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RESEARCH PAPER

Identifying climatic niche shifts using coarse-grained occurrence data: a test with non-native freshwater fish

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ABSTRACT

Aim We tested whether coarse-grained occurrence data can be used to detect climatic niche shifts between native and non-native ranges for a set of widely introduced freshwater fishes.

Location World-wide.

Methods We used a global database of freshwater fish occurrences at the river basin scale to identify native and non-native ranges for 18 of the most widely introduced fish species. We also examined climatic conditions within each river basin using fine-grained climate data. We combined this information to test whether climatic niche shifts have occurred between native and non-native ranges. We defined climatic niche shifts as instances where the ranges of a climatic variable within native and non-native basins exhibit zero overlap.

Results We detected at least one climatic niche shift for each of the 18 studied species. However, we did not detect common patterns in the thermal preference or biogeographic origin of the non-native fish, hence suggesting a species-specific response.

Main conclusions Coarse-grained occurrence data can be used to detect climatic niche shifts. They also enable the identification of the species experiencing niche shifts, although the mechanisms responsible for these shifts (e.g. local adaptation, dispersal limitation or physiological constraints) have yet to be determined. Furthermore, the coarse-grained approach, which highlights regions where climatic niche shifts have occurred, can be used to select specific river basins for more detailed, fine-grained studies.

Keywords
Bioclimatic models, climate mismatch, freshwater fish, invasion, risk assessment, river basins.

INTRODUCTION

Bioclimatic models of species distributions are increasingly being used to predict the establishment and spread of non-native species over new areas, and to forecast range shifts in invasive species due to climate change (e.g. Thuiller *et al.*, 2005; Jeschke & Strayer, 2008; Britton *et al.*, 2010). These models are built under the assumption that species are in equilibrium with the climatic conditions encountered in their native ranges (i.e. their realized niche; Hutchinson, 1957) and that they tend to maintain ancestral ecological requirements in their non-native range (i.e. niche conservatism; see Jeschke & Strayer, 2008). Under these assumptions, the climate range where a species can become established can be predicted by fitting models with climate data from its native range (i.e. climate matching). This climate or environmental matching approach has been widely applied in invasion risk assessment (e.g. Bomford *et al.*, 2009).

Such approaches have recently been criticized (e.g. Broennimann & Guisan, 2008) because the spatial distribution of a species is not only constrained by current climate but also by historical and biotic factors such as barriers to dispersion, biotic interactions and stochastic events (Jiménez-Valverde *et al.*, 2008). Consequently, a number of studies have shown that when models are trained (i.e. parameterized) using data from the

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native range, they tend to underpredict the non-native range, i.e. models were unable to predict the full extent of invasion (e.g. Broennimann *et al.*, 2007; Loo *et al.*, 2007; Medley, 2010). The reason is that species might be able to establish and spread into localities (or regions) that are climatically distinct from those encountered within the native range (i.e. a climatic niche shift).

Instances of climatic niche shifts have recently been reported for a wide range of plants and animals (e.g. Fitzpatrick *et al.*, 2008; Rödder & Lötters, 2009; Medley, 2010). These approaches typically use fine-grained data (e.g. 0.1° to 0.5° latitude and longitude grid cells), hence requiring the assembly of numerous local occurrence data in both the native and the non-native ranges. However, such detailed information is rarely available on a large scale (Pyšek *et al.*, 2008), limiting the identification of climatic niche shift to a restricted number of well-studied species. In contrast, much more information is available at a coarser spatial grain (e.g. ecoregion, country, province) through the use of natural history atlases or regional biodiversity assessments (e.g. DAISIE, 2009). Developing methods to identify niche shifts using these coarse-grained occurrence data would therefore considerably increase the pool of species for which a climatic niche shift can be identified.

We used a global database of freshwater fish to test whether coarse-grained occurrence data can be used to detect climatic niche shifts between native and non-native ranges. Specifically, we used river basins as our sampling unit (see Leprieur *et al.*, 2008). Freshwater fish distributions are influenced by many factors operating at different spatial scales (reviewed in Jackson *et al.*, 2001). Large scale (e.g. among river basins) present-day patterns of freshwater fish distribution are influenced by historical connections between river basins, Earth history events (e.g. Quaternary glaciations, orographic formation) and environmental constraints (e.g. climatic zones, biomes) (e.g. Jackson & Harvey, 1989; Leprieur *et al.*, 2009a). Smaller-scale patterns (e.g. within a given river basin) of fish distribution are mainly influenced by geometry of the river network and a combination of abiotic and biotic factors, including temperature and hydrology (Jackson *et al.*, 2001). In the present study, we analysed patterns of fish distribution among river basins for 18 introduced species that are known to be widely established beyond their native range.

