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Niche shift in invasive species: is it a case of "home away from home" or finding a "new home"?

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Abstract

In recent years, there has been a rather acrimonious debate on matters concerning the biology of invasive species, some as fundamental as the definition and what constitutes an invasive species. However, an abiding commonality of all invasive species is the fact that they have all moved away from their native ranges to newer and often non-native ranges. In plants, *Lantana camara* has shifted from its native South American range distribution to most other parts of the world. In animals, the African giant snail has dispersed from Africa to most parts of Asia. What do such niche shifts signify about the nature and quality of the habitats to which the invasive species have moved? In this paper, using the classical niche paradigm, we analyse if niche shifts of thirty-three of the world's top invasive species constitute just moving from one habitat to another similar habitat somewhere on the earth (home away from home) or that they have moved to totally new habitats (different from their native home). Surprisingly, our results show that for 90% of the world's top invasive species, movements have been largely restricted to homes away from home, rather than into alien homes. This clearly indicates the potential inertia that species might face in moving out of their fundamental niche. We discuss these results in the context of the overall debate on invasion biology and how niche conservatism may have played a role in dampening the rates of invasion.

Keywords Niche conservatism · Ecological niche · Invasive species · Niche modelling · *Lantana*

Introduction

One of the overriding commonalities of all invasive species is their movement from their native distribution to elsewhere (Hulme et al. 2017). There are extensive reports on such movements for numerous invasive plants and animals (Rouget et al. 2015; Capinha et al. 2016; Konowalik and Kolanowska 2018; Ahmed et al. 2019). The vectors of movements vary from natural means to those aided by human movements across geographies (Hulme

et al. 2008; Capinha et al. 2016). Thus, for one of the best-documented invasive species, *Lantana camara*, it is accepted today that the species was transported from its original sites of occurrence in South America to Africa and Asia by European colonizers for its perceived ornamental value (Bhagwat et al. 2012). Thereafter the species escaped into the wild to become one of the world's top hundred invasive species (Kannan et al. 2013). Yet another well-documented example is the case of the African Giant Snail, which moved from East Africa to Asia, mainly as a pet and also during the transport of agricultural and horticultural products (Nentwig 2008). Today, it has invaded much of south and south-east Asia and is considered a major agricultural and garden pest in countries such as India (Sarma et al. 2015; Sen et al. 2016). But to what extent do these movements from native sites of occurrence signify significant niche shifts by the invasive species? Several studies have addressed this question in the recent past, using a variety of tools, and have often shown significant niche shifts by invasives, across taxa (Broennimann et al. 2007; Rödder and Lötters 2009; Fitzpatrick et al. 2007; Beaumont et al. 2016; Tingley et al. 2014; Chapman et al. 2017; Qiao et al. 2016, 2017) question some of these findings and argue that a rigorous analysis of the overlap of the environmental ranges of the invaded habitat with that of the native habitat is required before affirming that niche shifts have occurred.

The argument of Qiao et al. (2016) could be summarised following Hutchinson's classical description of a niche. Every species is assumed to have a fundamental niche (N_f) of which only a proportion is realised by the species (N_r). The elements constituting N_r though cannot ever be exhaustively described and can only be approximated as a hypervolume of "n" biophysical parameters (Blonder et al. 2014). An invasive analogue of the species, by definition, is one that has moved out of the hypervolume that the species in its native range had been occupying (N_i). Accordingly, it is often assumed that $N_i \neq N_r$, thus constituting a niche shift. However, as shown by Qioa et al. (2016) such inequivalence may not necessarily always amount to a niche shift since the condition $N_i \neq N_r$, may still not be outside the set constituted by N_f of the species. In other words, though the invasive species has moved out of its native range, it could still be occupying the hypervolume constituted by the fundamental niche of the species (Qioa et al. 2017). Under these conditions, the said invasive species has merely, invaded into a proportion of the fundamental niche that had not been occupied by the species before it became 'invasive'. In summary, such invasions could merely represent a case of finding a "home away from home". However, if there is evidence that the invaded species has indeed moved in a manner that N_i is no longer a subset of N_f, then it could constitute a case of significant niche shift. In this case, the species could be referred to as having found an altogether new home, an alien home.

