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Broad-scale determinants of non-native fish species richness are context-dependent

Simon Blanchet[1,†], Fabien Leprieur[2,†], Olivier Beauchard[3], Jan Staes[3],
Thierry Oberdorff[2] and Sébastien Brosse[1,*]

[1]*Laboratoire d'Ecologie Fonctionnelle, UMR 5545, CNRS-Université Paul Sabatier, 118 route de Narbonne, 31062 Toulouse Cedex 4, France*
[2]*Institut de Recherche pour le Développement (UR131), Antenne au Muséum National d'Histoire Naturelle, 43 rue Cuvier, 75231 Paris Cedex, France*
[3]*Ecosystem Management Research Group, Department of Biology, Faculty of Sciences, University of Antwerp, Universiteitsplein 1, 2610 Antwerpen (Wilrijk), Belgium*

Identifying the factors determining the non-native species richness (NNSR) in a given area is essential for preventing species invasions. The relative importance of human-related and natural factors considered for explaining NNSR might depend upon both the spatial scale (i.e. the extent of the gradients sampled) and the historical context of the area surveyed. Here, using a worldwide database of freshwater fish occurrences, we tested whether the relative influence of human and ecological determinants of non-native fish species establishment at the scale of the biogeographic realm was consistent (i) with that observed worldwide, and (ii) among the different biogeographical realms. The prominent role of human activity in shaping the global (i.e. worldwide) pattern of NNSR cannot be directly extrapolated to the biogeographic realms. Furthermore, the relationships between human and ecological determinants and NNSR vary strikingly across biogeographic realms, revealing a strong context dependency of the determinants of NNSR. In particular, the human-related factors play a predominant role in explaining the establishment of non-native species in economically developed realms, while in the other realms environmental characteristics of the river basins best explained geographical patterns of NNSR. In the face of future biological invasions, considering both the spatial scale and the historical context of the surveyed area is crucial to adopt effective conservation strategies.

Keywords: species invasions; non-native species richness; human activity; context dependency; spatial extent

1. INTRODUCTION

By creating new routes and pathways for colonization, human activities have increasingly assisted species to overcome natural biogeographic barriers (Vitousek *et al.* 1997; Ricciardi 2007). Arguably, the probability that some non-native species become invasive and hence cause ecological damage is positively correlated to the pool of non-native species established in a region (Vander Zanden 2005; Ricciardi & Kipp 2008). Hence, identifying the factors determining the size of the regional pool of non-native species is a keystone challenge for predicting species invasions and ecological damage (Levine & D'Antonio 2003).

With regard to the establishment stage of the invasion process, three main hypotheses have been proposed to explain the geographical differences in non-native species richness (NNSR; Jeschke & Strayer 2005; Meyerson & Mooney 2007). First, the 'human activity' hypothesis predicts that, by disturbing natural landscapes and increasing the importation and dispersal of non-native species, human activities facilitate their establishment

(Taylor & Irwin 2004). Second, the 'biotic acceptance' hypothesis predicts that the establishment of non-native species will be greatest in areas that are rich in native species and with optimal environmental conditions for population growth (Fridley *et al.* 2007). Finally, the 'biotic resistance' hypothesis predicts that species-poor communities will host more non-native species than species-rich communities, the latter being highly competitive and hence liable to impede the establishment of non-native species (Levine 2000; Hooper *et al.* 2005).

Among these three hypotheses, the human activity hypothesis has been proven the most powerful in explaining the global (i.e. worldwide) patterns of NNSR for both island birds and freshwater fishes (Blackburn *et al.* 2008; Leprieur *et al.* 2008). This has led to the conclusion that NNSR is predominantly controlled by the intensity of human activities rather than by natural processes. However, changing the scale of spatial analyses is expected to greatly influence the mechanisms underlying the observed patterns (Blackburn & Gaston 2002; Rahbek 2005). Indeed, it has been shown for native species that the range of conditions along which the biota is surveyed can affect our perception of the importance of the determinants accounting for diversity patterns (Turner 1989; Rahbek & Graves 2001; Heino *et al.* 2005). For instance, Buckley & Jetz (2007) and Davies *et al.* (2007)

demonstrated that the relative importance of environmental determinants of native species richness of birds and amphibians cannot be extrapolated from one biogeographic realm to the globe. Moreover, for a given spatial scale, differences in regional evolutionary histories (i.e. speciation and extinction events) can trigger native species richness discrepancies among biogeographic realms (i.e. context dependency; Stephens & Wiens 2003; Buckley & Jetz 2007). Despite their crucial influence on setting up sound conservation strategies, the effects of both spatial scale and context dependency on perceptions of the determinants of NNSR have never been examined. When dealing with spatial scale in ecology, it is convenient to distinguish between 'grain' and 'extent' (Schneider 2001; Rahbek 2005). The grain refers to the sample units compared, while the extent refers to the geographical space over which comparisons are made. To date, much of the discussion regarding the determinants of NNSR has revolved around sample grain rather than extent (e.g. Davies *et al.* 2005; Fridley *et al.* 2007).

