmo trutta*)

Table 1. Mean direction (angle) and magnitude of isotopic niche shifts for each species between its introduced and native ranges with associated statistical analyses (Rayleigh's test). N_{pop}: global number of populations (in the native range only). N_{ind}: global mean number of individuals sampled within each population (in the native range only).

Family	Scientific name	Code	N_{pop}	N_{ind}	Angle	Magnitude	Ecosystem
Centrarchidae	Lepomis gibbosus	Legi	14 (4)	5.7 (8.0)	359.3***	3.0	Lentic
	Lepomis macrochirus	Lema	9 (4)	18.6 (27.7)	356.0***	2.6	Lentic
	Micropterus dolomieu	Mido	8 (2)	11.3 (17.5)	336.5*	2.1	Lentic
	Micropterus salmoides	Misa	14 (3)	8.1 (11.0)	269.5***	2.4	Lotic
Cichlidae	Oreochromis niloticus	Orni	20 (6)	17.2 (19.3)	13.0***	2.9	Lentic
	Tilapia zillii	Tizi	8 (4)	6.5 (5.5)	182**	4.7	Lentic
Cyprinidae	Carassius auratus	Caau	14 (11)	9.1 (9.5)	188.2***	2.4	Lentic
	Cyprinella lutrensis	Cylu	11 (5)	8.1 (5.6)	18.0***	1.6	Lotic
	Cyprinus carpio	Cyca	42 (19)	12.5 (11.3)	248.9***	2.0	Lentic
	Notemigonus crysoleucas	Nocr	10 (5)	5.9 (5.0)	336.2	2.5	Lentic
	Pimephales promelas	Pipr	8 (6)	8.9 (5.8)	47.6	1.6	Lentic
	Pseudorasbora parva	Pspa	6 (4)	12.0 (4.3)	237.4	3.6	Lentic
	Rutilus rutilus	Ruru	41 (39)	9.2 (9.2)	117.5***	1.7	Lentic
	Scardinius erythrophthalmus	Scer	27 (25)	9.3 (9.0)	127.2***	2.7	Lentic
Ictaluridae	Ameiurus nebulosus	Amne	12 (7)	7.3 (10.7)	269.4**	1.2	Lentic
	Ictalurus punctatus	Icpu	10 (3)	3.8 (4.0)	80.1***	2.4	Lotic
	Pylodictis olivaris	Pyol	6 (4)	5.8 (3.5)	233.1***	2.0	Lotic
Moronidae	Morone chrysops	Moch	5 (2)	37.0 (13.5)	141.2**	1.4	Lentic
Osmeridae	Osmerus mordax	Osmo	9 (3)	17.8 (3.7)	300.1**	2.4	Lentic
Percidae	Gymnocephalus cernua	Gyce	9 (4)	3.6 (5.0)	124.5	3.6	Lentic
	Perca flavescens	Pefl	23 (16)	23.8 (21.7)	177.2***	2.1	Lentic
	Sander lucioperca	Salu	15 (3)	5.1 (4.0)	41.7	2.0	Lentic
	Sander vitreus	Savi	12 (10)	28.7 (24.7)	12.6	1.2	Lentic
Poeciliidae	Gambusia holbrooki	Gaho	5 (3)	20.8 (31.7)	42.6**	2.4	Lotic
Salmonidae	Coregonus clupeaformis	Cocl	14 (11)	13.6 (13.5)	174.6***	3.0	Lentic
	Coregonus lavaretus	Cola	9 (7)	20.0 (16.6)	342.8***	3.4	Lentic
	Oncorhynchus mykiss	Onmy	7 (2)	16.3 (19.0)	157.9***	2.7	Lentic
	Oncorhynchus nerka	Onne	11 (7)	11.3 (9.3)	251.0***	1.9	Lentic
	Salmo trutta	Satr	8 (5)	11.1 (17.3)	101.6***	2.2	Lentic
	Salvelinus alpinus	Saal	10 (8)	36.4 (44.9)	62.4	4.2	Lentic
	Salvelinus fontinalis	Safo	10 (7)	6.9 (6.3)	193.9**	2.0	Lentic
	Salvelinus namaycush	Sana	29 (18)	16.1 (14.2)	228.1*	1.9	Lentic

Rayleigh's test: *$0.01 \leq p < 0.05$, **$0.001 \leq p < 0.01$, ***$p < 0.001$.

are included on the list of the '100 of the World's Worst Invasive Alien Species' (Lowe et al. 2004), and the majority have demonstrated significant ecological impacts in their introduced range (Cucherousset and Olden 2011).