In this paper, we analyse the distribution data of some of the world's top invasive plant and animal species and ask if these are associated with significant niche shifts or not. We analyse if their movements have been largely restricted to homes away from home, or into alien homes. We discuss these results in the context of the overall debate on invasion biology and how niche conservatism may have played a role in dampening the rates of invasion.

Materials and methods

Species occurrence and data collection

For this study, thirty-three most important invasive species of the world as per Global Invasive Species Database (GISD) were selected. The list of species with their native and introduced ranges is given in Supplementary Table 1. The distribution records for the thirty-three invasive species were obtained from the Global Biodiversity Information Facility database (GBIF; www.data.gbif.org) and included both native as well as the non-native ranges (introduced range). GBIF is the best open-source database and has been widely used for a variety of analyses. However, there have also been concerns about using the data for certain taxa where a small fraction of records have been identified as erroneous (4.2%; Zizka et al. 2020). The downloaded data were classified into native and introduced ranges as per the Centre for Agriculture and Bioscience International (CABI) database. Spatial filtering was used to remove duplicate records using the spThin package (Aiello-Lammens et al. 2015), and also removed points that were less than 5 km from each other to reduce the over-fitting of the model before running Species Distribution Modelling (SDM). The data were manually verified for any potential errors before running the model.

Climate data

The layers corresponding to the climate conditions were downloaded from Worldclim database version 2 (Supplementary Table S2; www.worldbioclim.org). This data is based on the climate parameters recorded between 1950 and 2000, at a resolution of 30 arc seconds (~ 1 km^2; Fick and Hijmans 2017). These global climatic data sets have been widely used in a number of studies and have been recommended for cross-continental tests of niche conservatism (Wiens and Graham 2005; Ahmed et al. 2019). These climatic variables represent combinations of temperature and precipitation, which are fundamental to species establishment and spread. A collinearity analysis was performed with all the nineteen bioclimatic variables using Pearson's Product Moment correlation. All variables which were correlated by |r| >0.75 were excluded from further analysis. Subsequently, the final sets of variables ranging from six to a maximum of ten were selected for each of the invasive species (Supplementary Table S2). There would be substantial differences in the correlations between bioclimatic variables when one considers the data across large geographical regions, which could have a potential impact on the model projections outside the calibration region. However, the most widely accepted method was followed to overcome some of these limitations (Barbosa et al. 2017; Ahamed et al. 2019; Lewis et al. 2019).

Species distribution modelling

The niche conservatism of the species was tested using the species distribution models (SDM) executed in Maxent (ver. 3.3.2 http://www.cs.princeton.edu/~shapire/Maxent; Phillips et al. 2006; Phillips and Dudík 2008). The model was run to predict the distribution of all the invasive species, but the result for only three species is provided to show complete shift, partial shift and no shift. Maxent uses presence-only data and estimates species distri-

bution by relating the environmental variables with the occurrence data. It gives a clog-log output based on the probability distribution of species presence (Elith et al. 2011).

The niche models were constructed by combining the bioclimatic variables with the distribution data of each of the species individually. For generating the models, 20% of the total occurrence points were randomly selected as testing data and the remaining 80% was used as training data with independent validation and 10,000 background points. The model was run using 10 replicates with 5000 iterations and used the clog-log output method. Model validation was performed using a subsampling strategy. The rest of the default settings were used for the prediction.

Model evaluation

The predictive power of each model was tested using an independent data set (20% of the total) in the range where it was calibrated, as well as in the range where it was projected, by comparing model predictions to real observations, using the area under the curve (AUC) of a receiver-operating characteristics (ROC) plot (Elith et al. 2006). The AUC allows testing of whether the pattern predicted by the model is significantly different from a random prediction in the same range.

