

Research article

All that changes is not shift: methodological choices influence niche shift detection in freshwater invasive species

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Species distribution models are often used to predict the potential distributions of invasive species outside their native ranges and rely on the assumption of realized niche conservatism. Analyses observed that freshwater invasive species often show high degrees of niche expansion, suggesting limited reliability of species distribution models. However, observed niche shifts can arise because of both actual niche shifts, determined by biological factors, and apparent shifts, due to methodological issues. We compared metrics of niche dynamics calculated using different sets of variables to identify factors that could influence the rate of niche shifts. We collected presence-only data for 40 freshwater invasive animal species, then measured niche shift dynamics using 14 different combinations of environmental variables. Shifts were assessed measuring niche overlap, expansion and unfilling, and testing for niche conservatism. We then built generalized linear mixed models relating niche shifts to methodological choices and biological features. Our results showed that methodological choices strongly affected all the considered niche dynamics metrics, while the effects of biological features were less prominent. Moreover, different niche dynamic measures sometimes provided contradictory assessments of niche conservatism. Niche analyses are powerful tools to predict areas at risk of invasion, but inappropriate methodological choices can lead to apparent niche shifts, questioning niche model reliability and biological interpretation. The high rate of niche expansion observed in freshwater invasive species highlights the importance of delineating objective criteria to determine the set of variables to be used in niche dynamic assessments.

Keywords: biological invasions, ecospat, invasive alien species, niche comparisons, niche conservatism, niche dynamics

Introduction

Freshwater environments are among the habitats most affected by invasive alien species (Strayer 2010). Freshwater invasive species (FIS) threaten local communities through multiple mechanisms, such as predation, hybridization, disease spread,



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food-web alterations and competition (Huxel 1999, Mooney and Cleland 2001, Ficetola et al. 2012, Falaschi et al. 2020). During the last decades, international trade has accelerated the rate of introductions of alien species (Westphal et al. 2008, Hulme 2009, Seebens et al. 2017). Additionally, global warming may facilitate the establishment of freshwater species outside their native ranges (Rahel and Olden 2008, Jourdan et al. 2018). Predicting potential FIS distributions is thus pivotal to prevent and/or limit their spread, since early detection and prompt control response represent the most effective strategy to eradicate an invasive species (Torres et al. 2018, Falaschi et al. 2020). A common strategy to predict the potential distribution of an invasive species is the use of occurrence data and selected environmental variables to approximate the species niche (Soberón 2007). These approaches, known as species distribution models (SDMs), are widely used; nevertheless, they present some limitations. Occurrences are only possible in environments where the local abiotic and biotic conditions are suitable for the species, and that are within the geographical area accessible to the species (Soberón and Peterson 2005, Barve et al. 2011). This means that niche assessments derived from occurrences can only give us information about the realized niche, i.e. the intersection between accessible, suitable abiotic and biotic conditions. The realized niche represents only a subset of the ensemble of the suitable abiotic conditions, namely the fundamental niche. Moreover, estimations of potential distribution performed using these models rely on several assumptions, such as niche conservatism between the native and the exotic range (Early and Sax 2014, Hill et al. 2017). The violation of the niche conservatism assumption may limit the ability of SDMs to accurately predict the potential distribution of non-native species (Early and Sax 2014, Pili et al. 2020, Atwater and Barney 2021). Assessing the pervasiveness of niche conservatism is thus a prerequisite for the broad application of SDMs in invasion biology. Previous assessments suggested that most invasive species conserve their niche (Petitpierre et al. 2012, Liu et al. 2020); nonetheless, some studies have reported relevant rates of niche shifts in some groups of invasive species (Lauzeral et al. 2011, Early and Sax 2014). FIS, for instance, show particularly strong niche shifts between native and exotic ranges (Torres et al. 2018, Liu et al. 2020).

Several processes can lead to the observation of niche divergence between native and invasive populations. First, adaptive evolution and different biotic interactions can allow invasive populations to occupy an environment that is not exploited in the native range (niche expansion; Guisan et al. 2014). Second, dispersal limitations, biotic interactions, and/or a recent introduction history can result in the exploitation of an environment in the native range but not in the exotic range (niche unfilling; Guisan et al. 2014). Furthermore, methodological issues related to the approaches used to compare niches among species/populations can lead to apparent niche shifts, even in the absence of true biological effects (apparent divergence; Strubbe and

Matthysen 2014, Torres et al. 2018, Atwater and Barney 2021; Fig. 1a). Niche unfilling does not represent a violation of the niche conservatism assumption and is usually expected to decline as the invasion continues, thus niche shifts are often described by quantifying the degree of niche expansion. Comparisons of the realized niches of native versus introduced populations of a species cannot prove whether an observed niche expansion is the result of changes in the fundamental niche or just in the realized niche. Moreover, the quantification of niche dynamics is only possible between analogous environments, i.e. environments shared by the native and the exotic geographical ranges. Indeed, when a species colonizes new environments unavailable in its native range, it is extremely challenging to determine whether this is caused by adaptive evolution or by other mechanisms (Guisan et al. 2014).

