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Niche shifts, low haplotype diversity and invasion potentials of invasive snail Lissachatina fulica (Gastropoda: Achatinidae)

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Abstract

Invasive alien species are one of the greatest threats to biodiversity, ecosystems, human economy and human health. Future climate change may result in niche expansion, contraction or range shift leading to changes in their geographic distribution. The Giant African snail, *Lissachatina fulica*, is one of the 100 worst invaders. This study uses a species distribution modelling approach to assess current and future potential global distribution for this pest species under two climate change scenarios (SSP2 and SSP5). We tested the niche conservatism hypothesis for this pest species by comparing native niche versus invaded niche. We also quantified niche overlap and niche dynamics such as expansion, stable and unfilling between the native and introduced ranges using PCA-env. Our results show that potentially suitable niches in the present and future climate change scenarios increase significantly. The results suggest that Bio 13 and Annual Mean Temperature (Bio1) are the two most important drivers in determining the potential distribution of this invasive species. Furthermore, we found evidence for niche shifts due to niche expansion across the continents, thus occurring in climatically distinct regions. Finally, the study identified the areas of high invasibility which help in managing this invasive species. This study has implications for understanding the range dynamics of *L. fulica* across continents despite having low mitochondrial haplotype diversity in the invaded regions.

1. Introduction

The invasive alien species are introduced to other parts of the world from their native ranges either deliberately or accidentally (IUCN, 2017). They are one of the primary causes of biodiversity loss, leading to changes in the structure and composition of the ecosystems (IUCN, 2017), ecosystem services, human well-being, agriculture and economic growth (Simberloff et al., 2013). They also act as hosts to pathogens and spread disease to humans, crops and native biodiversity (Barker, 2002; Simberloff et al., 2013). In conjunction with habitat loss, invasive species have been associated with nearly 60 percent of species extinctions in the last century (Bellard et al., 2016). With ever-increasing international trade, human-induced habitat destruction and climate change, the pressure caused by invasive species is only likely to increase in the future (Hulme, 2014).

Niche conservatism is the extent to which ecological niches are conserved through time and space (Wiens et al., 2010). Many studies have looked into the niche conservatism perspective (Wiens et al., 2005) and change in the fundamental or realised niche or both (Pearman et al., 2008) of the invasive species to understand the speciation effect of climate change due to biological invasions (Hulme, 2017). Several studies have suggested that climatic niche occupied by invasive species including plants (Broennimann et al., 2007; Holt et al., 1990; Dietz and Edwards 2006), insects (Fitzpatrick et al., 2009; Medley et al., 2010), fishes (Lauzeral et al., 2011) and amphibians (Tingley et al., 2014) may not be conserved between their native and introduced regions (Goncalves et al., 2014). In the case of invasive alien species, niche differences between native and introduced ranges are of three types, a) invasive species colonising novel environmental conditions relative to their native range, i.e., niche expansion, b) partial filling of the native niche in the invaded range, i.e., niche unfilling and c) proportion of the invaded

range overlapping with native niche, i.e., niche stability (Warren et al., 2008; Strubbe et al., 2015). One commonly discussed topic in ecology is niche shifts during biological invasions (Guisan et al., 2014; Broennimann et al., 2007). Generally, climatic niche shifts contradict the assumption of niche conservatism, which implies that species retain their niches in space and time (Wiens, 2005). This assumption underlies ecological niche modelling, the most commonly used approach for assessing the impact of climate change on biodiversity (Rodda, 2011). Comparisons between species' native and non-native climatic niches may identify species that have undergone adaptive evolutionary changes during the invasion process (e.g. change of the fundamental climatic niche) and lead to a better understanding of niche dynamics (Broennimann et al., 2007). The reproductive ability of the invasive species might influence the invasibility of the species. For example, asexual, parthenogenetic and hermaphroditic self-fertilising species might be more aggressive than sexually reproducing ones. However, a recent meta-analysis across taxa (both plants and animals) has shown no difference between them (Roman and Darling 2007).