Testing for climatic niche conservatism

To test for niche conservatism, a principal component analysis (envPCA) was carried out to compare the position of occurrences from the native and invaded range in the climatic space using the Ecospat package in R (Broennimann et al. 2012). For PCA, only those Bioclim data layers which were not auto-correlated were used for the analysis (Supplementary Table 2). The first two axes of this PCA were then used to examine the overlap between the species' native and introduced niches, taking into account the densities of occurrence records and climatic conditions within the species' range. To measure niche overlap between the native and introduced ranges, Schoener's D (Schoener 1970; Broennimann et al. 2012), a metric that represents a gradient between 0 (complete dissimilarity of niches) to 1 (complete overlap of niche), was used.

Reciprocal distribution model

A reciprocal distribution model (RDM; Fitzpatrick et al. 2007) was implemented, since modelling species distribution based only on native ranges is likely to underestimate the areas suitable for invasion (Fitzpatrick et al. 2007). For the forward-ENM, the model calibrated in the native range of invasive species (native model) was projected over the invaded range generating a prediction of the potential distribution of the species. This potential distribution was then contrasted with the current distribution that was predicted by the model calibrated with only the records from the invaded range of the species (invasive model). For the reverse-ENM, the invasive model was projected over the native range, generating a prediction of the potential native range of the species. This was then contrasted with the current distribution in the native range that was predicted by the native model. The best set of environmental variables for predicting species presences in Forward-ENM and Reverse-ENM was estimated using two tests generated by MaxEnt (Phillips et al. 2009) the relative

contribution of each variable during the model training process, and the gain in predictive power by the inclusion of each variable alone using the Jackknife test (Phillips et al. 2009).

Niche overlap between the native and introduced range

The overlap of the climatic niches between the native and the introduced ranges was assessed. Randomization tests were carried out to assess niche equivalency between the native and introduced ranges (Warren et al. 2008). These tests evaluated if the native and introduced niches were indistinguishable. The randomization tests were carried out using pseudo-replicates developed by pooling the occurrence data from both the native and introduced range and then randomly dividing them into two groups. For each of these pseudo-replicates, Schoener's D was calculated and compared with the observed D-value with a null distribution of 100 pseudo-replicated D values. This procedure was carried out 100 times in each direction (from the native range to the introduced range and from the introduced range to the native range) to generate two new null distributions of D-values. The niche equivalency hypothesis was rejected if the probability of the observed D-value fall-
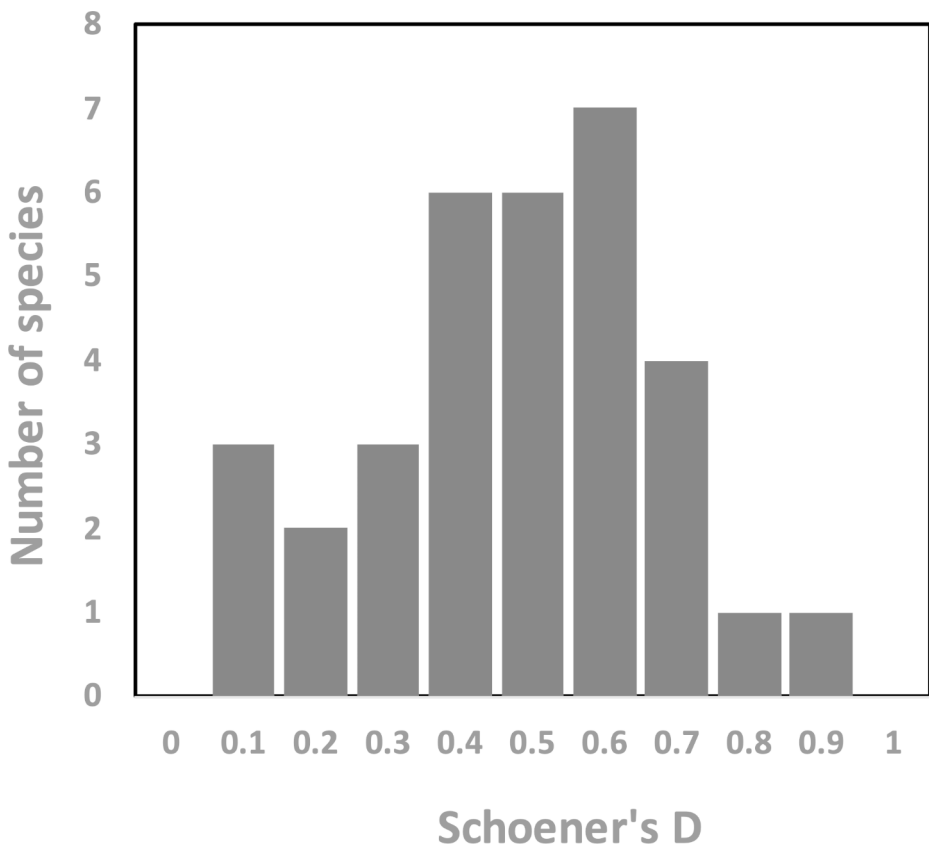