Several mechanisms, related to methodological choices, can bias niche comparisons, particularly for freshwater species, including:

- 1) Using biologically non-relevant variables. Using uninformative variables may increase the rate of apparent niche shifts (Rödder et al. 2009, Strubbe and Matthysen 2014, Torres et al. 2018). Niche comparisons are often based on broad-scale layers, such as WorldClim (Fick and Hijmans 2017) and CHELSA (Karger et al. 2020), which represent macroscale 'bioclimatic' conditions such as average annual temperature or annual precipitation. However, freshwater species live in specific microhabitats that are not necessarily affected by local conditions (e.g. the river regime can be affected by precipitation and snowmelt occurring hundreds of kilometres upstream), and in which temperature can strongly differ from nearby terrestrial environments. In turn, the use of bioclimatic layers that do not match the microhabitat experienced by animals can affect niche estimates (Ficetola et al. 2018, 2020). In addition to climate, other factors such as water chemistry shape the distribution of freshwater species (Jeschke and Strayer 2008). Nevertheless, there is evidence that bioclimatic variables are indeed appropriate to model aquatic species distributions (Frederico et al. 2014, McGarvey et al. 2018). Testing the effects of water chemistry variables on FIS niche shifts at a global level is challenging due to the lack of high-resolution global datasets (Loo et al. 2007, Torres et al. 2018).
- 2) Overparameterization. Including too many predictors can lead to inaccurate definitions of the relationships between species and environmental features, resulting in apparent niche shifts (Peterson 2011, Low et al. 2020). On the other hand, considering only a few variables might overestimate niche conservatism (Peterson 2011).
- 3) Selecting inappropriate backgrounds. Niche analyses usually select a geographical background to represent the environmental conditions accessible to the focal species. Background selection can deeply influence SDMs and niche quantifications and should be limited to areas accessible by the species (Godsoe 2010, Barve et al. 2011,

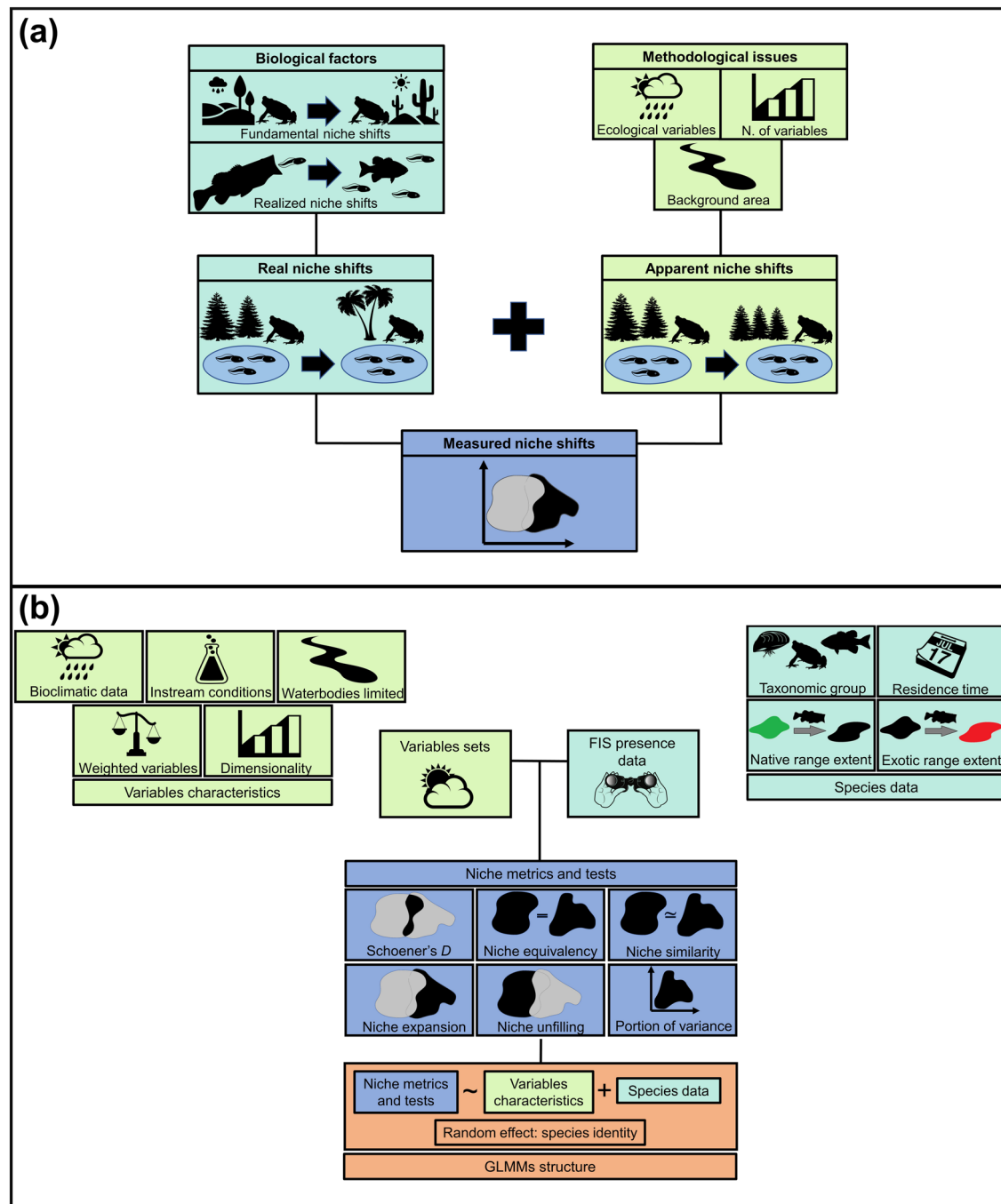


Figure 1. (a) Niche shifts detected by niche dynamics analyses can be the result of real niche shifts, caused by changes in the fundamental or in the realized niche, and/or apparent niche shifts, caused by methodological issues. (b) We used presence data for 40 freshwater invasive species (FIS) and 14 different sets of ecological variables to calculate six measures used in niche dynamic assessments. After that, each niche measure was used as the dependent variables in a generalized linear mixed model (GLMM), while five characteristics of the ecological variables and four commonly tested biological features of the species were used as independent variables. Drawings by: Natasha Sinegina (CC-SA 4.0 license; <https://creazilla.com/>), Creazilla, hamdolii, UnboxScience (Public Domain) and JoyPixel (CC-SA 4.0 license; www.joypixels.com/).