The adverse effects of invasive species may be intensified by climate change (Pyke et al., 2008). Negative impacts are further increased as invasive species are typically generalists with broad climatic tolerances; they are considered likely to cope with change in the climate, enabling them to expand into new areas (Walther et al., 2009). In recent times, there is growing evidence for the effects of climate change on invasive species distribution and is considered one of the main drivers of future invasions (Bellard et al., 2013). Studies involving various taxa have shown that climate change has serious impacts on the niche expansion and niche shift in invasive species (Ahmed et al. 209; Atwater et al. 2018; Wan et al., 2016). Forecasting responses of invasive species to climate change using ecological modelling or species distribution modelling has been extremely useful (Dillon et al., 2010; Gilman et al., 2010; Pereira et al., 2010; Salamin et al., 2010; Beaumont et al., 2011; Dawson et al., 2011; McMahon et al., 2011; Sarma et al., 2015) and play a vital role in identifying potential future risk areas and help in developing sound strategies to reduce future impacts on native biodiversity (Pereira et al., 2010; Parmesan et al., 2008). The ecological niche modelling tool is widely used to predict the geographical distribution of a given species based on correlations of species occurrence and suites of environmental and climatic variables (Philips et al., 2006). The species distribution models are also used to select the areas to determine the risk of species invasions under current and future climate scenarios (Guisan et al., 2013).

Lissachatina fulica, commonly known as the Giant African Snail, is one of the 100 worst invasive species in the world (Lowe et al., 2000; Raut and Barker, 2002). The native range of *L. fulica* is Ethiopia, Kenya and the United Republic of Tanzania (Bequaert, 1950a, in Raut and Barker 2002) and was introduced to other tropical and subtropical regions with warm and mild temperatures and high humidity. *Lissachatina fulica* is well adapted to various land use and land cover types such as agricultural areas, coastal areas, wetlands, natural forests, riparian forests, scrublands, shrublands, forest edges, plantations and modified forests (Raut, 2002; Moore, 2005) and even urban areas. This species is found to transmit diseases through spores (found in faeces) and is known to infect a variety of agricultural plants such as pepper, coconut, papaya and vanilla (Mead, 1961, 1979; Turner, 1964, 1967; Muniappan, 1983; Schotman, 1989). The snail *L. fulica* has a tremendous impact on native biodiversity, agriculture and horticultural crops and

is known to feed on more than 500 native plants and crop species (Raut and Baker 2002). It also competes with native snail species (Sharma et al., 2015). Thus, there is an urgent need to understand the relationship between climate change and *L. fulica* distributions since it has a significant impact on biodiversity and the livelihoods of farmers. A handful of studies have assessed invasion patterns of *L. fulica* using distribution models but are on a local or regional scale (Thiengo et al., 2007; Vogler et al., 2013; Sridhar et al., 2014; Sarma et al., 2015). A couple of recent studies at the global level shows that *L. fulica* has shown low haplotype diversity for mitochondrial markers in the invaded regions of the world (Fontanilla et al., 2014; Vijayan et al., 2020). In this study, we model the potential global distribution of *L. fulica* under present climatic conditions and future climate change scenarios using a maximum entropy algorithm. The following are the objectives of this study: (1) identify the potential distribution of *L. fulica* at a global scale (2) assess the impact of climate change on invasion patterns of *L. fulica* across continents, (3) test niche conservatism in invaded range and under climate change scenarios and (4) compare haplotype richness with habitat suitability derived from niche modelling in the invaded areas.

2. Materials And Methods

2.1 Distribution data: Global *L. fulica* occurrence data was compiled from Global Biodiversity Information Facility (GBIF 2021, http://www.gbif.org), India Biodiversity Portal (IBP, www.indiabiodiversity.org), iNaturalist (www.inaturalist.org), journals, published reports, (see Sarma et al., 2015) and field surveys by the first author. The compiled database was plotted in QGIS ver 3.18 and manually checked and cleaned for potential errors in geo-coordinates, duplicate records, and points falling outside the study region using the CABI database. Finally, spatial thinning was applied (see below).