Fish communities were then characterized according to several ecological and environmental factors. The intensity of competition was estimated through species richness, defined as the number of species (both native and nonnatives) in the local communities for which the isotopic values were quantified in the original publications. Although rare species may have been missed in some localities, we attempted to select only communities that had been comprehensively sampled (i.e. removing studies that stated that only a portion of the community was sampled or studies focused on other organisms than freshwater fish) and therefore assumed that such bias would be minimal. Comparison with the richness values reported at the river basin grain (Fish-SPRICH, Brosse et al. 2013) also reveal a positive relationship with our estimate ($R^2 = 0.15$; $p < 0.001$), indicating that the number of species estimated from the isotope data was likely to reflect global gradient in freshwater fish taxonomic richness. Absolute latitude based on the geographical coordinates of each fish community was used as a proxy for energy availability.

Trophic niches

Niche characterization
Species niches were characterized using stable isotopes ratios of $\delta^{13}C$ and $\delta^{15}N$, where $\delta^{13}C$ indicates the origin of the carbon in a consumer diet (relative contribution of pelagic versus littoral resources in lentic ecosystems and of autochthonous versus allochthonous resources in lotic ecosystems) and $\delta^{15}N$ is reflective of the trophic position of the consumer within the food web (Layman et al. 2012). We used assemblage centroid standardized isotope vector analysis (ACSIVA) to compare datasets from different spatial locations (Lujan et al. 2012). Isotopic niche positions, calculated as the mean $\delta^{13}C$ and $\delta^{15}N$ values, of native and introduced populations were described using vectors in the two-dimensional isotopic niche space and expressed relative to their local community centroid (see also Schmidt et al. 2011). In an attempt to avoid bias in the calculation of the centroids due to uncertainty in the sampled data and errors arising from the sampling process, we used a Monte Carlo simulations to sample 1000 $\delta^{13}C$ and $\delta^{15}N$ values for each species in the community from two normal distributions using their reported mean values and standard deviations along the two axes, including a precision error of $\pm 10^{-3}$ ‰. The mean

standardized vectors describing both the distance and angle of each population relative to the overall mean community centroid were then calculated.

Isotopic niche breadths of populations were estimated using the standard ellipse area approach (SEAc; Jackson et al. 2011). To control for the potential influence of varying sample sizes in estimating isotopic niche breadth (Syväranta et al. 2013), SEAc were regressed against the number of sampled individuals using an asymptotic model (pseudo $R^2 = 0.14$, p < 0.0001; log-likelihood ratio test; Supplementary material Appendix 2, Fig. A2). Regression residuals were then used in all subsequent analyses as estimates of isotopic niche breadth adjusted for sample size.

Quantifying consistency in niche shifts
Shifts in isotopic niche positions were quantified for each species as the mean differences in both direction and length of population-specific community centroid standardized vectors between each pair of introduced and native populations (i.e. introduced minus native). Consistency in the direction of shift was evaluated using Rayleigh's tests (Schmidt et al. 2007). Specific differences in both δ^{13}C and δ^{15}N were obtained by projecting the resulting vectors along the two isotopic axes and calculated as the vector length times the cosine and sine of the resulting angle, respectively. To ensure that any differences in isotopic niche positions were not an artifact of potential spatial variation in baseline isotopic values (Hoeinghaus and Zeug 2008), we calculated the mean differences in the rank occupied by the species within the communities along the two isotopic axes between their introduced and native ranges. To allow comparisons across communities displaying different number of species, we also reported differences in the relative rank of species, expressed as the rank of a species divided by the number of species within the community. In contrast to isotopic values, species rank within a community is independent from isotopic baselines (e.g. the same top-predator species in several communities will always have the lowest rank even if variation exists in isotopic baselines). This enabled us to test whether estimated niche shifts were related to actual shifts in trophic positions as opposed to representing a methodological artifact. Similarly, differences in isotopic niche breadth were quantified for each species as the mean pairwise differences in population niche breadths between their introduced and native ranges (i.e. introduced minus native).