Acevedo et al. 2012, Hill et al. 2017). For freshwater organisms, limiting the background area to freshwater environments could improve the transferability of SDMs and reduce apparent niche shifts between native and invasive populations (Nori and Rojas-Soto 2019).

Studies assessing niche dynamics in invasive species often use bioclimatic variables, do not subset the available variables and only rarely try to limit the background areas (Peterson 2011, Qiao et al. 2017, Nori and Rojas-Soto 2019, Liu et al. 2020); thus we hypothesize that a relevant portion

of observed niche shifts found in FIS is due to the inclusion of non-relevant variables, overparameterization and inappropriate background selection. These choices may affect niche analyses, possibly leading to strong apparent niche shifts in FIS, which in turn would affect the reliability of SDMs outside native ranges. The aim of our study was assessing the factors that determine observed niche shifts in FIS, testing whether and how a priori selection of different variables influences measures of niche dynamics.

Material and methods

Species records and ranges

We downloaded occurrence records for 40 FIS from the iNaturalist data portal (www.inaturalist.org/observations/export), filtering for 'Research Grade' data to reduce misidentification risk. We selected species with a large number of observations (range: 95–45 351; median: 1108.5; and with > 20 records for both the native and the invasive range) and included freshwater molluscs, crustaceans, fishes and tetrapod species (amphibians and reptiles; Supporting information) with occurrence records from the period 1962 to 2021. When available, we downloaded native ranges from the IUCN Red List website (IUCN 2022).

We used the Freshwater Ecoregions of the World (Abell et al. 2008) to select background areas for each species in both its native and introduced ranges. This allows an appropriate selection of background areas since they were delineated by considering physical and ecological dispersal limitations of freshwater species (particularly freshwater fish; Abell et al. 2008). For each species, native backgrounds were determined as those ecoregions that contained at least one record of the focal species and intersected the polygon of the IUCN native range. For those species whose distributions were not present on the IUCN website, other sources were used to determine native ranges (Supporting information). Subsequently, we determined the exotic background of each FIS as those ecoregions that contained at least one non-native record of the focal species in areas with bibliographical evidence of established populations. This criterion was used to avoid the inclusion of captive or semi-captive individuals and non-viable populations, because feral individuals of some FIS, e.g. turtle species, can survive for several years in sub-optimal habitats without establishing reproductive populations (Ficetola et al. 2008).

Environmental variables

To test the hypothesis that niche shifts detected between native and non-native ranges can derive from the variables used for analyses, we evaluated several datasets of environmental variables that could be used to model FIS niches. We aimed to understand whether and how niche metrics are affected by 1) using general (bioclimatic) versus more specific proxy variables, 2) selecting different numbers of variables and

3) limiting the background areas to waterbodies. To achieve this goal, we downloaded different raster datasets from two sources: WorldClim (Fick and Hijmans 2017) and EarthEnv (www.earthenv.org; Domisch et al. 2015). WorldClim provides global data for 19 different macroclimatic ('bioclimatic') variables at different resolutions, which well describe the features of terrestrial environments (Fick and Hijmans 2017). EarthEnv provides different near-global, standardized, 1-km resolution layers that can be used for niche modelling and other scientific purposes, and includes several river-specific variables (Domisch et al. 2015). We downloaded data from the near-global freshwater environmental variables dataset provided by EarthEnv through the 'sdmpredictors' R package (Bosch 2020). EarthEnv includes 19 bioclimatic variables derived from WorldClim; data on river drainage networks derived from HydroSHEDS (Lehner et al. 2008); and proxies for water chemistry derived from the soil properties maps of SoilGrids1km (Hengl et al. 2014). Both bioclimatic and water chemistry variables are provided as the average or sum of the upstream values and as inverse-distance weighted average or the inverse-distance weighted sum of the upstream values. The latter approximations aim to better represent local water conditions, although validation showed this it is not always the case (Domisch et al. 2015). The extent of all EarthEnv layers is 60° N to 5° S latitude, and 145° W to 180° E longitude.

We built 14 combinations of variables at the finest resolution available (0.008°; Table 1), because fine-scale niche shifts might not be detected when using coarse-resolution data (Petitpierre et al. 2012, Li et al. 2014; Supporting information). WorldClim rasters were cropped to the extent of EarthEnv ones.

Data preparation and analyses

For each species, we kept one presence point per grid cell. Presence points located more than 1 km away from waterbodies were discarded; points located < 1 km away from waterbodies were moved to the nearest cell inside a waterbody. This was done to avoid loss of information due to limited accuracy of coordinates or raster maps, or changes in stream and river shapes, and to include occurrences of semi-aquatic animals moving nearby main waterbodies. Presence points falling on cells associated with no value in at least one of the raster maps used were discarded.