2.2 Climatic variables: To predict present distribution, we used Bioclimatic variables downloaded from WorldClim database Ver 2 (http://www.worldclim.org/). For future scenarios, i.e., 2070 (average for 2061–2080), we used five general circulation models viz., BCC-CSM2-MR, CanESM5, CNRM-ESM2_1, IPSL-CM6A-LR, and MRI-ESM2_0 for two shared socio-economic pathways - SSP2 (2.6) representing a middle-of-the-road scenario (Strongly Declining Emissions) and SSP5 (8.5) representing Fossil-fueled Development (Rising Emissions thus, high challenges to mitigation, low challenges to adaptation). SSP data was downloaded from https://www.worldclim.org/data/cmip6/cmip6climate.html. All bioclimatic variables used had a spatial resolution of 5 km, i.e., 2.5 Arc minutes.

2.3 Ecological niche modelling: Current and future invasion risk at global scales was predicted using the maximum entropy principle implemented in MaxEnt algorithm v3.4.1k (Phillips, 2004, 2006). MaxEnt is a machine-learning technique that estimates the probability of species distribution in a given study area using a set of environmental variables and geocoded species presence data and provides an output on a scale of 0–1 indicating low to high suitable areas. The MaxEnt algorithm is a widely used algorithm to the model geographic distribution of species in particular invasive species. It has robust predictions that any other algorithms, and is relatively easy to use. The following settings were used in MaxEnt for species distribution modelling, namely cloglog output, 10,000 background points, 5,000 iterations,

subsampling and 15 replicates with other default settings. In addition, the jackknife procedure was selected to estimate the relative contribution of each variable in the final model.

Pearson's correlation was used to reduce multicollinearity and over parametrisation between different environmental variables. When a pair of environmental variables with a correlation coefficient greater than |r| > 0.70, one of the two highly correlated variables were excluded from the analysis. Finally, only nine variables (Bio 1, Bio 2, Bio 3, Bio 5, Bio 12, Bio 14, Bio 18, Bio 19.) were used for modelling (Table 1). Occurrence records are often associated with sampling biases which tend to bias the models. Therefore, distribution records were spatially thinned to 10 km^2 using the SpThin package (Aiello-Lammens et al., 2015) in R (R Core Team, 2017) to remove the effect of sampling bias. Spatial thinning retains the fewest records while retaining the information necessary to build robust models (Pearson et al., 2007; Syfert et al., 2013; Verbruggen et al., 2013; Boria et al., 2014; Fourcade et al., 2014). Of the 10,132 points, 8,956 were retained after thinning for further analysis. Habitat suitability models were developed using known occurrence records from the invasive range (invasive model), native range (native model) and combined invasive and native ranges (global model) as proposed by Warren et al. (2008) and projected for two future climate change scenarios. This paper presents the models and analysis based on occurrence records for the global model. We choose both native and invaded occurrence records because the model has the advantages of using records that are likely to be in equilibrium with the native environment and introduced region. This leads to robust models helpful in providing information on the expansion of the realised niche (Broennimann and Guisan, 2008; Arcelino et al., 2015; Shabani and Kumar 2015; Wan et al., 2017).

Table 1
Model performance for three types of analysis

Models	10% training threshold	AUC Test	AUC Train	AUC_{DIFF}	pAUC
Global	0.456	0.909	0.907	0.001	0.923
Native	0.299	0.995	0.990	0.005	0.485
Non-native	0.448	0.908	0.905	0.003	0.922

2.4 Model evaluation: The model was evaluated by the Area Under Receiver Operating Curve (ROC), popularly known as AUC (Swets 1988), by setting 25% of occurrence records for testing and 75% of the records were used for training the modelling. The AUC values vary from 0–1, where values < 0.5 signify that the model is worse than random, 0.5–0.7 signifies poor performance, 0.7–0.9 signifies moderate performance, and > 0.9 signifies high performance (Kumar et al., 2014). The final model obtained showed high-performance values indicating that performance was good. pAUC and AUC_{diff} were calculated as per Lira-Noriega et al. (2020).