MATERIALS AND METHODS

The use of coarse-grained occurrence data (i.e. river basin-scale occurrence data) to detect potential climatic niche shifts can present major limitations. For instance, averaging values of a climatic variable (e.g. annual precipitation) over large and heterogeneous areas may strongly bias the estimation of the climatic niche of a freshwater fish and lead to false claims of niche shifts between native and non-native habitats. To overcome such limitations, we simultaneously analysed coarse-grained fish occurrence data at the river basin scale and fine-grained climate data (i.e. 0.5° × 0.5° gridded climate data that account for the full range of climatic variation within a river basin). Thus, we assumed that a species present in a given river basin can exist anywhere within that basin, and that it is compatible with the full range of climatic or environmental conditions encountered throughout the basin. Climatic niche shifts were then defined as instances where the range of an environmental variable within the native basins exhibited zero overlap with the same variable's range in at least one non-native basin. Notably, this conservative method will increase the probability of Type II error (i.e. failing to detect climatic niche shifts when they have, in fact, occurred), but it is also robust to Type I error (i.e. falsely claiming that climatic niche shifts have occurred).

We used the database of Leprieur *et al.* (2008), which documents occurrences of the world's freshwater fishes at the river basin scale (i.e. complete rivers, from the headwaters to the ocean). Among the 1055 river basins available in our database, the geographic extent of 938 basins dispersed throughout the world was available in a digital format.

For each of the 938 river basins, we collected values of eight climatic variables over the whole surface area from 0.5° × 0.5° gridded climate data (Leemans & Cramer, 1991; New *et al.*, 1999): precipitation in the driest month ($P_{\min}$); precipitation in the wettest month ($P_{\max}$); coefficient of variation of the monthly precipitation (P_{cv}); number of rainy days (N_{rd}); mean temperature of the coldest month ($T_{\min}$); mean temperature of the warmest month ($T_{\max}$); coefficient of variation of mean monthly temperature (T_{cv}); and mean annual temperature range (T_{ampl}). These climatic variables are often used in broad-scale studies of freshwater fish distributions (e.g. Minns & Moore, 1995; Chu *et al.*, 2005; Leprieur *et al.*, 2009a), because broad-scale physiological and ecological requirements of freshwater fish species are largely related to temperature and hydrology (Matthews, 1998). Moreover, the Pearson correlations between the eight variables remain low. Although all of the 28 determination coefficients were significant ($P < 0.05$), all were lower than 0.65, except $T_{\min} - T_{cv}$ (see Table S1). However, we kept these two variables to maintain a similar approach for temperature and precipitation patterns. For the same reason, overall mean values of temperature and precipitation were not used as they were highly redundant with $T_{\min}$ [Pearson determination coefficient r^2 ($T_{\min} - T_{mean}$) = 0.96; $P < 0.001$] and $P_{\max}$ [Pearson determination coefficient r^2 ($P_{\max} - P_{mean}$) = 0.81; $P < 0.001$]. Air temperatures were used as a substitute for water temperatures, which are not currently available for many river basins. This is generally acceptable because streams and rivers are well-mixed water bodies that readily exchange heat with the atmosphere, and it has been empirically demonstrated that air and river water temperatures are strongly positively correlated (e.g. Caissie, 2006).

We then selected fish species that had been widely introduced outside their native range (Lever, 1996) and that are native to more than 15 river basins to ensure that the native basins available in our dataset are representative of a substantial part of the native range. *Gambusia affinis* and *Gambusia holbrooki* were considered together due to their uncertain taxonomic status in the literature and to their similar ecological requirements (Pyke, 2008). For the 18 resulting fish species (see Table 1), we gathered species occurrences per river basin and distinguished between

Table 1 Native and non-native species occurrences (i.e. number of basins) and percentage of non-native basins experiencing a niche shift for at least one climate variable.