Following Hill et al. (2017), we selected 10 000 random cells as the background for each species in both the native and exotic range. For WorldClim variables, background points were selected across the entire background areas, whereas for the EarthEnv variables the background points were selected within waterbodies. Subsequently, we extracted the variable values for both presence and background points. Each resulting dataset was used to describe the native and exotic niches using the centroid shift, overlap, unfilling, expansion (COUE) framework, an ordination approach to quantify niche changes (Guisan et al. 2014). Following Broennimann et al. (2012), we performed a principal component analysis (PCA)

Table 1. The 14 combinations of environmental variables used to assess niche metrics and quantify niche shifts. Each combination was used to calculate niche metrics for the 40 freshwater invasive species. The different variables were obtained from WorldClim (Fick and Hijmans 2017) and EarthEnv (Domisch et al. 2015).

Variables set	Bioclimatic variables	Instream conditions proxies	Distance-weighted variables	Limited backgrounds	Number of variables
bioclim6	Yes	No	No	No	6
bioclim19	Yes	No	No	No	19
climriv6	Yes	No	No	Yes	6
climriv19	Yes	No	No	Yes	19
climrivw6	Yes	No	Yes	Yes	6
climrivw19	Yes	No	Yes	Yes	19
riv5	No	Yes	No	Yes	5
riv13	No	Yes	No	Yes	13
rivw5	No	Yes	Yes	Yes	5
rivw13	No	Yes	Yes	Yes	13
rivall11	Yes	Yes	No	Yes	11
rivall32	Yes	Yes	No	Yes	32
rivallw11	Yes	Yes	Yes	Yes	11
rivallw32	Yes	Yes	Yes	Yes	32

on the environmental space of the native and exotic ranges. Occurrence densities of the species in the native and invasive ranges were then calculated with kernel smoothing methods to limit sampling biases and projected onto the gridded PCA environmental space. We used the 75th percentile of environmental densities as a threshold to eliminate rare environments from our analyses (Petitpierre et al. 2012, Guisan et al. 2014, Li et al. 2014, Liu et al. 2017). Niches were then defined by using 95% of the species occurrences to avoid the inclusion of the most marginal populations.

Subsequently, we calculated the adjusted Schoener's D, a measure of niche overlap (Broennimann et al. 2012). Low Schoener's D values are a first indication of limited niche overlap; nonetheless, large Schoener's D values do not necessarily imply the absence of niche shifts (Guisan et al. 2014). After that, we performed niche equivalency and similarity tests. Niche equivalency tests consist in pooling all occurrences and splitting them into two datasets, calculating Schoener's D and repeating the process N-times; niche similarity tests were performed by randomly shifting the entire observed density of occurrences in the exotic range and calculating the overlap of the simulated niche with the observed niche in the native range (Broennimann et al. 2012). Both tests were run with 1000 random replicates using the 'ecospat' (ver. 3.2) R package (Di Cola et al. 2017). When testing for niche conservatism, a significant ($p < 0.05$) equivalency test implies that overlap between native and exotic niches is higher than expected under randomness, while a significant similarity test implies that the focal species occupies environments in the native and exotic range that are more similar than would be expected by chance. Finally, we calculated niche expansion, i.e. the proportion of the exotic niche non-overlapping with the native niche, and niche unfilling, i.e. the proportion of conditions inside the native niche but outside the exotic niche (Guisan et al. 2014). Niche expansion is often considered to be the only measure that truly describes shifts in the realized niche (Petitpierre et al. 2012, Strubbe et al. 2013, Li et al. 2014, Liu et al. 2020).

We used generalized linear mixed models (GLMMs) to test the effects of variable selection, overparameterization and background area limitation on the measures of niche dynamics (Fig. 1b). Moreover, we also considered the effects of 'biological' features of invasive species commonly used in similar studies, to evaluate whether the effects of these predictors are stronger or weaker than the ones related to methodological choices. Previous analyses found relationships between niche conservatism and the extent of invasive species ranges (Early and Sax 2014, Li et al. 2014, Hill et al. 2017, Liu et al. 2017), thus we included the log-transformed number of raster cells occupied in the native range and in the exotic range as independent variables. The year of first introduction of each FIS was obtained from Seebens et al. (2017) and used to calculate residence time in the exotic ranges, another frequently considered factor in niche dynamic studies (Cardador and Blackburn 2020, Liu et al. 2020). Finally, we included the taxonomic group (invertebrate, fish or tetrapod) as a fixed factor. We ran six separate GLMMs with different independent variables: Schoener's D, the significance of statistical comparisons between native and invasive niches (equivalency and similarity tests; non-significant versus significant), the relevance of niche expansion and niche unfilling, and the portion of variance explained by the first two principal components (PCs). Niche expansion and unfilling are usually considered to be relevant when > 0.10 (Hill et al. 2017, Torres et al. 2018), thus we used this value as a threshold and treated these two metrics as binomial variables. Results of equivalency and similarity tests were also treated as binomial variables (significant versus non-significant tests), while the proportion of variance explained by the first two PCs and Schoener's D values were modelled using beta regressions (Ferrari and Cribari-Neto 2004). We expected the proportion of variance explained by the PCs to be directly linked to collinearity between the selected variables, thus we modelled it using the methodological approaches as the only independent variables. Each GLMM included: a niche metric as dependent variables; five variables representing the typology

of environmental characteristics and four variables representing species features as independent variables (Fig. 1b), and species identity as a random effect. GLMMs were run using the 'lme4' (Bates et al. 2015) and the 'GLMMtmb' packages (Brooks et al. 2017). The significance of independent variables was assessed using likelihood ratio tests.