Fig. 1 Niche overlap (Schoener's D) for the 33 species; 1b. Niche overlap (Schoener's D) for the three groups, plants, invertebrates and vertebrates

ing in the null distribution was lower than 0.05 (P<0.05). Schoener's D index is calculated based on occupation (occurrence density corrected by environmental availability) of the environmental space, which is represented by the first two axes of the PCA (Warren et al. 2008; Broennimann et al. 2012; PCA-env). Schoener's D index varies between 0 (no overlap) and 1 (total overlap). This metric is independent of grid resolution because it is based on kernel functions. We used the PCAenv package in R as proposed by Broennimann et al. (2012) to directly measure niche overlap between the native and invaded ranges in a gridded environmental space.

Results

Patterns of Niche Shifts

The species distribution models using Maxent showed three different types of niche shifts based on Schoener's D in the species studied. Of the thirty-three species analyzed across the different taxonomic groups, the model indicated that for eight species there was very little to
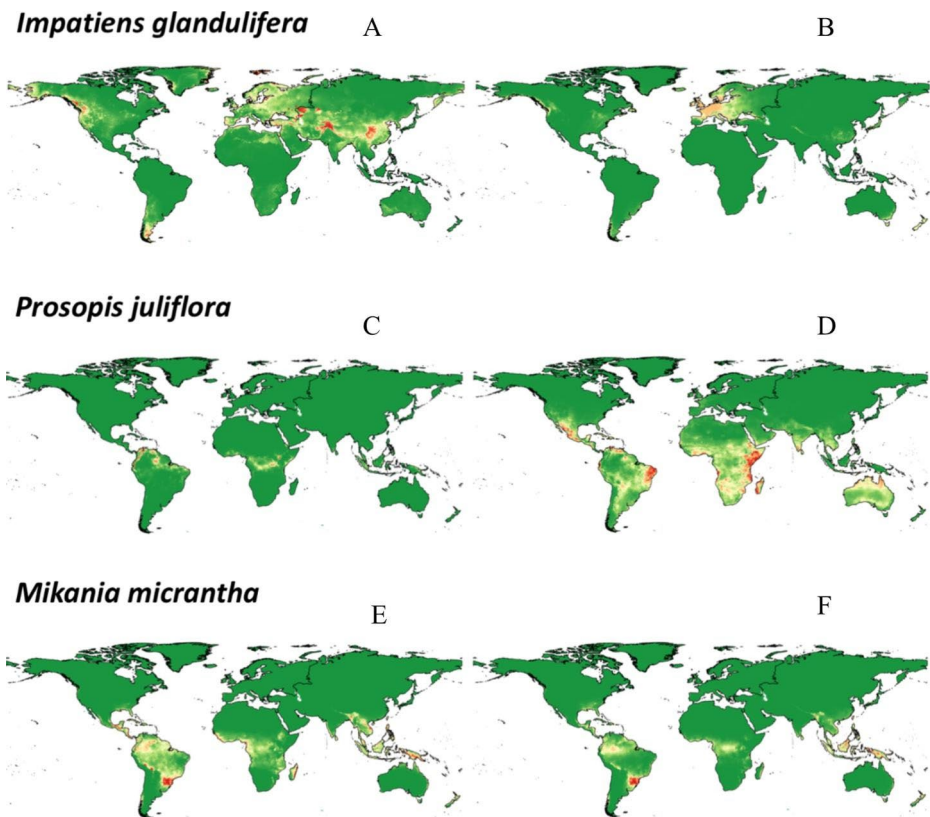