In the present study, we first tested for an effect of the spatial extent on the determinants of freshwater fish NNSR. To do this, we used an extensive worldwide dataset of freshwater fish occurrences at the river basin level (i.e. the sample unit), with information for both native species and successfully established non-native species (Leprieur *et al.* 2008). In particular, we tested whether the relative influence of human and ecological determinants of fish NNSR at the biogeographic realm extent was consistent with that previously reported on the global extent by Leprieur *et al.* (2008; i.e. spatial extent effects). We then tested whether the relative influence of the determinants of fish NNSR varied among the different biogeographic realms (i.e. context-dependent effects). Since the gross domestic product (GDP) has been identified as the main determinant of fish NNSR on the global extent (Leprieur *et al.* 2008), we expected that between-extent and between-realm differences in the range of this variable would trigger discrepancy in the determinants of NNSR. This prediction is based on a recent study (Davies *et al.* 2006) showing that the relative influence of human impacts on extinction risk in birds was inconsistent between biogeographic realms due to an incomplete representation of the worldwide human impact gradient within the realms.

2. MATERIAL AND METHODS

(a) *Species data*
The database was built by conducting an extensive literature survey of native and non-native freshwater fish species checklists. Only complete species lists at the river basin level were considered. River basin here refers to all the connected drainage systems upstream of an outlet that enters an ocean or an inland 'sea' (e.g. lakes). The full list of river basins used in our analysis can be consulted in Leprieur *et al.* (2008). In regional freshwater fish biogeography, the river basin is the most appropriate sampling unit because each river basin can be considered as a biogeographic island with specific species pools (Hugueny 1989; Guegan *et al.* 1998). The database contains species occurrence data for the world's freshwater fish fauna ($n = 597$ river basins). To our knowledge, it constitutes the largest database for a group of invaders. A species was considered non-native when (i) it did not

historically occur in a given basin and (ii) it was successfully established (i.e. self-reproducing populations). Estuarine species with no freshwater life stage were not considered in our analyses. Details on the data and bibliographical sources are given in Leprieur *et al.* (2008). Data on native species richness and NNSR per river basin will be available at the end of the research programme 'Freshwater Fish Diversity' (ANR-06-BDIV-010: 2007-2010).

(b) *Environmental and human activity-related variables*
Three environmental variables and three human activity related variables were determined for each river basin. The surface area of each river basin (km^2) was taken from Leprieur *et al.* (2008). The altitudinal range (m) for each river basin was determined from a geographical atlas and expressed as a semi-quantitative metric (ranging from 1 to 8). We calculated the mean value of net primary production (kg-carbon $m^{-2} yr^{-1}$), the human population density (number of people km^{-2}), the purchasing power parity GDP (US $) and the percentage of urban area over the surface area of each basin from $0.5° \times 0.5°$ grid data available in CIESIN (Center for International Earth Science Information Network; http://islscp2.sesda.com/ISLSCP2_1/html_pages/groups/soc/gdp_xdeg.html; 2005) and the Atlas of Biosphere (Centre for Sustainability and the Global Environment; http://www.sage.wisc.edu; 2002). In addition, we reported the number of native freshwater fish species (from our species database) for each river basin. The 597 river basins considered in this study cover almost all terrestrial areas of the globe and account for 72 basins for the Afrotropical realm, 94 for the Australian realm, 127 for the Nearctic realm, 68 for the Neotropical realm, 29 for the Oriental realm and 207 for the Palaearctic realm.

These environmental and human activity-related variables, as well as the number of native species per river basin, were previously used by Leprieur *et al.* (2008) to test: (i) the human activity hypothesis, which predicts a positive relationship between the human activity-related variables (human population density, percentage of urban area and GDP) and NNSR in a given river basin (e.g. Taylor & Irwin 2004); (ii) the biotic resistance hypothesis, which predicts a negative relationship between the native species richness and the NNSR (Levine 2000; Hooper *et al.* 2005); and (iii) the biotic acceptance hypothesis, which predicts a positive relationship between the native species richness and the NNSR (Fridley *et al.* 2007), due to similar responses of native and NNSR to environmental gradients (altitudinal range, basin area and net primary productivity).

(c) *Statistical analyses*
We used a generalized linear model (GLM) framework to explain the fish NNSR per river basin. This approach was similar to that used by Leprieur *et al.* (2008) and was applied to each realm independently. Using this approach allowed (i) comparison of our results, obtained at the biogeographic realm extent, to those of Leprieur *et al.* (2008) derived at the global extent (i.e. spatial extent effects), and (ii) comparison of the results between biogeographic realms (i.e. context-dependent effects).

(i) *GLM framework*
We first tested the form and strength of the relationship (positive or negative) between the NNSR and each explanatory