Species	Native occurrences	Non-native occurrences	Percentage of non-native basins with niche shift
Ameiurus melas	18	49	14.3
Carassius auratus	49	164	12.8
Carassius carassius	30	54	55.6
Cyprinus carpio	34	245	20.4
Gambusia sp.	52	206	20.4
Ictalurus punctatus	33	44	25.0
Lepomis cyanellus	20	46	23.9
Lepomis gibbosus	28	52	23.1
Lepomis macrochirus	44	63	19.0
Micropterus salmoides	48	100	24.0
Oncorhynchus mykiss	56	189	27.5
Perca fluviatilis	103	64	42.2
Pseudorasbora parva	29	45	15.6
Salmo trutta	141	131	21.4
Salvelinus fontinalis	66	71	40.8
Sander lucioperca	32	48	43.8
Thymallus thymallus	35	33	12.1
Tinca tinca	79	46	10.9

native and non-native occurrences. A species was considered non-native when: (1) it did not historically occur in a given basin, and (2) it was successfully established (i.e. had self-reproducing populations) (see Leprieur *et al.*, 2008; Blanchet *et al.*, 2009). For a few basins (no more than four per species) the native or non-native status was uncertain in the literature, and the species was considered as native in these basins to avoid identifying undue niche shifts.

We assumed that if a species is present (native or non-native) in a river basin, it is potentially present in all of the 0.5° × 0.5° grid cells encompassed by the river basin. We then defined climatic niche shifts as instances where the climate characteristics of one or more non-native basins exhibited zero overlap with climate conditions observed throughout the native range. As a climatic niche shift can result from either an increase or a decrease in a climatic variable, we distinguished between positive and negative shifts. For each species and for each climatic variable, we determined the percentage of non-native basins for which a positive or negative climatic niche shift was identified. To test for potential bias due to native occurrence sampling of each species we measured the relationship (Pearson's correlation) between the per species percentage of non-native basins experiencing climatic niche shifts and: (1) the number of basins in the native range, and (2) the native range area measured as the number of pixels of 0.5° × 0.5°.

We then tested for a common pattern of climatic niche shifts among species depending on their biogeographic origin (i.e. Nearctic versus Palaearctic) and their thermal guild (i.e. cold water versus cool water; Scott & Crossman, 1973; Keith & Allardi, 2001). We compared the per species percentage of non-native basins experiencing climatic niche shifts between the defined groups using a Mann–Whitney test. For each climate variable, positive and negative shifts were considered as distinct, hence resulting in 10 climate variables (as two variables exhibited both positive and negative shifts).

RESULTS

Climatic niche shifts were identified for each of the 18 studied species (Table 1). Using the eight selected climatic variables, each species experienced a shift between native and non-native ranges for at least one climate variable in, on average, 25% of its non-native basins. There was, however, large variation among species (see Table 1). For instance, the tench (*Tinca tinca*) exhibited climatic niche shifts in about 10% of its non-native basins whereas the crucian carp (*Carassius carassius*) exhibited climatic niche shifts in more than half of its non-native basins. The percentage of non-native basins presenting climatic niche shifts was not significantly correlated with the number of basins in the native range (Pearson correlation $r = 0.063$; $P = 0.81$) nor to the native range area (Pearson correlation $r = 0.329$; $P = 0.18$). Five out of the 18 species exhibited a climatic niche shift for more than half of the eight climate variables (Figs 1 & S1). For instance, the rainbow trout (*Oncorhynchus mykiss*) exhibited a climatic niche shift for each climatic variable (Fig. 1a). The introduction patterns of that species are largely documented (Fausch *et al.*, 2001; Crawford & Muir, 2008), and although its establishment success remains uncertain in some places, it has become established in large areas throughout the world (Fig. 1b). Some of these river basins are characterized by a lower temperature and precipitation variability and by a warmer winter temperature than the basins where that species is native (Fig. 1a).