Fig. 2 Reciprocal distribution model for three invasive species (left panel: Native model; Right panel: Invasive model)

no shift in the niche between the native and introduced; for twenty-three species, there was a partial shift (less than 30%); and for two species there was a significant shift in the niche occupied (more than 30%) (Fig. 1).

Reciprocal distribution model

The reciprocal distribution model showed a complete shift for *Impatiens glandulifera*, partial shift for *Prosopis juliflora* and no shift for *Mikania micrantha* (Fig. 2). The result shows that for *I. glandulifera*, the native model (Fig. 2a) significantly underpredicts the invaded regions in Europe. Similarly, for the invasive model, there is hardly any prediction in the
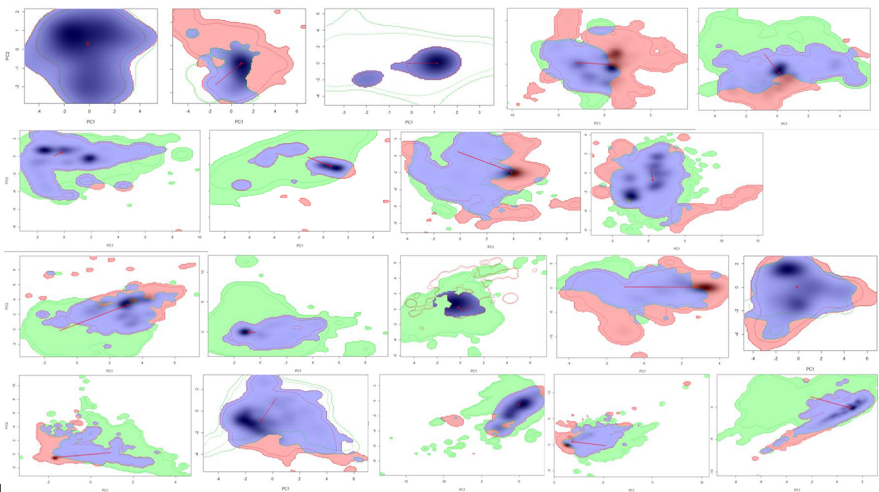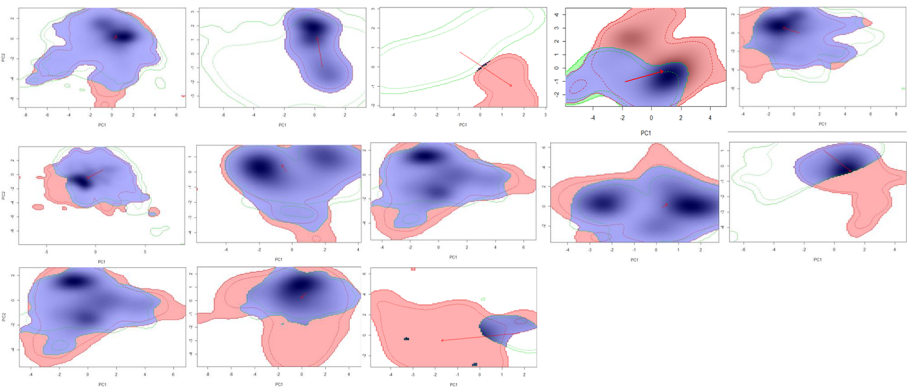