variable by performing a series of partial regression analyses (see Chiron *et al.* 2008; Leprieur *et al.* 2008). Indeed, the three hypotheses considered are not necessarily mutually exclusive and we therefore checked for confounding effects of the other hypotheses when testing the form of each individual hypothesis. To test the human activity hypothesis, we first extracted the residuals from a GLM (Poisson error term) linking NNSR and the independent variables related to the biotic resistance and biotic acceptance hypotheses (i.e. number of native species, altitudinal range, basin area and net primary productivity). We then analysed the form and the significance of the relationship between the residuals of the former GLM with each variable related to the human activity hypothesis (i.e. GDP, percentage of urban area and population density). This allowed us to test the human activity hypothesis while controlling for the effects of environmental conditions and native species richness. To test the biotic acceptance hypothesis, we first extracted the residuals from a GLM (Poisson error term) linking NNSR and the independent variables related to the human activity hypothesis (i.e. GDP, percentage of urban area and population density). We then analysed the form and the significance of the relationship between the residuals of the former GLM with each variable related to the biotic acceptance hypothesis (i.e. number of native species, altitudinal range, basin area and net primary productivity). This allowed us to test the biotic acceptance hypothesis while controlling for the effects of propagule pressure and habitat disturbance. Finally, to test the biotic resistance hypothesis, we first extracted the residuals from a GLM (Poisson error term) linking NNSR and the independent variables related to the biotic acceptance and human activity hypotheses (i.e. altitudinal range, basin area, net primary productivity, GDP, percentage of urban area and population density). We then analysed the form and the significance of the relationship between the residuals of the former GLM with the variable related to the biotic resistance hypothesis (i.e. number of native species). This allowed us to test the biotic resistance hypothesis while controlling for the effects of environmental conditions, propagule pressure and habitat disturbance. To test the relationship between residuals and each explanatory variable, we performed a Spearman rank correlation test, because residuals were not normally distributed. We corrected for multiple comparisons using Bonferroni corrections ($\alpha = 0.05/48 = 0.001$).

Next, we applied hierarchical partitioning to quantify the independent and joint explanatory power of each variable related to the three hypotheses tested (Chevan & Sutherland 1991; Mac Nally 2000). This modelling technique is particularly appropriate when the explanatory variables are collinear (Chevan & Sutherland 1991; Mac Nally 2000). In hierarchical partitioning, all possible models (i.e. submodels) in a multiple regression setting are considered jointly to identify the most likely causal factor. This process involved computation of the increase in the fit of all models with a particular variable compared with the equivalent model without that variable (for more details, see Chevan & Sutherland 1991; Mac Nally 2000; Leprieur *et al.* 2008). Hierarchical partitioning allows each explanatory variable to identify an independent contribution and a joint contribution, each expressed as the percentage of the total deviance explained by the submodels. Joint contributions represent the percentage of deviance that is explained by a given variable in association with at least one other variable. Independent contributions represent the percentage of deviance that is

explained by a given variable irrespective of the other variables. To account for potential bias due to differences in sampling effort between biogeographic realms, hierarchical partitioning was run on 1000 random subsets of one-third of the total number of basins available for each realm. For each realm independently, we quantified the average independent contribution of each explanatory variable from the 1000 random subsets. We then compared each average independent contribution with the contribution observed when all river basins within a realm were considered. We expressed the bootstrap estimate of bias as the difference between the average and observed independent contribution values (Quinn & Keough 2004).

(ii) *Spatial extent effects*
To compare the influence of each environmental or human determinant worldwide and on the biogeographic realm extent, we used a meta-analysis approach (Rosenberg *et al.* 2000). Fisher's z-transformed Spearman rank correlation (r_s) values obtained from the partial regression analyses (see above) were used to evaluate the effect size (z, the magnitude of an effect) of each determinant for each realm (for formulae, see Rosenberg *et al.* 2000). We then calculated the cumulative effect size ($\bar{E}$) and the 95% confidence interval of each determinant. This procedure allows the calculation of a mean effect size weighted for differential sampling sizes among realms and hence enables sampling size variability to be checked (Rosenberg *et al.* 2000). Following this procedure, we calculated the effect size (z) of each determinant on the global extent (r_s from table 2 in Leprieur *et al.* 2008) and verified whether it fell within the 95% confidence interval calculated on the biogeographic realm extent. Finally, we evaluated whether the set of effect sizes calculated for the realm extent was homogeneous across realms. The total heterogeneity of a sample (Q_t) was calculated as described in Rosenberg *et al.* (2000) and its significance was tested using χ^2 statistics.

(iii) *Context-dependent effects*
We tested the hypothesis that potential differences observed between biogeographic realms in the determinants of NNSR are triggered by between-realm differences in the GDP range (i.e. the main determinant of fish NNSR on the global extent; Leprieur *et al.* 2008). To do so, we used a subset of our dataset in which we restricted the range of GDP in each realm, so that it was equalized among realms. Specifically, we selected river basins so that in each realm the range of GDP ($\log(x+1)$ transformed) was between 8 and 12 units (i.e. the range of the Afrotropical realm, which displays the lowest observed range of GDP; figure 1). Using this restricted dataset, we again ran the hierarchical partitioning procedure as described above. These results were compared with those obtained when using the full dataset. If GDP is indeed a major reason explaining why the determinants of NNSR differ among biogeographic realms, we expect that, by holding GDP within a constant range, the determinants of NNSR should be similar among realms.