2.5 Niche shift analysis: To test for potential shifts for *L. fulica* in native and introduced continents (Africa, Asia, North America, Oceania and South America), we performed Principal Component Analysis (PCA-env) approach as proposed by Broennimann et al. (2012). PCA method transforms environmental variables into two-dimensional space projected onto 100x100 PCA grids of cells bounded by minimum and maximum PCA values of background data. Niche overlap was measured using Schoener's D metric to measure the niche overlap, which varies from 0 (no overlap) to 1 (complete overlap). Niche equivalency and similarity are statistically tested from the density in environmental space (Broennimann et al., 2012). The niche equivalency test was used to assess whether the niches of two entities being compared are equal (display constant overlap), moderately similar (show some overlap) or significantly different (display no overlap) when occurrences are randomly shuffled across the ranges. The equivalency was performed by comparing the overlap (D) for native and introduced ranges with a null distribution. If the observed niche values were lower than the overlap value from the null distribution ($P < 0.05$), then the null hypothesis of niche equivalency was rejected (Broennimann et al., 2012). The niche equivalency test is limited by the fact that evaluation is not accounting for environmental conditions of the surrounding space of available habitat (Warren et al., 2008). Hence, the niche similarity test was adopted to assess whether the niches of two entities are more similar or different than would be expected by chance (Warren et al., 2008). This analysis was carried out using the "Ecospat" package (Di Cola et al., 2016) in R (R core team 2018) with 100 replicates to ensure that the null hypothesis can be rejected with high confidence. Further, this approach is considered robust as it uses kernel density smoothing to mitigate the effects of sampling bias (Petitpierre et al., 2012).

2.6 Range contraction and expansion: We calculated the percentage change in habitat suitability for current and future models. We categorised the final model arbitrarily into four suitable categories according to Hamid et al. (2018): Not suitable habitat (0.0–0.25) where the probability of occurrence of species is not greater than 25% in a given grid. Low suitable habitats (0.25–0.50) where the probability of occurrence of species is between 25–50%. Moderately suitable habitat (0.50–0.75) where the probability of occurrence of species is 50–75% and highly suitable habitat (0.75–1.00) where the probability of occurrence of species range from 75–100%. We used DIVA-GIS (Hijmans et al. 2001) to calculate the percentage of area change by simple subtracting.

2.7 Haplotype analysis: *Lissachatina fulica* haplotype richness data for two mitochondrial markers viz., 16S rRNA and Cytochrome oxidase I (CoI) was compiled from Fontanilla et al. (2014) and Vijayan et al. (2020), respectively. For each site, habitat suitability value was extracted from niche modelling output for the current scenario using the point-sampling tool in QGIS ver 3.08. Linear regression was performed for habitat suitability value with haplotype richness in PAST (Hammer et al., 2001).

3. Results

3.1 Model performance and variable contribution: The MaxEnt output for all three models (global, native and invasive ranges) showed a good fit with AUC values of 0.909, 0.995 and 0.908, respectively (Table 1). Partial AUC is also high for a global and invasive model except for the native model (Table 1). The analysis of variable contribution showed that Mean Precipitation (Bio 12; 66 percent) and Annual Mean Temperature (Bio 1; 23.6 percent) contributed 89.6 per cent to the model. Rest 10.5 per cent is contributed by Bio 2, Bio 3, Bio 5, Bio 14, Bio 18 and Bio 19.

3.2 Current global invasion hotspot: Under the current climatic condition, the suitable area for *L. fulica* is seen in most part South America (except southern regions), south-eastern parts of North America, the central part of the African continent and Madagascar, part of the south and south-east Asia, eastern China, the northern part of Australia and all most all oceanic islands are vulnerable to invasion (Fig. 1a).