Magnitude of niche shifts
To assess the magnitude of the observed niche shifts compared to natural niche variations, we first tested whether the differences in isotopic niche positions and breadth between introduced and native ranges calculated exceeded the mean pairwise differences exhibited across populations within the native ranges calculated using the same procedure than above. The significance was tested using phylogenetic paired t-tests (Linderfors et al. 2010). Then, we assessed the magnitude of the observed niche differences between introduced and native ranges compared to the variation exhibited across community members. For each species, we calculated the mean pairwise differences in isotopic niche positions and breadth with all the species with which they co-occurred

within their native range and compared them to observed shifts using phylogenetic paired t-tests.

Ecological and environmental correlates of niche shifts
We used phylogenetic generalized least-squares models (PGLS) accounting for potential phylogenetic non-independence among related species (Freckleton et al. 2002) to test for associations between observed niche shifts and 1) the isotopic attributes of species in their native range (i.e. mean δ^{13}C and δ^{15}N values and niche breadth), 2) differences in community species richness (i.e. mean differences in species richness ranging from –10.7 to 5.1), 3) changes in resource availability (i.e. mean difference in absolute latitude ranging from –21.8 to 16.0°), or 4) transient dynamic of introduced populations (i.e. mean time since introduction varying from 26.5 to 338.4 yr) [values for each species are provided in Supplementary material Appendix 2, Table A1]. For each response variable describing different aspects of niche shifts, we developed models with all the combinations of variables for a maximum number of three predictors. We also included models with two-way interactions between the mean isotopic attributes and the ecological and environmental predictors. The variance inflation factors ranged between 1.0 and 1.5, indicating limited evidence for multicollinearity among the predictors in the models. All variables were scaled to mean of zero and standard deviations of one to standardize slope coefficients (β). We then identified the best set of models using the differences in the Akaike information criterion adjusted for small sample sizes (AICc) calculated between each model and the model demonstrating the lowest AICc value. All models with ΔAICc ≤ 2 were then retained as potential candidate models. To account for model uncertainty, we performed model averaging of coefficients within the best set of models using the Akaike weights, including zeros when predictors did not occur in a particular model. The effects of the predictors were then assessed using the 95% confidence interval of the estimated model-averaged coefficients.

All analyses were performed in R ver. 3.1.2 (R Development Core Team) using the packages 'ape' (Paradis et al. 2004), 'nlme' (Pinheiro et al. 2015), 'phytools' (Revell 2012), and 'siar' (Jackson et al. 2011).

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.6q036> (Comte et al. 2016).