In all statistical analyses, each explanatory variable was log transformed to meet the assumptions of normality and homoscedasticity. All statistical analyses were performed with R v. 2.6.0 (R Development Core Team 2005), except the meta-analysis, which was performed using METAWIN v. 2.0 (Rosenberg *et al.* 2000).
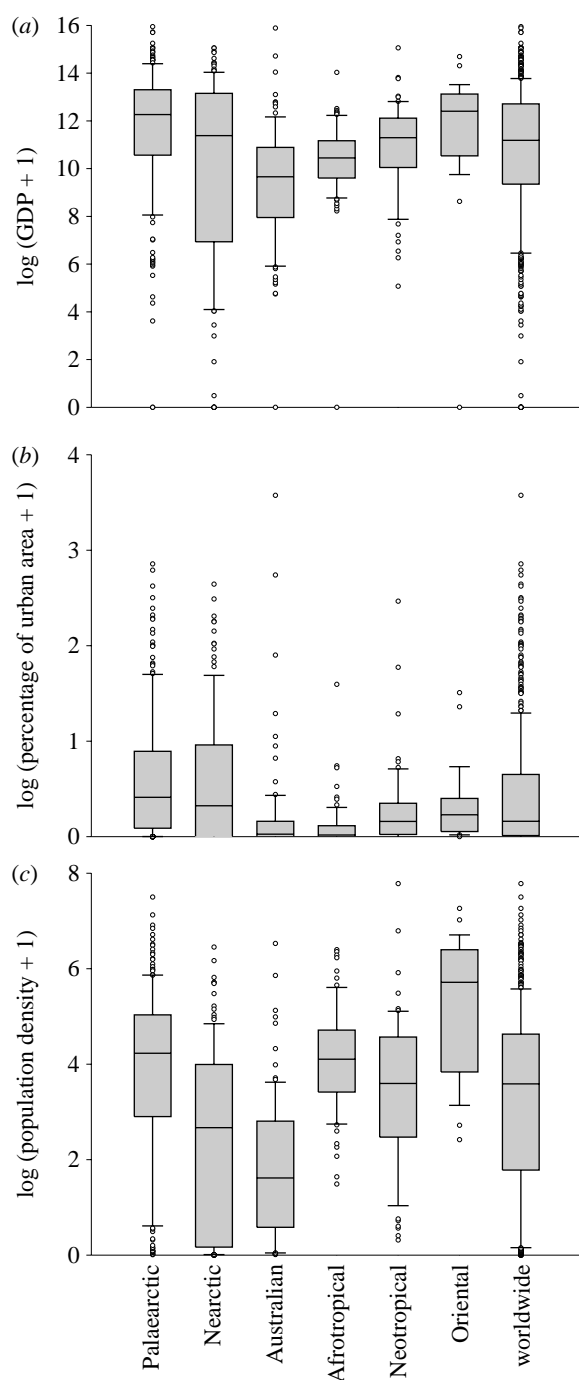
Figure 1. Variations in the GDP, human population density and percentage of urban area among biogeographic realms. (*a*) Average GDP (log scaled) per river basin. (*b*) Average percentage of urban area (log scaled) per river basin. (*c*) Average human population density (log scaled) per river basin. Horizontal bars represent medians, boxes indicate the 25th (upper box) and 75th (lower box) percentiles, whiskers are 1.5 times the interquartile range of the data and points are outliers.

3. RESULTS

Using a meta-analytical framework, we showed that the relative importance of the ecological and human activity-related variables in predicting NNSR were similar across spatial extents (figure 2). Indeed, at both the biogeographic realm and global extents, the variables related to the human activity hypothesis had average effect sizes that were higher than the other two hypotheses (figure 2). However, it should be noted that a spatial extent effect

occurred for three variables (GDP, percentage of urban area and native species richness). Their effect sizes reported at the global extent were either significantly higher or lower than those observed at the biogeographic realm extent (figure 2). Moreover, we found a significant heterogeneity of the effect sizes between the realms for all the variables ($14.86 < Q_t < 56.42$, d.f.$=5$, $0.001 < p < 0.01$; results not detailed), suggesting that the spatial extent effect might depend upon the realm considered.

Such a trend was confirmed using an approach of partial regression analyses applied to each biogeographic realm independently. Indeed, the strength and shape of the variables explaining NNSR exhibited a strong between-realm variation (table 1). For the Palaearctic, Nearctic and Australian realms, the relationships between each variable related to the human activity hypothesis and the NNSR were positive and highly significant (table 1). By contrast, none of these relationships were significant in the Afrotropical, Neotropical or Oriental realms (table 1), suggesting a weak influence of the variables related to the human activity hypothesis in these realms. In all the biogeographic realms (except for the Australian realm), at least one of the variables related to the biotic acceptance hypothesis was significant after Bonferroni corrections (table 1). It is worth noting that, for the biotic acceptance hypothesis to be accepted, a positive relationship between the native species richness and the NNSR must be verified, which holds for the Palaearctic, Nearctic and Oriental realms (table 1). Finally, the negative relationship between native species richness and NNSR, which is expected under the biotic resistance hypothesis, was not significant in any of the realms (table 1).