All the species we selected had at least 20 records for both the native and the invasive range before spatial filtering; however, after spatial filtering, seven species retained fewer than 20 records for either the native or the invasive range (range: 6–19 records). The COUE approach is thought to be robust even with small sample sizes, and niche comparisons can be performed with as few as five occurrences in either range (Liu et al. 2017, Torres et al. 2018). Nevertheless, we repeated GLMMs removing the seven species with fewer than 20 observations to assess the robustness of our conclusions.

Results

Overall, we obtained data from seven molluscs, five crustaceans, 19 fishes and nine tetrapod species (six amphibians and three reptiles; Supporting information). After spatial filtering, the mean number of retained records per species \pm SD was 1413 ± 2337 (range: 61–10 321). The mean number of raster cells occupied in the native range was 853 ± 1969

(15–10 199), while the mean number of occupied cells in the invaded range was 561 ± 798 (6–3494). The average residence time was $153 \text{ years} \pm 89$ (42–525). Residence time was not correlated to invaded range extent (Pearson's $r_{38} = 0.219$, $p = 0.175$). For each species, each niche dynamic measure was calculated multiple times, using different sets of ecological variables. We obtained a total of 560 values for each niche dynamic measure (40 species \times 14 sets of variables). The GLMMs relating niche parameters to the different predictors explained a good amount of variation (R^2 ranging from 0.33 to 0.93); see Supporting information for details. In nearly all cases, the models excluding species with < 20 occurrences in at least one of the two ranges were highly consistent with the ones including all the species (Supporting information).

Variance explained by the first principal components

On average, the first two principal components explained $65.3 \pm 13.2\%$ of variance of environmental variables. The amount of explained variance was strongly affected by methodological choices (Fig. 2), as it increased when we used terrestrial bioclimatic data ($B = 0.482$, $\chi^2_1 = 288.3$, $p < 0.001$), as well as when we limited background to waterbodies ($B = 0.083$, $\chi^2_1 = 7.2$, $p = 0.007$). Furthermore, the first two principal components explained a lower proportion



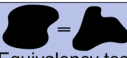












	 Portion of variance	 Schoener's D	 Equivalency test	 Similarity test	 Niche expansion	 Niche unfilling
 Bioclimatic variables	$B = 0.48$ $\chi^2_1 = 288.3$ $p < 0.001$	$B = -0.05$ $\chi^2_1 = 0.3$ $p = 0.521$	$B = -0.34$ $\chi^2_1 = 1.0$ $p = 0.312$	$B = 0.37$ $\chi^2_1 = 1.3$ $p = 0.245$	$B = -0.85$ $\chi^2_1 = 5.3$ $p = 0.021$	$B = -0.17$ $\chi^2_1 = 0.2$ $p = 0.649$
 Instream conditions	$B = -0.70$ $\chi^2_1 = 507.2$ $p < 0.001$	$B = 0.13$ $\chi^2_1 = 3.3$ $p = 0.070$	$B = -0.05$ $\chi^2_1 = 0.0$ $p = 0.867$	$B = 0.00$ $\chi^2_1 = 0.0$ $p = 0.986$	$B = -0.03$ $\chi^2_1 = 0.0$ $p = 0.926$	$B = -0.63$ $\chi^2_1 = 3.2$ $p = 0.073$
 Weighted variables	$B = -0.07$ $\chi^2_1 = 17.7$ $p < 0.001$	$B = 0.36$ $\chi^2_1 = 38.9$ $p < 0.001$	$B = 0.87$ $\chi^2_1 = 13.8$ $p < 0.001$	$B = 1.06$ $\chi^2_1 = 21.8$ $p < 0.001$	$B = 1.72$ $\chi^2_1 = 43.5$ $p < 0.001$	$B = 0.95$ $\chi^2_1 = 12.6$ $p < 0.001$
 Limited background	$B = 0.08$ $\chi^2_1 = 7.2$ $p = 0.007$	$B = -0.45$ $\chi^2_1 = 24.0$ $p < 0.001$	$B = -1.18$ $\chi^2_1 = 10.6$ $p = 0.001$	$B = -1.29$ $\chi^2_1 = 14.3$ $p < 0.001$	$B = -1.58$ $\chi^2_1 = 15.2$ $p < 0.001$	$B = -1.2$ $\chi^2_1 = 8.2$ $p = 0.004$
 N. of variables	$B = -1.10$ $\chi^2_1 = 498.9$ $p < 0.001$	$B = -0.06$ $\chi^2_1 = 4.2$ $p = 0.041$	$B = -0.08$ $\chi^2_1 = 0.5$ $p = 0.499$	$B = -0.05$ $\chi^2_1 = 0.1$ $p = 0.695$	$B = 0.03$ $\chi^2_1 = 0.1$ $p = 0.803$	$B = 0.41$ $\chi^2_1 = 7.9$ $p = 0.005$
 Native range extent	/	$B = 0.41$ $\chi^2_1 = 25.3$ $p < 0.001$	$B = 0.60$ $\chi^2_1 = 5.6$ $p = 0.018$	$B = 0.31$ $\chi^2_1 = 2.2$ $p = 0.139$	$B = -1.37$ $\chi^2_1 = 14.0$ $p < 0.001$	$B = -0.04$ $\chi^2_1 = 0.0$ $p = 0.905$
 Exotic range extent	/	$B = 0.08$ $\chi^2_1 = 1.4$ $p = 0.238$	$B = -0.07$ $\chi^2_1 = 0.1$ $p = 0.757$	$B = 0.49$ $\chi^2_1 = 5.8$ $p = 0.016$	$B = -0.14$ $\chi^2_1 = 0.2$ $p = 0.659$	$B = -2.62$ $\chi^2_1 = 39.6$ $p < 0.001$
 Residence time	/	$B = 0.03$ $\chi^2_1 = 0.3$ $p = 0.566$	$B = 0.58$ $\chi^2_1 = 6.7$ $p = 0.009$	$B = 0.05$ $\chi^2_1 = 0.1$ $p = 0.804$	$B = 0.88$ $\chi^2_1 = 8.0$ $p = 0.005$	$B = 0.08$ $\chi^2_1 = 0.1$ $p = 0.789$
 Taxonomic group	/	$\chi^2_2 = 6.6$ $p = 0.036$	$\chi^2_2 = 2.7$ $p = 0.255$	$\chi^2_2 = 0.6$ $p = 0.743$	$\chi^2_2 = 5.5$ $p = 0.063$	$\chi^2_2 = 3.5$ $p = 0.173$