Results

We found little evidence for trophic niche conservatism of freshwater fishes across the globe. The majority of species shifted their isotopic niche positions in a consistent direction from their native to their introduced ranges for both ecosystem types (Rayleigh test, p < 0.05) (Table 1 and Supplementary material Appendix 2, Fig. 1A, Table A1). The magnitude of shifts was comparable along the δ^{13}C and the δ^{15}N axes (phylogenetic paired t-test, p = 0.28) and spanned 4.7 and 3.7‰, respectively. Both expansion and contraction in isotopic niche breadths (from –4.6 to 9.3) were also observed when comparing introduced and native ranges. Importantly, we did not find evidence that niche shifts were
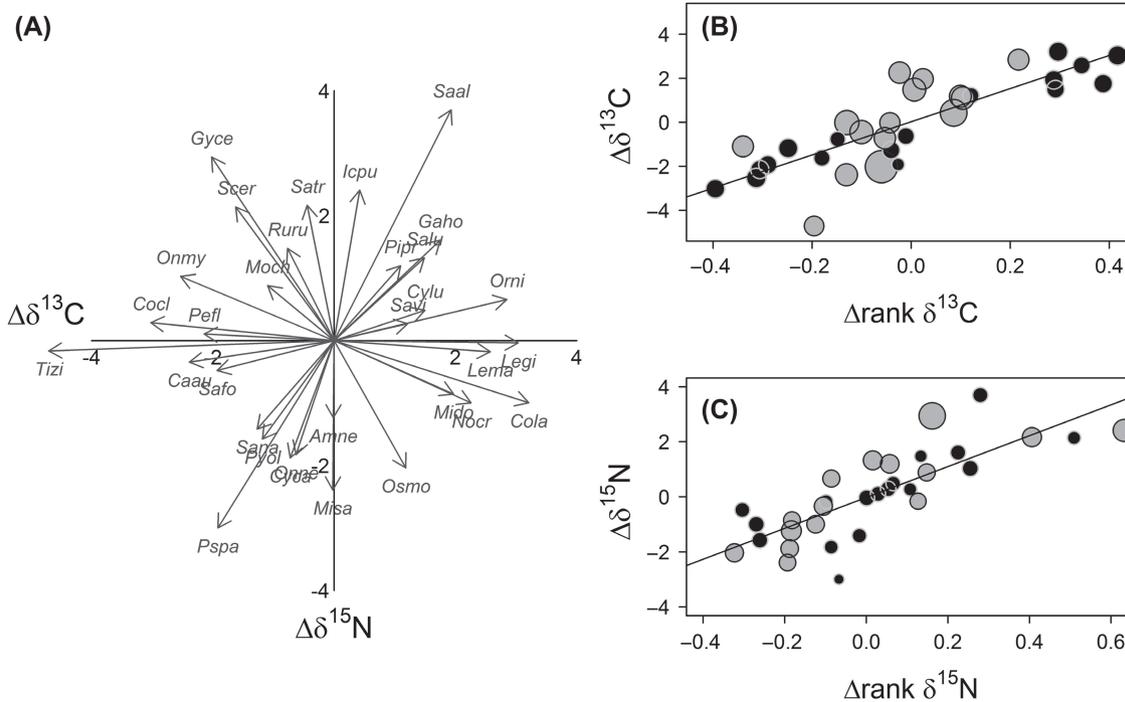
Figure 1. Trophic niche shifts between the introduced and native ranges (introduced minus native). (A) Direction and magnitude of shifts within the δ^{13}C and δ^{15}N isotopic space. Differences in (B) δ^{13}C and (C) δ^{15}N niche positions as a function of changes in the relative rank of species within their local communities. The size of the circles represents the differences in isotopic niche breadth, where black indicates a contraction and grey indicates an expansion. Lines are the fitted relationships using PGLS (p < 0.001). Species codes are available in Table 1.

related to variation in sample size between the introduced and native ranges (Supplementary material Appendix 2, Fig. A4). Further, we found that shifts in isotopic niche positions were associated with changes in the rank occupied by the species along their respective isotopic dimensions, expressed as either ordinal (Supplementary material Appendix 2, Fig. A4) or relative rank (Fig. 1B, C; PGLS, pseudo $R^2 = 0.69$ and 0.62, p < 0.001). This indicated that observed shifts were unlikely to be an artifact of spatial variations in isotopic baselines as the trophic positions of the species relatively to other species in the community also shifted between their introduced and native ranges. By contrast, we found that the relationships between shifts in isotopic niche positions and niche breadth were not statistically significant for δ^{13}C (p = 0.80) and δ^{15}N (p = 0.06) (PGLS), suggesting that niche shifts were not directly driven by changes in intraspecific trophic variability.

The magnitude of shifts in isotopic niche positions from native to introduced ranges exceeded the observed variability across sites within the native range along both δ^{13}C and δ^{15}N axes (Fig. 2A; phylogenetic paired t-test, p < 0.001), and were comparable to the differences observed with co-occurring species (phylogenetic paired t-test, p = 0.14 and p = 0.64). By contrast, the magnitude of changes in niche breadth was not different from the degree of variability observed within the native range (Fig. 2B; phylogenetic paired t-test, p = 0.82) or with co-occurring species (phylogenetic paired t-test, p = 0.67). Similar conclusions were obtained using the untransformed values regarding the variability observed within the native range (phylogenetic paired t-test, p = 0.16) or with co-occurring species (phylogenetic

paired t-test, p = 0.39) (Supplementary material Appendix 2, Fig. A3).