Considering climatic variables for the overall set of species revealed little consistency among the species: two variables ($P_{\max}$ and N_{rd}) exhibited both negative and positive climate shifts,

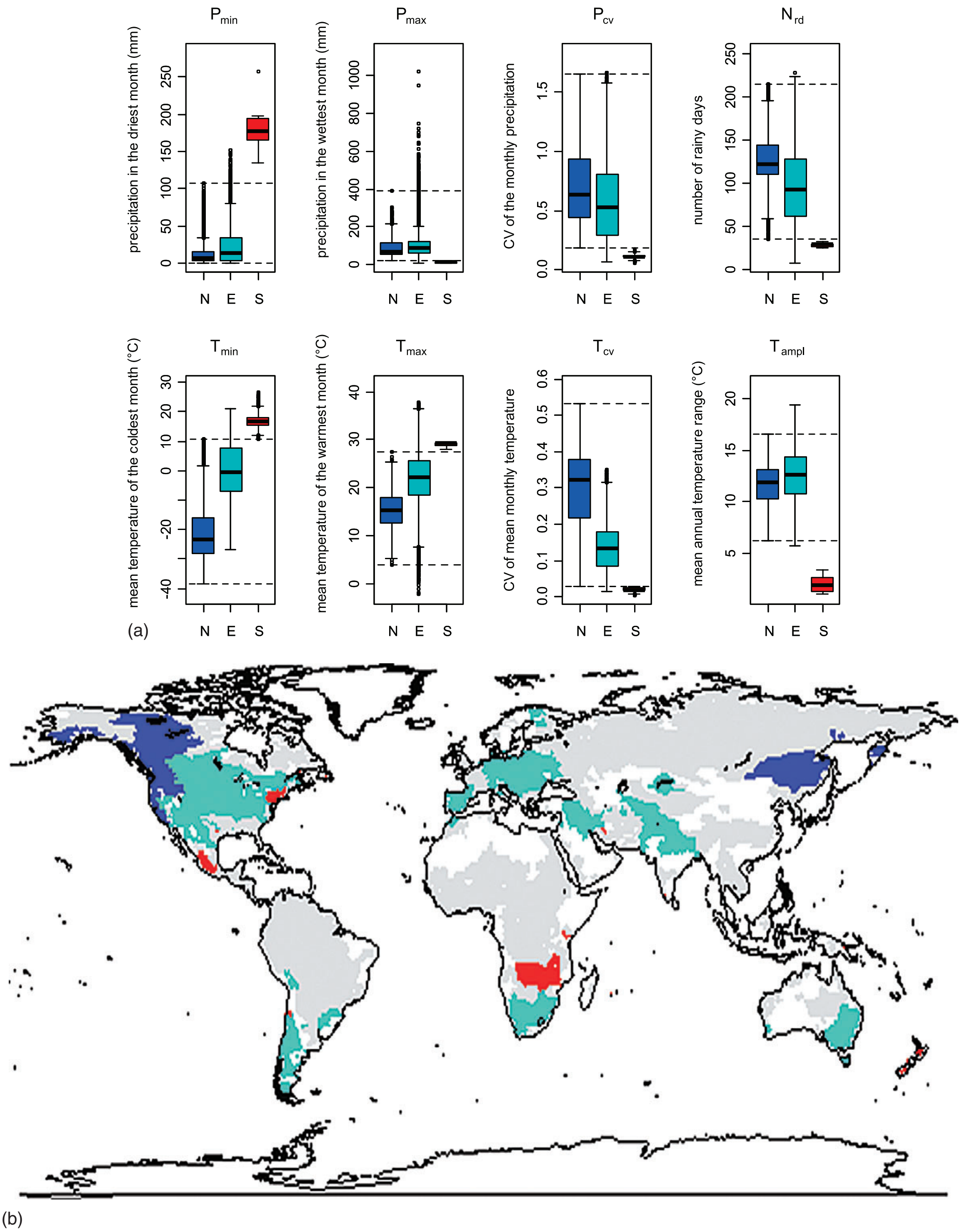

Figure 1 (a) Boxplots representing the climatic range of the rainbow trout *Oncorhynchus mykiss*: For each climate variable, native basins (N, blue), non-native basins without climatic shift (E, turquoise) and non-native basins with climatic shift (S, red) were separated. A climatic niche shift is observed when all the values inside a basin lie outside the two horizontal lines (corresponding to the extreme values inside the native area). The variables used are: precipitation of the driest month (P_{min}); precipitation of the wettest month (P_{max}); coefficient of variation of the monthly precipitation (P_{cv}); number of rainy days (N_{rd}); mean temperature of the coldest month (T_{min}); mean temperature of the warmest month (T_{max}); coefficient of variation of mean monthly temperature (T_{cv}); and mean annual temperature range (T_{ampl}). (b) World-wide distribution of *O. mykiss* based on the 938 basins considered: native basins, non-native basins without climatic shift or non-native basins with climatic shift. Basins available in our database where *O. mykiss* is absent are in grey, areas not covered by our database are in white. Note that the native or non-native status of rainbow trout remains uncertain in the west of the Kamchatka Peninsula basins. To avoid identifying undue niche shift rainbow trout was considered as native in these basins.