3.3 Future global invasion hotspot: Under SSP 2.6 climate change scenario, there is a significant increase in the habitat suitability for *L. fulica* across its invaded ranges. Already moderately suitable areas are likely to become highly suitable, as seen in regions such as South America and South and south-east Asia (Fig. 2b). A similar trend was observed under SSP 8.5 scenario as well (Fig. 2c). Under SSP 8.5, the expansion occurs in most parts of India, eastern China, eastern USA, southern South America, equatorial Africa, and northern and eastern Australia. There is a northward shift in the suitable areas (Fig. 2b). According to the niche model, under SSP 8.5, most parts of western and south-western Europe will become moderately suitable for *L. fulica* invasion. The analysis of area changes reveals a significant increase in the suitable area by 15% (168,490 km2) and 47% (539,067 km2) respectively in SSP 2.6 and SSP 8.5 (Fig. 2c) in the current scenario. Very small suitable areas show contraction under changing climate.

3.4. Test for niche conservatism: Niche overlap measured using Schoener's D between the native and invaded regions for *L. fulica* was found to be 21%, 29%, 34%, and 38% between current and future scenarios for Asia, Africa (introduced), South America and North America and Oceania respectively (Table 2). The PCAenv analysis showed that the PC1 retained the maximum variation (native vs introduced regions) ranging from 28% (for North America) to 38.68% (for Asia). In contrast, the maximum variation retained by the PC2 ranged from 22.12% (for South America) to 25.10% (for Africa) (Table 2). The niche conservatism test between the native and invaded regions revealed that the species had undergone shifts in its climatic niche only in North America. The native African and Asian, South American and African (introduced) niches completely overlap. However, our result shows that there is a considerable expansion into new environments in these regions. For North America, there is a niche shift by about 50% (Fig. 3). The analysis shows niche expansion in Africa (introduced), South America and Asia compared to unfilling value. In these continents, the *L. fulica* occupied a wide range of climatic conditions compared to the native region. *Lissachatina fulica* successfully colonises novel environmental conditions across invaded regions (Niche expansion) by 46.3%, 55.4%, 48%, and 29% in Africa (introduced), Asia, North America and South America, respectively. Niche comparisons for native

and introduced regions showed that the null hypotheses for niche equivalency were not rejected for all continents (non-significant, P > 0.05). The results from the niche equivalency tests showed that the niche inhabited by *L. fulica* was identical in the case of Asia, South America and Africa (introduced) and not identical in the cases of North America. In addition to this, the niche similarity test for *L. fulica*, the null hypothesis was not rejected (P < 0.05) for North America (Fig. 2; Table 2), and the climate niches in Africa (introduced), Asia and Southern America are no more similar than expected by chance (no significant, P > 0.05). The results for North America shows that *L. fulica* could occupy most of the areas with the similar climatic condition to those found in Africa (native range). Niche similarity tests also showed that *L. fulica* occupies similar conditions in invaded regions.

Table 2
Evidence of invasion potential and niche shift in *L. fulica* across different regions of the world.

Region	Africa (Introduced)	Asia	North America	South America
Schoener's D	0.287	0.210	0.383	0.340
Equivalency (p=)	1.000	0.976	0.537	0.700
Similarity (p=)	0.224	0.072	0.002	0.210
Expansion	0.463	0.554	0.479	0.294
Stability	0.537	0.446	0.521	0.706
Unfilling	0.000	0.000	0.643	0.000
PC Axis 1	36.43	38.68	28.10	39.40
PC Axis 2	25.10	23.80	22.73	22.12

Table 2
Changes in the habitat suitability of *L. fulica* under different climate change scenarios.

Habitat Suitability	Area (km^2)			
	0.1–0.25	**0.25–0.50**	**0.50–0.75**	**0.75–1.0**
Present	173,71,708.00 (62.14%)	80,52,665.00 (28.80%)	20,43,588.00 (7.31%)	4,89,154.00 (1.75%)
RCP 2.6	161,28,611.00 (59.83%)	78,35,824.00 (29.97%)	25,18,470.00 (9.34%)	4,72,963.00 (1.75%)
RCP 8.5	157,58,551.00 (62.09%)	71,53,268.00 (28.18%)	20,52,038.00 (8.09%)	4,16,680.00 (1.64%)