Figure 2. Results of generalized linear mixed models (GLMMs) relating niche metrics to methodological choices and biological factors. All niche shift measures were modelled as a function of methodological choices and biological factors; the amount of variance explained by the two principal components was modelled as a function of methodological choices only. Significant positive effects are shaded in red, while significant negative effects are shaded in blue. Asterisks indicate those effects whose significance disappeared when removing the species with small sample size. Drawings by: Natasha Sinagina (CC-SA 4.0 license; <https://creazilla.com/>), Creazilla, hamdolii, UnboxScience, loritheladybug7 (Public Domain) and JoyPixel (CC-SA 4.0 license; www.joypixels.com/).

of variation when we considered a larger number of environmental variables ($B = -0.398$, $\chi^2_1 = 740.5$, $p < 0.001$), when we used variables representing instream conditions ($B = -0.696$, $\chi^2_1 = 507.2$, $p < 0.001$) and when using distance-weighted measures ($B = -0.075$, $\chi^2_1 = 17.7$, $p < 0.001$) (Fig. 2; Supporting information).

Factors affecting niche overlap

The niche overlap between native and non-native ranges (Schoener's D) showed a strong variation across species and sets of variables (average 0.256 ± 0.147 ; range 0.003 – 0.596). Niche overlap was significantly larger when using distance-weighted variables ($B = 0.364$, $\chi^2_1 = 38.9$, $p < 0.001$), while overlap decreased when using backgrounds limited to waterbodies ($B = -0.446$, $\chi^2_1 = 24.0$, $p < 0.001$) and when we increased parameterization ($B = -0.063$, $\chi^2_1 = 4.2$, $p = 0.041$). Species with a greater native range showed larger overlap between native and invasive range ($B = 0.410$, $\chi^2_1 = 25.3$, $p < 0.001$). We also detected significant differences between taxonomic groups (likelihood ratio test: $\chi^2_2 = 6.6$, $p = 0.036$), with tetrapod species showing significantly lower D values than invertebrates (Tukey test: $B = -0.484$, $p = 0.021$) (Fig. 2; Supporting information). Finally, using water conditions proxies slightly increased niche overlap, but this effect was significant at the 0.05% level only after removing species with small sample sizes ($B = 0.184$, $\chi^2_1 = 5.4$, $p = 0.020$).

Factors affecting niche equivalency tests

We obtained 158 out of 560 significant niche equivalency tests. The niche equivalency hypothesis was accepted more frequently when using distance-weighted values ($B = 0.872$, $\chi^2_1 = 13.8$, $p < 0.001$), while it was more frequently rejected when using waterbody-limited backgrounds ($B = -1.177$, $\chi^2_1 = 10.6$, $p = 0.001$; Fig. 2). Large native ranges ($B = 0.604$, $\chi^2_1 = 5.6$, $p = 0.018$) and long residence times ($B = 0.581$, $\chi^2_1 = 6.7$, $p = 0.009$) were associated with higher levels of niche equivalency, but the significances of both these effects disappeared when removing species with few occurrences (Fig. 2; Supporting information).

Factors affecting niche similarity tests

We obtained 176 out of 560 significant niche similarity tests. Similarity rates were higher when using distance-weighted variables ($B = 1.055$, $\chi^2_1 = 21.8$, $p < 0.001$) and for species with wide exotic ranges ($B = 0.489$, $\chi^2_1 = 5.8$, $p = 0.016$). Conversely, similarity tests were less frequently significant when using waterbody-limited variables ($B = -1.294$, $\chi^2_1 = 14.3$, $p < 0.001$) (Fig. 2; Supporting information).