Plate 1
FIRST ROW: *Achatina fulica, Dreissena polymorpha, Pomacea canaliculata, Solenopsis Invicta, Lymantria dispar*
SECOND ROW: *Wasmannia auropunctata, Clarias batrachus, Gambusia affinis, Micropterus salmoides*
THIRD ROW: *Oncorhynchus mykiss , Oreochromis mossambicus, Lithobates catesbeianus, Rhinella marina, Trachemys scripta elegans*
FOURTH ROW: Psittacula krameria, *Acridotheres tristis, Rattus rattus, Sus scrofa, Sciurus carolinensis*

Plate 2
FIRST ROW: *Mesosphaerum suaveolens, Conyza canadensis, Impatiens glandulifera, Eichhornia crassipes, Mimosa pigra*
SECOND ROW: *Lantana camara, Mikania micrantha, Mimosa diplotricha, Parthenium hysterophorus, Prosopis juliflora*
THIRD ROW: *Solanum mauritianum, Chromolaena odorata, Centaurea biebersteinii, Acacia mearnsii*

Fig. 3 PCA-env for 33 invasive species in native and invaded region

native range (Fig. 2b). In the case of *P. juliflora*, the invasive model shows more areas of suitability than the native model (Fig. 2c and d). For *M. micrantha* both native and invasive models show similar areas of suitability (Fig. 2e and f).

Niche overlap between native and invaded ranges

Environmental Principal component analysis (envPCA) showed three different patterns viz., less niche shift, marginal shift and complete or significant shift from the centroid. A complete niche shift was observed in *I. glandulifera*, which is an introduced species from the Himalayas to Europe. Among plants, *P. juliflora* and *Centaurea biebersteinii* had a partial shift. Most of the other species either had no shift in the niche or very little shift (Fig. 3).

Table 1 Extent of niche shift across the thirty three species

Category	Species	Taxa
No shift (0%)	*Achatina fulica*	Mollusc
	Pomacea canaliculata	Mollusc
	Clarias batrachus	Fish
	Lithobates catesbeianus	Amphibian
	Oreochromis mossambicus	Fish
	Conyza canadensis	Plant
Partial shift (<30%)	*Rattus rattus*	Mammal
	Wasmannia auropunctata	Insect
	Acridotheres tristis	Bird
	Mesosphaerum suaveolens	Plant
	Lantana camara	Plant
	Mikania micrantha	Plant
	Mimosa pigra	Plant
	Mimosa diplotricha	Plant
	Parthenium hysterophorus	Plant
	Acacia mearnsii	Plant
	Gambusia affinis	Fish
	Lymantria dispar	Insect
	Oncorhynchus mykiss	Fish
	Solanum mauritianum	Plant
	Psittacula krameri	Bird
	Sciurus carolinensis	Mammal
	Oncorhynchus mykiss	Fish
	Sus scrofa	Mammal
Significant shift (>30%)	*Dreissena polymorpha*	Mollusc
	Rhinella marina	Amphibian
	Centaurea biebersteinii	Plant
	Prosopis juliflora	Plant
	Eichhornia crassipes	Plant
	Micropterus salmoides	Fish
	Trachemys scripta elegans	Reptile
	Solenopsis invicta	Insect
	Chromolaena odorata	Plant
Complete shift (100%)	*Impatiens glandulifera*	Plant

Table 2 Extent of niche shift and Schoener's D between native and non-native ranges