These results were concordant with those obtained by a hierarchical partitioning method that allows the relative importance of each variable to be determined in explaining NNSR (see table S1 in the electronic supplementary material; figure 3). Regarding biogeographic realms (figure 3), the percentage of deviance explained by the seven ecological and human activity-related variables, varied between 41.02 per cent (for the Neotropical realm) and 77.02 per cent (for the Oriental realm). In all realms except the Australian, the independent contribution of the explanatory variable in explaining NNSR was higher than the joint contribution (see table S1 in the electronic supplementary material). More precisely, the independent and joint effects of the human activity-related variables (i.e. GDP, population density and percentage of urban area) on NNSR were high in three of the six biogeographic realms, namely the Nearctic, Palaearctic and Australian realms (figure 3*a*–*c*). Among the human activity-related variables, the GDP had the greatest explanatory power in these realms (figure 3*a*–*c*). For the same three realms, the independent contribution of the ecological variables was weak for all except the Palaearctic realm, for which the surface area (biotic acceptance hypothesis) accounted for approximately 20 per cent of the total explained deviance (figure 3*b*). By contrast, for the other three realms (i.e. Oriental, Neotropical and Afrotropical), the human activity-related variables had a weak effect on NNSR, while environmental variables such as basin area and altitudinal range accounted for most of the variation (figure 3*d*–*f*). In the Oriental realm, surface area and native species richness best explained the NNSR (figure 3*d*). For the Neotropical realm, both altitudinal
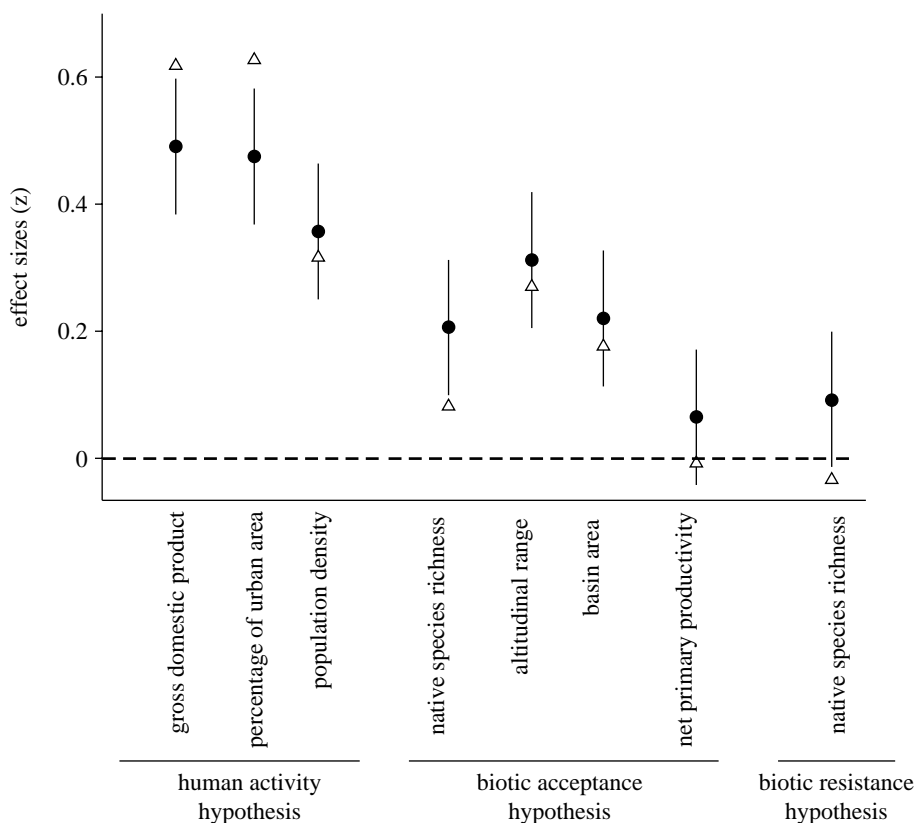
Figure 2. Effect sizes (measured as Fisher's z-transformation, z) of each determinant of NNSR measured either at the global (triangles) or biogeographic realm extent (circles). The effect sizes at the biogeographic realm extent (i.e. effect sizes measured for the Palaearctic, Nearctic, Australian, Neotropical, Afrotropical and Oriental realms independently) are summarized as a cumulative effect size ($\bar{E}$) that allows differential sample sizes to be calculated among realms. At the biogeographic realm extent, the 95% confidence interval of each determinant was assessed. We assumed that significantly different effect sizes occur between the global and realm spatial extents when the effect size for a given determinant on the global extent falls outside the 95% confidence interval calculated on the biogeographic realm extent. Determinants were grouped according to the hypotheses proposed to explain spatial patterns of NNSR (see the main text).

range and surface area best explained the NNSR (figure 3*e*). Finally, altitudinal range accounted for most of the variation in NNSR in the Afrotropical realm (figure 3*f*). These results strongly suggest that the strength of the determinants of NNSR is context-dependent. It is noteworthy that for all biogeographic realms bootstrap estimations of biases were very weak, indicating that the difference in sampling effort among realms had only slight effect on the above results (see table S2 in the electronic supplementary material).

Finally, we tested whether the differences in the determinants of NNSR noted between biogeographic realms might be triggered by between-realm differences in the range of the GDP (i.e. the main determinant of fish NNSR at the global extent; Leprieur *et al.* 2008). To do so, we used a subset of our data in which we restricted the range of GDP in each realm, so that it equalized among realms (see §2). As expected, when using this restricted dataset, the relative influence of each variable differed strongly from the situation in which the full dataset was used (figure 4). Indeed, the joint and independent effects of human activity-related variables became weak for the three biogeographic realms in which we had previously shown that these variables had a strong effect (i.e. Nearctic, Palaearctic and Australian realms; figures 3 and 4). Instead, the effect of the ecological variables increasingly accounted for the NNSR. However, the whole

pattern remained unchanged for the two other realms (i.e. Oriental and Neotropical), the ecological variables still accounting for most of the variation in NNSR (figure 4).