Table 2 Environmental variables, percentage of species exhibiting shifts and percentage of basins in which at least one species exhibited a shift.

Environmental variable	Percentage of shifting species	Percentage of exotic shifting basins
P_{min}+	22.2	1.1
P_{max}+	22.2	3.5
P_{max}–	22.2	1.3
N_{rd}+	11.1	1.3
N_{rd}–	66.7	9.7
T_{min}+	38.9	10.4
T_{max}+	5.6	0.2
P_{cv}–	27.8	9.1
T_{cv}–	88.9	26.3
T_{ampl}–	50.0	8.6

The variables used are: precipitation of the driest month (P_{min}); precipitation of the wettest month (P_{max}); coefficient of variation of the monthly precipitation (P_{cv}); number of rainy days (N_{rd}); mean temperature of the coldest month (T_{min}); mean temperature of the warmest month (T_{max}); coefficient of variation of mean monthly temperature (T_{cv}); mean annual temperature range (T_{ampl}). + corresponds to positive shifts, – to negative shifts. The variables experiencing no shift have been removed.

depending on the species. Three other variables (P_{cv}, T_{cv} and T_{ampl}) exhibited only negative shifts, and the three remaining variables (P_{min}, T_{min} and T_{max}) exhibited positive shifts (Table 2). The distribution of shifts also differed: T_{cv} and N_{rd} exhibited at least one shift for more than two-thirds of the species (89% and 67%), whereas T_{cv} exhibited shifts in about one-quarter of the basins and N_{rd} exhibited shifts only in 10% of the basins (Table 2).

Mann–Whitney tests revealed no significant differences between fish species according to their thermal requirements (coldwater versus coolwater species) for any of the 10 climatic variables. With regard to the biogeographic origin of species, Mann–Whitney tests revealed a significant difference between species for only one variable, namely the number of rainy days ($P < 0.01$). Actually, Nearctic species exhibited a much greater number of rainy days shifts than Palaearctic ones. Many of these shifts were located in the south of the United States and in Mexico (i.e. around the native area), except for *Gambusia* sp. which also exhibited numerous shifts in central Asia.

DISCUSSION

For all the species considered in this study, our results showed a niche shift between native and non-native ranges for at least one climatic variable. With these results, the growing literature on climate mismatch for a wide variety of organisms (Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2008; Beaumont *et al.*, 2009; Rödder & Lötters, 2009; Medley, 2010) is now extended to freshwater fish. The fact that all the considered species are experiencing a niche shift is probably linked to the fact that their realized niches actually don't encompass their entire physiological and ecological ranges (Rosenfield, 2002). Indeed, native species distribution is strongly limited by species incapacity to cross dry land or survive in marine environment (Hugueny, 1989). Our results also show that climatic niche shifts can be detected using coarse-grained data. Importantly, these niche shifts were detected even though we used a highly conservative procedure (i.e. zero overlap in environmental variables between native and non-native basins). It should, however, be noted that our method probably overestimated species climate ranges, as species were assumed to be ubiquitous throughout each river basin. It is therefore highly likely that we underestimated the frequency of climatic niche shifts. It is also possible that sampling artefacts occurred due to incomplete environmental sampling in the native area. This bias is, however, unlikely, because no relationship was found between the surface area (or the number of river basins) in the native range and the percentage of non-native river basins experiencing climatic niche shifts.