Species	Group	Number of records		Schoener's D	Equivalency	Similarity
		Native	Invasive			
Hyptis suaveolens	Plant (Herb)	879	2445	0.666	**0.007**	0.022
Conyza canadensis	Plant (Herb)	297	1441	0.511	0.401	0.039
Impatiens glandulifera	Plant (Herb)	66	55,648	**0.008**	**0.001**	0.744
Eichhornia crassipes	Plant (Herb)	286	2062	0.5	0.038	0.154
Mimosa pigra	Plant (Shrub)	1252	924	0.51	0.169	0.039
Lantana camara	Plant (Shrub)	2830	10,840	0.294	0.109	0.054
Mikania micrantha	Plant (Shrub)	1360	251	0.759	0.073	0.02
Mimosa diplotricha	Plant (Shrub)	174	174	0.521	0.377	0.007
Parthenium hysterophorus	Plant (Shrub)	1131	495	0.679	0.522	0.005
Prosopis juliflora	Plant (Shrub)	517	122	0.281	0.374	0.049
Solanum mauritianum	Plant (Shrub)	22	2228	0.521	0.385	0.006
Chromolaena odorata	Plant (Shrub)	1030	484	0.419	0.509	0.019
Centaurea biebersteinii	Plant (Shrub)	1195	34	0.12	0.066	0.481
Acacia mearnsii	Plant (Shrub)	1652	445	0.3919	0.384	0.346
Wasmannia auropunctata	Animal (Insect)	8688	3593	0.6261	0.038	0.077
Lymantria dispar	Animal (Insect)	4281	9479	0.4834	0.038	0.038
Solenopsis invicta	Animal (Insect)	124	8292	0.3852	0.038	0.038
Pomacea canaliculata	Animal (Mollusc)	151	2225	0.809	**0.002**	0.002
Achatina fulica	Animal (Mollusc)	188	153	0.056	**0.001**	0.415
Dreissena polymorpha	Animal (Mollusc)	4661	5896	0.056	0.296	0.405
Clarias batrachus	Animal (Fish)	212	971	0.2209	0.962	0.077
Gambusia affinis	Animal (Fish)	32,277	2321	0.1608	0.038	0.038
Micropterus salmoides	Animal (Fish)	111,125	7249	0.6621	0.038	0.038
Oncorhynchus mykiss	Animal (Fish)	112,410	6335	0.4714	0.038	0.038
Oreochromis mossambicus	Animal (Fish)	3491	2024	0.3182	1	0.038
Lithobates catesbeianus	Animal (Amphibian)	39,219	10,021	0.3613	0.615	0.077
Rhinella marina	Animal (Amphibian)	5876	6023	0.5210	0.386	0.003
Trachemys scripta elegans	Animal (Reptile)	21,188	7547	0.5301	0.038	0.077
Psittacula krameri	Animal (Bird)	271,699	185,706	0.4444	0.038	0.115
Acridotheres tristis	Animal (Bird)	439,113	527,132	0.343	0.401	0.011
Rattus rattus	Animal (Mammal)	26,808	263	0.4061	0.038	0.038
Sus scrofa	Animal (Mammal)	156,448	18,058	0.5126	0.038	0.077
Sciurus carolinensis	Animal (Mammal)	48,974	150,428	0.3404	0.038	0.077

Niche overlap, equivalency and similarity test showed that *I. glandulifera* had very low niche overlap between native and invaded range (D=0.008), followed by two mollusc species – *Lissachatina fulica* and *Dreissena polymorpha* (D=0.056). The highest niche overlap was observed in *Pomacea canaliculata* (D=0.809) and *M. micrantha* (D=0.759). A complete list of species with Schoener's D index is given in Table 1.