Factors affecting niche expansion

The selected FIS showed relevant (> 0.1) niche expansions in 331 out of 560 comparisons, with a mean value of 0.251 ± 0.244 . Relevant niche expansions were less frequently found

when using terrestrial bioclimatic variables ($B = -0.851$, $\chi^2_1 = 5.3$, $p = 0.021$), and when limiting backgrounds to waterbodies ($B = -1.581$, $\chi^2_1 = 15.2$, $p < 0.001$). Conversely, using distance-weighted variables increased niche expansion ($B = 1.725$, $\chi^2_1 = 43.5$, $p < 0.001$). Residence time had a significant positive effect on this measure ($B = 0.883$, $\chi^2_1 = 8.0$, $p = 0.005$), while the number of cells occupied in the native range had a negative effect on it ($B = -1.374$, $\chi^2_1 = 14.0$, $p < 0.001$) (Fig. 2; Supporting information).

Factors affecting niche unfilling

Niche unfilling was relevant (> 0.1) in 277 out of 560 comparisons, with a mean value of 0.198 ± 0.232 . Unfilling was less frequent when selecting waterbody-limited backgrounds ($B = -1.209$, $\chi^2_1 = 8.2$, $p = 0.004$), and for species with broad exotic ranges ($B = -2.652$, $\chi^2_1 = 39.6$, $p < 0.001$). Conversely, unfilling was inflated by using distance-weighted variables ($B = 0.947$, $\chi^2_1 = 12.6$, $p < 0.001$) and by over-parameterization ($B = 0.407$, $\chi^2_1 = 7.9$, $p = 0.005$) (Fig. 2; Supporting information).

Discussion

The majority of the 560 niche comparisons showed significant niche shifts between native and invasive range, with frequent niche expansion and limited values of overlap. Nevertheless, detections of niche shifts strongly depended on methodological choices, including background selection, the use of distance-weighted variables or the use of a large number of variables. This suggests that a priori choices of environmental predictors have strong impacts on the detection of niche shifts and some choices might inflate the probability of observing apparent shifts. The effects of these methodological choices seem to be stronger than potential biological factors, such as residence time or the extent of native range.

Effects of methodological choices

Methodological choices appear to be extremely relevant in influencing niche metrics (Fig. 2). These findings pose a challenge to the interpretation of meta-analyses on niche comparisons since niche conservatism and shifts may be linked to differences across studies in modelling techniques, instead of actual biological processes. This underlines once more the urgent need for objective criteria in selecting the most appropriate variables for niche comparisons, particularly for those species, such as FIS, whose realized niches are likely to be influenced by complex interactions between climatic, chemical and dispersal factors.

Traditionally, niche modelling for FIS and other invasive species was based on easily accessible bioclimatic variables, such as air temperature or annual precipitation (Torres et al. 2018, Mori et al. 2021). Bioclimatic variables are often highly collinear, thus in most works principal components explain a great proportion of the variance of these variables. Bioclimatic

data are particularly suitable for ordination approaches such as the COUE scheme, still they do not necessarily describe the environmental features truly affecting organism occurrences. Therefore, it is pivotal to select variables that better represent the environment experienced by organisms, such as instream conditions, soil temperature or other micro-habitat features (Bramer et al. 2018, Lembrechts et al. 2021). Unfortunately, an accurate representation of microhabitat features over broad spatial scales can be extremely challenging because of the limitations of remote sensing when trying to derive extremely fine-grained information (Lembrechts et al. 2021). Datasets aiming to represent instream conditions at a global level are broad-scale estimates, mostly based on soil chemistry and geological features of nearby environments, and hence in some cases they may not accurately represent the actual conditions experienced by organisms. Moreover, several water chemistry parameters relevant for FIS distribution (e.g. calcium concentrations for molluscs) are not always available at high resolution at the global scale (Jeschke and Strayer 2008).

Distance-weighted variables led to contrasting results. While their use increased niche overlap, equivalency and similarity between native and invaded ranges, it also increased niche expansion and unfilling. Validation exercises suggested that distance-weighted variables may represent some instream conditions less accurately than the unweighted ones (Domisch et al. 2015), possibly inflating niche expansion and unfilling. On the other hand, weighted variables might be particularly appropriate for parameters such as precipitation, for which downstream conditions are more tightly linked to drainage-based processes.

Limiting the background to the accessible area should improve the representation of the movement constraints of the species (Godsoe 2010, Barve et al. 2011, Nori and Rojas-Soto 2019). This may be particularly important for modelling FIS, which often are strongly affected by dispersal barriers (Jeschke and Strayer 2008). In fact, the use of a limited background resulted in low rates of niche expansion and unfilling compared to the 'traditional' background. This suggests that this approach can minimize the detection of apparent differences between native and exotic niches, consistently with results of previous studies on invasive turtles (Nori and Rojas-Soto 2019). Nevertheless, the constrained background also reduced niche overlap and the significance of equivalency and similarity tests between native and invasive ranges compared to 'traditional' background (Nori and Rojas-Soto 2019). This probably occurred because limiting the background to waterbodies also drastically reduces the number of points available to estimate background abiotic conditions, decreasing the statistical power of tests (Nori and Rojas-Soto 2019). This highlights the risk of obtaining contrasting results with different niche metrics when background areas are limited to different extents.

The number of ecological variables has long been recognized as a major methodological issue of distribution modelling. Many approaches are available to reduce dimensionality, such as excluding those variables that are supposed to be not

relevant for the target species, that show strong correlations with other variables or that are secondly derived from other variables (Peterson 2011, Low et al. 2020). Increasing dimensionality is expected to decrease the amount of variation explained by the first two PCs, hence limiting the effectiveness of ordination analyses. Moreover, using too many ecologically variables can lead to apparent niche shifts (Strubbe and Matthysen 2014, Torres et al. 2018). Our results remark the importance of avoiding over-parameterization, and the need for objective methods to define an appropriate number of ecological variables used to define species niche, particularly for FIS.