3.5 Haplotype richness vs habitat suitability

The haplotype richness for both markers (CoI and 16S) for *L. fulica* shows that except populations from Mayotte, Tanzania, and UAE, a significant number of sites have low richness occurring in highly suitable areas (Fig. 4). On the other hand, all Indian, south-east Asian and South American populations have very low haplotype richness occurring in relatively high suitable areas. Furthermore, the analysis carried out for the CoI marker shows that there is a significant negative relationship between haplotype richness and habitat suitability ($r= -0.645, p < 0.001, n = 25$) and for 16S rRNA, the relationship is not significant ($r = 0.128, p > 0.05, n = 34$; Fig. 3; Table 4).

4. Discussion

Globally worst invasive species are the greatest threat to biodiversity, economy, ecosystems and human health. *Lissachatina fulica* species is widely distributed in over 70 countries (CABI, 2021) across all continents except the Arctic and Antarctic. Management of this species is paramount, given its impact. Species distribution models or ecological niche models are a simple and robust method for providing early warnings of the potential spread of invasive species and are widely used to prevent, detect, and assess invasive risk (Petitpierre et al., 2012; Fernandes et al., 2014). This study used the species distribution model to assess the global invasion potential of *L. fulica*, one of the 100 worst invasive species in the world (Lowe et al., 2000) and explored niche dynamics. Its rapid spread into many places worldwide is an issue of great concern for agriculture, economy, and native biodiversity (Raut and Barker, 2002). The broad climatic tolerance, large size, high reproductive output, voracious and varied food preferences make *L. fulica* a successful invader across continents (Raut and Baker 2002; Thiengo et al., 2007; Gregoric et al., 2011; Sarma et al., 2015). This study showed the potential region of invasion under present and two future climate change scenarios that can be used to manage this highly invasive species along with the environmental drivers of distribution. In our study, precipitation and warm

temperatures were the most important climatic factors driving *L. fulica* distribution, which is consistent with variables explaining other land snail distributions. The model predictions for present and future climatic conditions revealed that the Southern parts of North America and Central America as well as northern parts of South America, central Africa, South and South-east Asia, Northern Australia and Oceanic Islands are highly suitable, indicating that *L. fulica* can spread and colonise regions with novel climatic condition (see below).

Species distribution model results showed a significant increase in the suitable area under two climate change scenarios assessed here. The increase in the range under climate change scenarios ranges from 15 percent to 47 percent. There is also an increase in the total area of invasion under both climate change scenarios to the extent of one million to 3.5 million km^2. Earlier modelling efforts by Sarma et al. (2015) for India showed an increase of up to seven per cent. Thus, many parts of tropical regions of the world will become highly vulnerable to invasion in the near future. On the other hand, in Australia, the *L. fulica* is a regulated pest and not present at the moment (Walker, 2005), but this area is highly vulnerable to invasion and should be prepared to prevent future deliberate and/or accidental introduction.

4.1 Niche shift and niche overlap

The results on niche comparison studies for *L. fulica* across multiple continents provides strong evidence of expansion across all continents and niche shifts between native Africa and North America, indicating that this species has the potential to occupy the novel climatic conditions. Our analysis revealed that the native occupied climatic niche of *L. fulica* has not remained entirely conserved in introduced ranges across continents. Niche shifts and expansion have been demonstrated in a wide variety of taxa, including plants and animals (Broennimann et al., 2007; Gallagher et al., 2010; Strubbe 2013; Guisan et al., 2013; Ihlow et al., 2016; Atwater et al., 2018; Datta et al., 2019) and our results are in agreement with previous studies. Our study showed that *L. fulica* can invade regions with both similar and different climatic conditions than those found in its native range in Africa. Several examples across taxonomic groups have shown that many invasive species occupy different climatic niches once introduced (Dreyer et al., 2019; Lopez et al., 2017). Our results also infer that species with narrower climatic niches in native ranges show significantly higher rates of niche expansion in the introduced range. These results agree with other similar studies on pests such as *Delia antiqua* and *Phenacoccus solenopsis* (Wei, 2017; Ning et al., 2017). The study shows a significant niche expansion in South America, Asia and Africa. A small proportion of the niche in North America remains unfilled. This will have an implication on the future spread of this species. Comparisons between native African versus global introduced niche revealed a considerable amount of unoccupied niche space in the species native range. A high amount of unoccupied niche space in the native range may be explained by the presence of natural enemies such as carnivorous snails and Carabid beetles (Davis and Butler Jr, 1964). The absence of natural enemies in the introduced ranges might have facilitated the observed niche expansion and, in turn, the spread of *L. fulica* throughout the globe. Given the wide range of food preferences, simultaneous hermaphroditism nature, high reproductive output and low genetic diversity among the introduced populations make *L. fulica* more invasive rather than basic evolutionary process in