Discussion

Our analyses show that for most of the species examined (90%), there is no evidence of significant niche shifts. In fact, for these species, as is evident by the reciprocal distribution model, the native and invaded habitats were interchangeable with respect to their predictability of each other. Thus, for these species which have made it into the world's top 100 invasive species, their invasiveness is merely a movement from one home in their native range to another home on some other part of the earth, but all within the fundamental niche of the species. So here the N_i (the invaded niche)=N_r (the realized niche of the species) both of which in turn are subsumed by N_f (the fundamental niche of the species). This observation supports the well-articulated hypothesis of niche conservatism, wherein species tend to exhibit inertia and hence tend to move only into those habitats or niches that resemble most of their parental or native niches (Wiens et al. 2010; Liu et al. 2020). Accordingly, the invasion risk of a species is likely to be highest in regions that have the greatest similarity to their respective native range in terms of climate and/or other environmental factors (Petitpierre et al. 2012; Strubbe et al. 2013). Indirect yet reasonably strong evidence for such niche conservatism also comes from the fact that for most of the 70% of the species analysed in the study, the movements (from their native to invaded niches) have been along the longitudinal than the latitudinal axis. For these species, and for the reasons argued above, ecological niche modelling tools would be expected to provide reliable range expansion predictions. If at all the predictions of range expansion and invasions do not match with the empirical data of actual invasions of these species, it is likely that this could be due to constraints other than climatic, such as biotic interactions and competitions (Rosche et al. 2019).

The remaining 10% of the species that do not show niche conservation, where $N_i \neq N_r$, sare likely to have found a new home, an alien home, that is outside the fundamental niche in which the species evolved. *I. glandulifera* best exemplifies this situation. A native plant of the Himalayas, the species is today an important invasive in most parts of Western Europe (Hagenbald et al. 2015). As indicated by our analysis, there is almost no overlap between the native and the invaded niches, and therefore the reciprocal distribution model fails to predict each other. The other species showing such shifts are *D. polymorpha, C. biebersteinii, P. juliflora* and *Chromolaena odorata*. Similarly, *M. gigas*, a non-indigenous species rapidly shifted its niche in its introduced range in a span of fifty years (Pack et al. 2022). For all of these plants and animals, historical contingencies, either natural or aided by humans, have enabled them to move and survive in habitats that are clearly not the habitats in which they evolved.

Understanding the process of niche diversification in such species would open up a number of interesting questions, both related to their historical biogeography as well as the proximate mechanisms that may have led to their adaptation to novel niches. For example, how did these species jump from one adaptive peak (their native niche) to the other (their

invaded niche)? Were such jumps in hoops or were they linear with an ever-increasing arc of occupation that finally landed the species in a niche that bears no climatic resemblance to that of their nativity? To what extent does genetic adaptability or homeostasis accompany such jumps? Finally, for precisely the reason that $N_i \neq N_r$ in these species, ecological niche modelling tools would not be useful in modelling the niche expansion of these species.

In conclusion, our study extends and opens up an interesting debate on niche shifts in invasive species and calls for a studied caution in deciding whether a species has just extended its home range from one home to the other, or found an entirely alien home. While either of them is not going to be forgiving on what impact they could have on the existing species dynamics in their new niches, it is important to bear in mind, that such a nuanced approach could actually have implications that might not have been considered so far. Our findings also have implications for species distribution modelling as these have a strong assumption of niche conservation. Our results show that for 90% of the invasive species this assumption is largely true. These models provide fairly robust predictions even under different climate change scenarios and are reliable. However, there are also some caveats in predicting distribution given niche shifts and environmental non-equilibrium (Pili et al. 2022). Nevertheless, despite their caveats, they may be widely used for predicting the spread of invasive species.

Data Availability (data transparency): The data obtained is freely available from www.data.gbif.org.

Code Availability (software application or custom code): The analysis has been carried out using Maxent software that can be freely downloaded -MAXENT (ver. 3.3.2 http://www.cs.princeton.edu/~shapire/Maxent; Phillips et al. 2006; Phillips and Dudík 2008).

Declarations

Conflict of interest The authors declare that they do not have any conflict of interest with the results.

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