4. DISCUSSION

Our findings show that the prominent role of human activity in shaping the global pattern of fish NNSR (Leprieur *et al.* 2008) cannot be directly extrapolated to a smaller spatial extent, namely the biogeographic realm. Indeed, the human activity hypothesis was only verified for the Australian, Nearctic and Palaearctic realms. In these realms, the level of economic activity within river basins (i.e. the GDP) strongly determined the establishment of non-native species, and it is noteworthy that the geographical variation in GDP was high and similar to that observed worldwide (figure 1). However, for the Afrotropical, Neotropical and Oriental biogeographic realms, which have limited geographical variation in GDP, environmental characteristics of river basins, such as area and altitudinal range, accounted for the geographical patterning of NNSR. Several previous studies have highlighted a strong spatial-scale dependency of the determinants of NNSR. However, many of these studies focused on the effects of grain size (Collingham *et al.* 2000; Lloret *et al.* 2004; Hamilton *et al.* 2005; Pauchard & Shea 2006; Fridley *et al.* 2007). Here, we provide evidence that the spatial extent can also greatly

Table 1. Spearman rank correlation (r_s) between the NNSR (residuals) and each determinant related to the human activity, biotic acceptance and biotic resistance hypotheses. (The coefficients of correlation and the associated *p*-values are presented for each realm independently. Italic values indicate coefficients that were significant after Bonferroni corrections ($\alpha = 0.05/48 = 0.001$).)

	Nearctic		Palaearctic		Australian		Oriental		Neotropical		Afrotropical	
	r_s	*p*-value	r_s	*p*-value	r_s	*p*-value	r_s	*p*-value	r_s	*p*-value	r_s	*p*-value
human activity hypothesis												
gross domestic product	*0.680*	<0.0001	*0.514*	<0.0001	*0.471*	<0.0001	0.087	0.651	0.216	0.075	0.133	0.265
percentage of urban area	*0.584*	<0.0001	*0.533*	<0.0001	*0.397*	<0.0001	0.162	0.400	0.291	0.015	0.130	0.274
population density	*0.666*	<0.0001	*0.371*	<0.0001	*0.370*	<0.0001	−0.014	0.941	0.142	0.245	−0.236	0.045
biotic acceptance hypothesis												
native species richness	*0.301*	0.0005	*0.326*	<0.0001	0.144	0.166	*0.489*	<0.0001	−0.259	0.032	−0.065	0.586
altitudinal range	*0.407*	<0.0001	0.150	0.031	0.242	0.018	0.174	0.365	*0.400*	<0.0001	*0.544*	<0.0001
basin area	0.104	0.243	0.246	<0.0001	0.032	0.759	*0.785*	<0.0001	0.233	0.054	0.250	0.034
net primary productivity	−0.012	0.887	0.284	<0.0001	0.222	0.031	0.174	0.365	*−0.519*	<0.0001	−0.124	0.296
biotic resistance hypothesis												
native species richness	0.191	0.030	0.185	0.007	0.068	0.514	0.122	0.527	−0.356	0.003	−0.002	0.982

influence our perception of the determinants of NNSR, which constitutes a step forward to understand the spatial-scale dependency of the mechanisms explaining invasion success (Cadotte *et al.* 2006).

However, the observed spatial-extent effect strongly depended upon the biogeographic realm considered, suggesting an additional strong context dependency of the processes driving NNSR. Indeed, all things being equal, we showed that the relationship between NNSR and ecological and human activity-related factors varies strikingly across biogeographic realms, and does not permit generalization of the patterns from only one biogeographic realm to others. Among the abundant literature relating NNSR to environmental and human factors over large geographical areas (i.e. multi-country regions and continents), most concluded that human activity has a prominent role in explaining the gradients of NNSR (McKinney 2001; Taylor & Irwin 2004; Qian & Ricklefs 2006; Lin *et al.* 2007; Chiron *et al.* 2008; Gravuer *et al.* 2008). Our results call into question the generality of this view since we failed to verify such a pattern in biogeographic realms with a limited range of human disturbance.