Niche shifts along the δ^{13}C (four selected models, $R^2 = 0.35$–0.48; Supplementary material Appendix 3, Table A2) and δ^{15}N (three selected models, $R^2 = 0.49$–0.53; Supplementary material Appendix 3, Table A2) axes were significantly and negatively associated with the mean δ^{13}C and δ^{15}N values of species in their native range, respectively (Fig. 3 and Supplementary material Appendix 3, Fig. A6). This indicated convergence for all species in their introduced environments towards a more balanced acquisition of resources with mixed origins and at intermediate trophic positions. Differences in mean absolute latitude were also significantly and negatively associated to shifts along the δ^{15}N axis, indicating that species introduced into potentially more productive habitats (i.e. at lower latitude) tended to increase their trophic position (Fig. 3 and Supplementary material Appendix 3, Fig. A6). By contrast, factors related to changes in community species richness, time since introduction or the interaction between isotopic attributes of species and the ecological and environmental factors were poor predictors of niche shifts. All our results and main conclusions remained unchanged using analyses not accounting for phylogeny (Supplementary material Appendix 5).

Discussion

We demonstrated that introduced freshwater fishes exhibited little evidence for trophic niche conservatism and instead
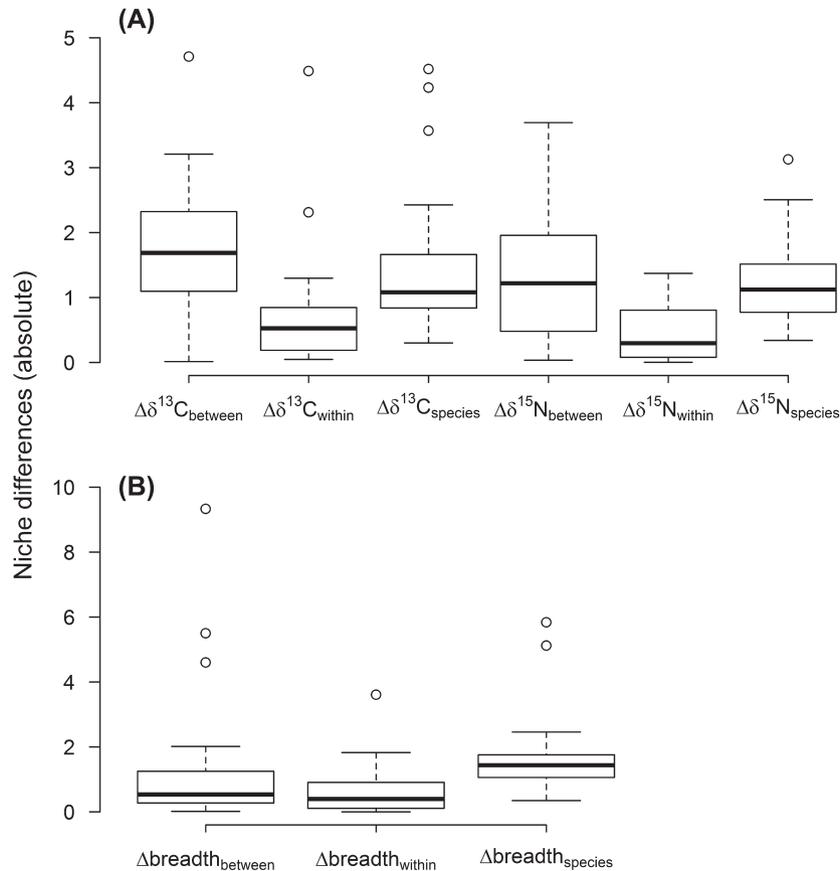
Figure 2. Comparisons of the between- versus within-ranges and across-species trophic niche differences in (A) δ^{13}C and δ^{15}N niche positions and (B) isotopic niche breadth. Within-range and across-species variability were calculated within the native range.

displayed trophic flexibility when compared to their native ranges. At the global scale, we documented shifts in both the origin of the resources used and the trophic position above the levels of natural variability observed in species native ranges.