Focusing on individual species and specific locations might help to better understand the climatic niche shifts observed. For example, the rainbow trout (and the brown trout) was largely introduced in New Zealand streams and rivers (Townsend, 1996) encountering a more stable climate, which explains a shift toward lower amplitude of temperature and lower coefficients of variation. Here the establishment of trout may have been facilitated by the lack of native enemies, diseases and competitors resulting in a higher tolerance over a wider range of environmental conditions in novel habitats (Moyle & Light, 1996; Townsend, 1996). Moreover, elevated winter temperatures have positive effects on juvenile growth (Morgan *et al.*, 1998) and rainbow trout acquire a higher thermal tolerance for hatching and egg development under a warmer climate (Ineno *et al.*, 2005), which parallels our present temperature mismatch findings: the shift of the rainbow trout to higher minimal temperature in some Mexican and African river basins. From a broader point of view, climate niche shifts have been attributed to three non-mutually exclusive mechanisms: (1) the rapid evolution of species when introduced to novel environments, which may allow them to advance beyond the limits of their climate distribution in their native range (Pearman *et al.*, 2008); (2) physiologically suitable environmental conditions in the non-native range which are not found in native habitats because of historical or geographical constraints on colonization (Jiménez-Valverde *et al.*, 2008; Leprieur *et al.*, 2009a); and (3) the lack of native predators, diseases and competitors (i.e. enemy release), which can result in higher tolerance to extreme biotic or abiotic conditions (Moyle & Light, 1996; Townsend, 1996). Our coarse-grained data did not allow the relative roles of these three mechanisms to be disentangled, but complementary experimental and fine-grained field studies could help to determine and quantify the mechanisms responsible for climatic niche shifts. Extending these considerations to a multispecies context, there was little similarity between species concerning the climate features to do with climatic niche shift variables, nor in the way they vary. Neither geographical origin nor thermal preferences appear as a strongly significant factor explaining a multispecies response, leaving open the question of the causes of climatic niche shifts (local adaptation, dispersal limitation or physiological tolerance). For instance, we recommend further studies to disentangle the causes of climatic niche shifts focusing on a per species analysis, rather than adopting a multispecies approach.

Overall, our results have important implications for the application of both bioclimatic models and invasion risk assessments. Bioclimatic models are increasingly being used by conservation biologists to forecast the future ranges of both native and non-native species in the face of climate change (Jeschke & Strayer, 2008). Our results suggest, however, that bioclimatic models are likely to underestimate the spread of colonizing species when they are trained or parameterized using environmental data from species native ranges, especially under projected climate change scenarios. Such discrepancies have been recently highlighted for particular plant and invertebrate taxa (i.e. Broennimann *et al.*, 2007; Loo *et al.*, 2007; Fitzpatrick *et al.*, 2008; Medley, 2010). With regard to freshwater fish, we strongly recommend that future studies using bioclimatic models consider climatic conditions found in both native and known non-native ranges so as to consider: (1) a wider sampling of environmental variation (see Menke *et al.*, 2009), and (2) a wider range of climatic conditions in which the species has become established. For instance, this will give a clearer picture of the potential climatic range and hence will reduce uncertainty when assessing the risks posed by non-native freshwater fish (Leprieur *et al.*, 2009b). By the same logic, however, we must caution that such a procedure will be much less informative for potential invaders that have not yet expanded or that have been rarely introduced out of their native range. For such species, bioclimatic models might produce an incomplete picture of their colonization potential (e.g. Loo *et al.*, 2007).

As demonstrated here, coarse-grained occurrence data can be used to identify climatic niche shifts. This is important because a vast number of coarse-grained occurrence data have been published in regional atlases, for a wide variety of taxonomic groups (e.g. DAISIE, 2009). These data can facilitate invasion risk assessments when detailed, local-scale occurrence data are lacking, which is the case for many freshwater fishes but also for most organisms on Earth (Pyšek *et al.*, 2008; Leprieur *et al.*, 2009b). It should, however, be noted that our coarse-scale approach probably underestimates climatic niche shifts. We therefore suggest that it can serve as a first step to identify species experiencing climatic niche shifts, or be used to predict regions where climatic shifts are likely to occur. It might then guide future fine-grained studies in identifying the exact nature and extent of the climatic niche shift observed (see Pearman *et al.*, 2008) and in determining which mechanisms underlie observed patterns (e.g. local adaptation, dispersal limitation or physiological constraints).

To conclude, our study has demonstrated that climatic niche shifts can be identified using coarse-grained species occurrence data. However, the establishment of a species outside its native range is driven by multiple biotic and abiotic factors acting at different spatial resolutions (Lockwood *et al.*, 2007). We thus strongly encourage future studies to extend the present results by applying a multiscale approach. The development of global-scale databases at both fine and coarse spatial resolutions is urgently needed to draw baseline generalities in invasion ecology (Cadotte *et al.*, 2006) which would help managers to prevent future species invasions.

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SUPPORTING INFORMATION

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

Figure S1 Climatic range and world-wide distribution of 17 freshwater fish species.

Table S1 Bivariate correlation matrix between the climate variables.

BIOSKETCHES

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