Context dependency has long been recognized as a problem hindering the efficiency of generalizations in ecology and conservation biology (Rahbek & Graves 2001; Willis & Whittaker 2002; Heino *et al.* 2005; Davies *et al.* 2007). The discrepancy in the determinants of NNSR reported here cannot readily be attributed to evolutionary events since most human-mediated species introductions have been recent (i.e. generally less than a few hundred years ago; Vitousek *et al.* 1997; Sax & Gaines 2008). The discrepancy probably does not result from preferential introduction pathways between biogeographic realms as almost half of the established non-native fish species are translocated species (i.e. species introduced from one river basin to another within the same biogeographic realm; see table S3 in the electronic supplementary material). Rather, two non-mutually exclusive explanations can be put forward. First, our analyses using the restricted range of GDP in each biogeographic realm suggested that a sampling effect is very likely to explain the observed context dependency in the determinants of fish NNSR (Turner 1989; Rahbek & Graves 2001; Willis & Whittaker 2002; Heino *et al.* 2005). Indeed, when the range of GDP (i.e. the main determinant of fish NNSR worldwide; Leprieur *et al.* 2008) was held constant across the six biogeographic realms, we found that the environmental characteristics of river basins, such as the altitudinal range and surface area, became the most important factors for explaining the geographical pattern of NNSR, while the role of human activity-related factors became more marginal. Similarly, Davies *et al.* (2006) found that the relative influence of human impact on extinction risk in birds was inconsistent between biogeographic realms due to an incomplete representation of the worldwide human impact gradients within each biogeographic realm. Overall, our results thus suggest that the range of variation in human factors over which NNSR is estimated might affect the significance of the determinants of NNSR. Second, the observed discrepancy in the determinants of NNSR between biogeographic realms may result from between-realms differences in the history of basin-level anthropogenic disturbance (e.g. fragmentation and flow
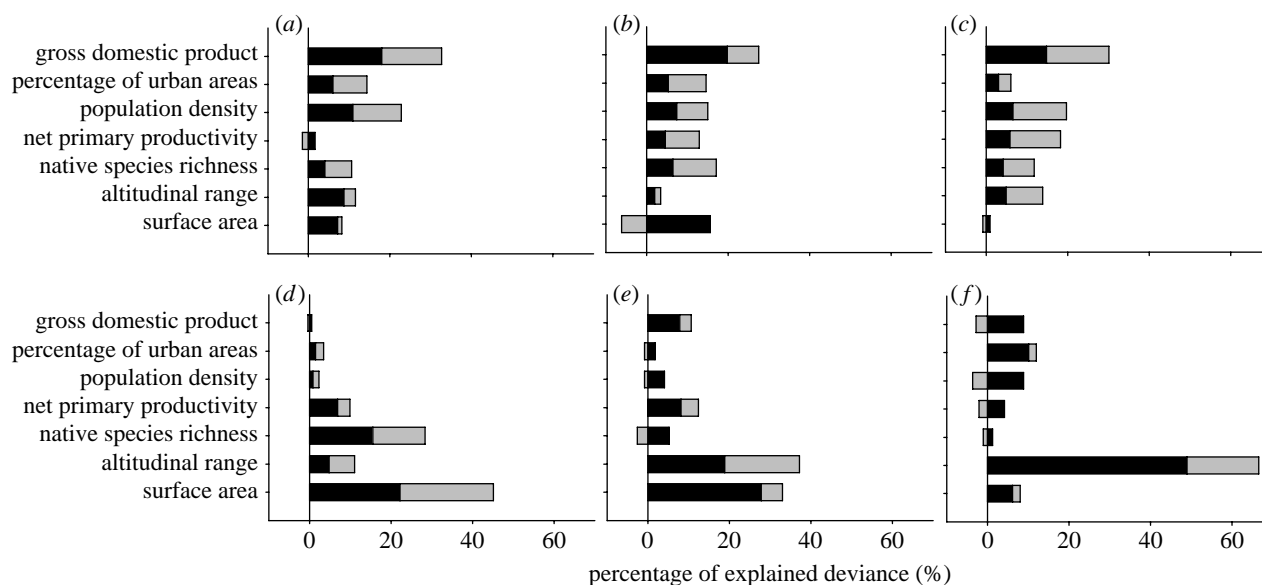
Figure 3. Hierarchical partitioning results showing the independent (black bars) and joint (grey bars) contributions (given as the percentage of the total explained deviance) of the seven determinants selected to explain the NNSR at the biogeographic realm extent. The contributions for each biogeographic realm are represented independently (dev. = percentage of explained deviance of the whole model integrating all determinants of NNSR): (*a*) Nearctic, dev. = 73.39%; (*b*) Palaearctic, dev. = 48.08%; (*c*) Australian, dev. = 43.38%; (*d*) Oriental, dev. = 77.02%; (*e*) Neotropical, dev. = 41.02%; and (*f*) Afrotropical, dev. = 56.69%.
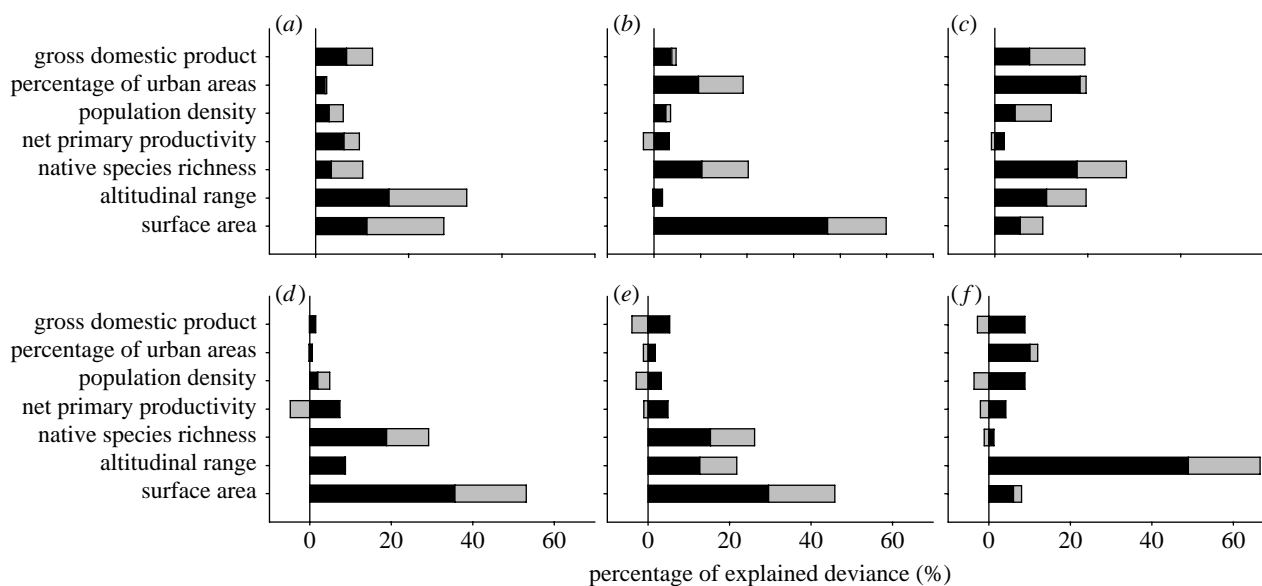