Across all species, we found a consistent shift towards increased diversification of resource origins and intermediate trophic positions. This suggested that species in their introduced ranges displayed more generalist and omnivorous foraging strategies, potentially exploiting multiple food chains based on different carbon sources (multi-chain omnivores; Vadeboncoeur et al. 2005). Although a shift to sub-optimal resources has been proposed as a general mechanism accompanying the establishment of nonnative species (Gido and Franssen 2007, Tillberg et al. 2007), we found that decreases in trophic position in the introduced range may not be a universal phenomenon. For instance, among the four most globally-introduced fish species present in our
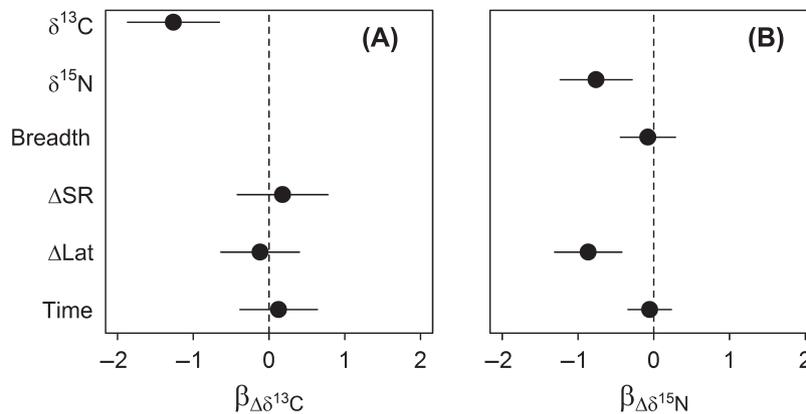

Figure 3. Model-averaged coefficients (β) and associated 95% confidence intervals of the PGLS relating trophic niche shifts in (A) δ^{13}C and (B) δ^{15}N niche positions to isotopic attributes of species in their native range (δ^{13}C, δ^{15}N and isotopic niche breadth), differences in specific richness (ΔSR), differences in mean latitude (ΔLat) and time since introduction (Time). Only variables that entered in the set of best models are indicated (ΔAICc ≤ 2).

database (Lowe et al. 2004), we found that the common carp *Cyprinus carpio* and the largemouth bass *Micropterus salmoides* shifted toward lower trophic positions, whereas rainbow trout *Onchorynchus mykiss* and brown trout *Salmo trutta* displayed a higher trophic positions in their introduced range. Optimal foraging theory predicts that consumers adjust their feeding behavior to maximize their expected fitness as a result of changes in resource availability and predation levels (Stephens and Krebs 1986). As such, adaptive omnivorous behaviors are expected to arise from multiple environmental and ecological pressures and for different combinations of traits (Chubaty et al. 2014). Convergence towards a 'take what you can get' strategy by exploiting alternative resources may therefore be relatively profitable for nonnative species, with the potential to induce rapid evolutionary adjustments in ways that improve competitive abilities, invasion success and associated ecological impacts on native organisms and recipient ecosystems.

It was striking that the documented shifts in isotopic niche positions exceeded the variability observed within the native range of species. The magnitude of shifts corresponded to the differences observed across different co-occurring species, with the maximal shifts being comparable to differences observed between distinct carbon basal sources (e.g. 4.7‰ observed for δ13C vs ~ 6.7‰ between pelagic and littoral food chains across 25 lakes; Post 2002, ~ 4.1‰ between autochthonous and allochthonous food chains across 10 streams; Evangelista et al. 2014) and about one trophic level (e.g. 3.7‰ observed for δ15N vs ~3.4‰; Post 2002). The fact that niche shifts were unrelated to the time since introduction suggest a persistent, rather than transient, phenomenon occurring early in the invasion process (Strayer et al. 2006). We also found that niche breadth of many species in their introduced range were well within the range of variability recorded across native populations, and that changes in niche breadth occurred independently from shifts in isotopic niche positions. These findings suggest that conservatism in niche breadth may be decoupled from changes in niche position. Consequently, broad Eltonian niches, which are often cited as a characteristic of successful invaders (Romanuk et al. 2009), might actually be an artifact of the introduction process rather than an intrinsic attribute of nonnative species. In support to this assertion, we found that the isotopic niche breadth of the 32 selected nonnative species did not differ from those of native species with which they co-occurred within their introduced range, even after excluding native species that are known to have been introduced outside of their native range (see Supplementary material Appendix 4 for further discussions on this aspect). Although this result remains to be generalized using other sources of data and other organisms, it indicates that using trait-based approaches to assess invasion risk based on the mean trophic characteristics of species may be of limited value in certain circumstances.