Comparison between methodological and biological factors

Previous work has reported that several biological features can significantly affect niche shift measures. A broad native range has been found to increase niche overlap and reduce niche expansion (Early and Sax 2014, Li et al. 2014, Liu et al. 2017, 2020), while several studies observed a negative relationship between the extent of invaded ranges and niche unfilling, and a positive effect of residence time on niche expansion (Li et al. 2014, Liu et al. 2020). These patterns have been explained by several biological processes. A positive relationship between residence time and climatic niche shifts has been taken as a confirmation that these shifts can be related to a release from dispersal limitations within the invasive range (Li et al. 2014); nevertheless, the interpretation of the role of residence time is subjected to several pitfalls, as similar studies with small methodological differences showed contrasting results (Liu et al. 2017, 2020). In fact, in our analysis the effect of residence time on niche equivalency found by our models disappeared when removing species with small sample size, suggesting that it might be an artifact.

Freshwater invasive species with broad native ranges often are generalist species that already exploit a wide range of environments, meaning that their exotic populations are more likely to be introduced in environments with similar conditions just by chance, and are unlikely to further expand their niche. Similarly, species that have been able to exploit broad invasive areas are expected to reduce their unfilling compared to the native range. Our results were consistent with these expectations, regardless of the methodological approach, confirming the potential importance of these processes (Fig. 2). Nevertheless, in most cases biological factors explained less deviance in niche metrics, compared to methodological choices (Supporting information). As methodological choices can outweigh biological effects, the risk of apparent niche shifts should be carefully considered when planning the analysis, and researchers should pay special attention to testing the robustness of their conclusions. Direct measures of actual niche shifts, such as experimental approaches that approximate the fundamental niche and/or genomic analyses, would be extremely helpful to verify whether observed shifts represent actual evolutionary processes (Kearney and Porter 2009, Sherpa et al. 2022).

Additional factors influencing observed shifts

Regardless of the robustness of modelling designs, niche modelling has some inherent weaknesses that are difficult to overcome. Global analyses are based on large databases of species distribution. These databases do not necessarily represent the actual distribution of the species, owing to geographical biases in data collection, uneven search efforts and reporting biases (van Strien et al. 2013, Uyeda et al. 2020). Approaches like the COUE scheme are thought to limit the effects of sampling bias by calculating smooth densities of species occurrences in a gridded environmental space (Broennimann et al. 2012, Guisan et al. 2014), but there are other biases that can undermine the reliability of models.

Occurrences of dispersing individuals or non-viable populations, such as continuously restocked fish populations that occupy sub-optimal environments, should be excluded from analyses to avoid niche overestimation. To limit this issue, we only selected observations from countries where the considered FIS are known to be established, and excluded marginal observations from niche analyses. However, niche overestimation caused by non-breeding populations might have occurred in large countries and for species with wide distributions. Finally, even the best global datasets of ecological variables currently available have some limitations, and they can provide an imperfect representation of conditions experienced by organisms (Domisch et al. 2015). The development of high-quality datasets that well represent microhabitat conditions is one of the major issues for modelling studies, and recent broad-scale efforts promise improvements that will be extremely useful for future studies (Potter et al. 2013, Bennie et al. 2014, Lembrechts et al. 2021, Marta et al. 2022). The increased resolution of recently available waterbody maps (Allen and Pavelsky 2018) might soon allow the realistic accounting for dispersal limitation while retaining high statistical power.

Conclusion

An appropriate selection of environmental variables is pivotal when performing niche analyses and can have major consequences on the detection of niche shifts. The differences in niche comparisons linked to different methodological choices can be extremely relevant for niche conservatism assessments. Identifying the best approach to quantify niche dynamics can greatly improve our ability to predict FIS distribution, improving the effectiveness of prevention and/or containment measures, and enhancing predictions under climate change scenarios.

Apparent niche shifts can be reduced by using appropriate ecological variables and avoiding overparameterization. Therefore, a better understanding of the drivers of FIS distribution, the availability of global high-resolution maps of these drivers and objective methods for selecting the appropriate number of variables are essential prerequisites for reliable niche modelling. Moreover, drawing biological inference

from niche modelling without accounting for the weaknesses of this approach can lead to misleading conclusions. Experimental approaches, and physiological and genomic data, when available, can greatly help to refine niche modelling and SDMs. Meeting these challenges will also help conservationists to face the ongoing threats in freshwater environments in a more appropriate and effective way.

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Author contributions

Elia Lo Parrino: Conceptualization (lead); Formal analysis (lead); Methodology (lead); Validation (equal); Visualization (equal); Writing – original draft (lead). **Mattia Falaschi:** Conceptualization (equal); Formal analysis (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (equal). **Raoul Manenti:** Methodology (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (equal). **Gentile Francesco Ficetola:** Conceptualization (equal); Formal analysis (equal); Methodology (equal); Supervision (lead); Visualization (equal); Writing – original draft (equal).

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Data availability statement

The presence-only data, the areas used as backgrounds for the native and the invasive ranges of the considered species, as well as data and scripts used for niche comparisons and GLMMs are available at: https://figshare.com/articles/online_resource/Datasets_and_script_for_niche_comparisons_and_GLMMs/19388282 (Lo Parrino et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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