Figure 4. Hierarchical partitioning results showing the independent (black bars) and joint (grey bars) contributions (given as a percentage of the total explained deviance) of the seven determinants selected to explain the NNSR on the biogeographic realm extent. Here, the datasets were restricted so that the range of the GDP in each biogeographic realm was equalized among realms (see the text and figure 1). This was done to test the hypothesis that potential differences observed between biogeographic realms (figure 3) in the determinants of NNSR might be triggered by differences in the GDP range between biogeographic realms. The contributions of each biogeographic realm are represented independently (dev. = percentage of explained deviance of the whole model integrating all determinants of NNSR): (*a*) Nearctic, dev. = 82.36%; (*b*) Palaearctic, dev. = 35.82%; (*c*) Australian, dev. = 40.30%; (*d*) Oriental, dev. = 81.21%; (*e*) Neotropical, dev. = 25.88%; and (*f*) Afrotropical, dev. = 56.69%. Note that the pattern for the Afrotropical realm is similar to that of the full dataset analysis (see figure 3 and §2), since its range of GDP has not changed.

regulation associated with dam construction) and species introduction. Indeed, the Nearctic and Palaearctic realms experienced earlier industrial development (Hannah *et al.* 1995) and species introduction (Lever 1996) than the Afrotropical, Neotropical and Oriental realms. According to this hypothesis, in the near future we can expect a shift from natural to human-based determinants of NNSR in the economically growing biogeographic realms (Gilland 1995). Time-series analyses of long-term data are

currently needed for verifying this expectation. For instance, it would be helpful to undergo surveys in river basins from the Neotropical and Oriental realms where large dams are planned or under construction (Nilsson *et al.* 2005), because dams are known to facilitate the establishment of non-native species (Havel *et al.* 2005; Johnsson *et al.* 2008).

When restricting the range of GDP in each biogeographic realm to that observed in the Afrotropical realm

(i.e. the lowest range of GDP; figure 1), the environmental factors related to habitat heterogeneity (basin area and altitudinal range) were found to be the most important in explaining the geographical pattern of NNSR. Concerning basin area, two non-mutually exclusive mechanisms may explain its influence on NNSR. First, passive sampling surely plays a role since propagule pressure (i.e. the number of individuals released as well as the number of introduction events) is likely to increase with area. Second, it is expected that larger river basins will provide a greater range of available habitats (e.g. from cold-water upland streams to warm-water lowland rivers) for non-native freshwater fishes.

Finally, the relationship between altitudinal range and NNSR in the Afrotropical and Neotropical realms are probably not causal, but rather result from the influence of river basin topography on the occurrence of restricted-range species. Hence, at least one-third of the non-native species in these two tropical realms originate from temperate regions (Nearctic and Palaearctic; see table S3 in the electronic supplementary material). Most of these species can only become established under particular environmental settings and therefore have a restricted range distribution. For instance, salmonid species that have been widely introduced for sport fishing in the high-altitude lakes and streams of the Afrotropical and Neotropical realms (Lever 1996) typically have an ecological niche strongly constrained by temperature and oxygen availability (Crawford & Muir 2008).

Among the competing biotic acceptance and biotic resistance hypotheses, the latter was not verified in any of the six biogeographic realms, which is consistent with numerous macroecological studies (Lonsdale 1999; Evans 2004; Fridley et al. 2007; Leprieur et al. 2008). However, the absence of strong signs of biotic resistance when analysing broad spatial grains such as river basins would not signify that biotic resistance is a weak mechanism in determining invasion success (Smith et al. 2004). Rather, it may suggest that other structuring factors such as propagule pressure, disturbance regime and resource availability outweigh the effects of species richness on invasion success, often leading to positive correlations between native and non-native species richness (Hooper et al. 2005; Fridley et al. 2007). This hypothesis is highly concordant with recent theoretical developments and empirical studies showing that the relationship between native and non-native species richness turns from negative at small spatial grains to positive at broad spatial grains (Fridley et al. 2007).

5. CONCLUSION

For the first time, we have compared the determinants of NNSR across biogeographic realms and between regional and global spatial extents. Our study revealed a strong context dependency of the processes driving the NNSR of freshwater fishes, which limits the generalization that can be made from realm to realm. An interaction between the effects of spatial extent and the anthropogenic history of the biogeographic realms may well explain the strong context dependency we report here. Indeed, when scaling down from the global to the biogeographic realm, the range of the values of the

major determinants is not only reduced but also heterogeneously distributed according to the historical context of each biogeographic realm. This induces both a context and a spatial dependency of the determinants of NNSR.

Most previous studies have focused on economically developed biogeographic realms (i.e. Palaearctic, Nearctic and Australian; Taylor & Irwin 2004; Chiron et al. 2008), and a general paradigm implying a strong role of human-related factors in predicting NNSR is emerging (Chiron et al. 2008). Here, we show that such a widely accepted pattern might, in fact, not be as general as previously thought, since it does not hold for more than half of the continental surface of the Earth, at least for freshwater fishes. This implies that the current knowledge about regional determinants of NNSR is biased towards economically developed regions of the world. Owing to the urgent need to conserve ecosystems and biodiversity, we hope that our work will motivate others to undergo complementary studies in developing countries.

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