Alternatively, as its Grinellian counterpart, it is possible to distinguish between potential and realized Eltonian niches, the former covering the trophic interactions that a given species is able to engage in based on its morphological and physiological characteristics and the latter only the interactions that actually occur (Soberón 2007, Devictor et al. 2010). Introduced species may therefore be functionally able to consume a large array of food items in their native range, but their niche breadth may be constrained by a trade-off between prey profitability and availability (Stephens and Krebs 1986). Ultimately, this constraint may change when species are introduced to new environments, resulting in a shift in isotopic niche positions (Jackson and Britton 2014). In support to this hypothesis, we found that shifts in trophic position were associated with differences in absolute latitude, suggesting underlying connections between ecosystem productivity and the placement of nonnative species into the recipient food-webs. Nonetheless, both kind of shifts can arise from the same underlying processes and plasticity in resource use itself may have a genetic basis that can evolve in response to the selection pressures in the new environment (Robinson and Wilson 1994, Bolnick et al. 2010). For instance, the relationship between the trophic niche shifts and the latitudinal gradient might also indicate that species introduced to climates that differed from their native range also displayed the greatest trophic adjustments. Collectively, our results thus suggested that trophic adaptability may play an important but underappreciated role in the establishment and integration phase of biological invasions. This research area deserves further attention.

It is worth highlighting that we cannot completely rule out the possibility that isotopic niche shifts may have arisen from changes in the stable isotope values of baselines between introduced and native species ranges (Hoeinghaus and Zeug 2008). Our analysis was conducted at a broad geographical scale and used many different data sources for which such information was not available. Given that trophic niche metrics were standardized with respect to the local communities (Schmidt et al. 2011, Lujan et al. 2012) and that niche shifts were highly consistent across sites according to both absolute versus relative (rank) isotopic values along the two axes, we believe that such bias would be minimal and unlikely to obscure our main conclusions. However, some rare species have certainly not been collected in some localities, which may have increased the level of uncertainty around our quantitative estimates of niche shifts and subsequent analyses. Therefore, using stable isotope data of prey along with statistical models to reconstruct diet in both their native and introduced range may be a step forward in resolving the underlying determinants of trophic niche shifts. Another potential caveat of our study is that we relied on a limited number of pairwise comparisons to document potential trophic niche shifts for several species, and using a relatively small number of individuals. Small sample size can affect estimates of niche breadth, along with natural variation typically associated with stable isotope data (Syväranta et al. 2013). Although we attempted to control for the varying sample sizes across sites, such imprecision probably resulted in considerable uncertainty in estimating changes in niche breadth between introduced and native ranges. Understanding the patterns of conservatism in trophic niche breadth would therefore benefit from further examinations across a larger number of sites and incorporating more individuals.

A burgeoning challenge in ecology is to gain insight into the new biotic interactions, and resulting implications for ecosystem processes, that may arise from shifting species distributions in the future (Van der Putten et al. 2010, Woodward et al. 2010). Although it represents a tremendous

task, considerable progress have already been made in considering trophic relationships when inferring global change impacts (Albouy et al. 2014). If the processes underlying the success of nonnative species do not fundamentally differ from those involved in native range expansions (Van der Putten et al. 2010, Moran and Alexander 2014), then it is reasonable to expect that many species may adapt their trophic behavior in the future. Foraging-switching strategies may rapidly restructure food webs, with potential consequences for evolutionary trajectories of species and ecosystem functioning (Strauss et al. 2006, Tunney et al. 2014). We therefore propose that more accurate predictions for species responses to climate change may benefit from acknowledging that both Grinellian and Eltonian niches may shift in space and time.

With respect to freshwater fishes at the global scale, it is premature at this stage to assume that the direction or magnitude of changes in trophic niche will be consistent. Before doing so, understanding whether the innate trophic and evolutionary characteristics of nonnative species fundamentally differ from the native ones and how trophic niche flexibility contribute to invasion success and the ecological impacts induced would be required. Given evidence that both the rates of phylogenetic and between-range disparity in Grinellian and Eltonian niches may be decoupled (Larson et al. 2010, Pearman et al. 2014), a comprehensive analysis of the synchronism in niche conservatism along these two dimensions could also provide valuable guidance in that direction. We hope that this research for global freshwater fishes will inspire more detailed examinations of the physiological and ecological mechanisms underlying patterns in niche conservatism, and the extent to which trophic niche shifts might be crucial components of future range shifts of both native and nonnative species.

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Supplementary material (Appendix ECOG-02007 at < www. ecography.org/appendix/ecog-02007 >). Appendix 1–5.