niche expansion in the introduced regions. *Lissachatina fulica's* nature of adapting to the different climatic conditions would be a cause of worry as this species can invade to the new regions with different climatic conditions in the future. It is worth looking at the new potential areas of adaptability and formulating effective management strategies to prevent socio-economic and biodiversity risks.

The niche overlap of *L. fulica* was very low, ranging from 1.10 percent (South America) to 18.91 percent (Africa), indicating that this *L. fulica* adapted well to different environmental conditions in this non-native range. The present study showed that the shift observed in the climatic niches of *L. fulica* in Asia and Southern America is mainly due to niche expansion. Hence, the presence of *L. fulica* in novel environmental conditions in its introduced regions suggest that its niche has not been conserved during the process of invasion. Our results suggest that the species has the capacity to invade more new regions than previously thought.

4.2 Genetic diversity and invasion

From a global perspective, one can see that the native range has higher *L. fulica* haplotype richness (Tanzania) than invaded ranges for both markers. An earlier study has revealed the presence of 16 COI haplotypes of *L. fulica* in Asia and Africa. The UAE showed the highest haplotype and nucleotide diversities (Vijayan et al., 2020) among the introduced ranges. For 16S, the 18 haplotypes varied across 20 sites (Table 2). Eight haplotypes were found in Uganda and Tanzania. The study indicated that the majority of the haplotypes are found in East Africa and the Indian Ocean islands (Fontanilla et al., 2014). Our results show that all regions where *L. fulica* has invaded have very low genetic diversity for both the mitochondrial markers. A similar pattern was seen in *Corbicula flumea* where the invaded region has low genetic diversity compared to native ranges (Gomes et al., 206). In apple snails, Yang et al. (2018) found that haplotype diversities were lower in *Pomacea maculata* populations in China than in the native range. Similarly, low genetic diversity was also reported from the introduced population of *Impatiens glandulifera* in Europe (Hagenblad et al., 2015). However, these studies didn't consider ENM analysis to check if high habitat suitability regions have higher or lower genetic diversity. In future, studies using more mitochondrial markers might give us better insight into the genetic diversity in relation to invasion.

A large number of studies comparing the genetic diversity of invasive plants in their native and introduced ranges have been carried out in different species across the world (Hagenblad et al., 2015). The review of studies indicates that, in general, there is a loss in genetic diversity upon invasion (Hagenblad et al., 2015). Recent global haplotype network analysis of *L. fulica* has revealed very low genetic differentiation among invaded populations (Fontanilla et al., 2014). Low genetic diversity and high invasibility of introduced species have been shown in other taxa (Hagenblad et al., 2015; Edelaar et al., 2015). Despite low genetic diversity, the capacity of invasive species to spread may be due to high phenotypic plasticity (Hagenblad et al., 2015). More studies are required to assess the nature of plasticity exhibited by *L. fulica* in its introduced ranges.

4.3 Management of *L. fulica*

Management of one of the greatest invertebrate invaders is challenging for the forest managers and farmers. Several chemical, biological and manual control methods have been tried to manage this species, but at a local or a small scale but with limited success (Raut and Baker 2002). There is a need to use a combination of these methods such as manual collection and killing, use of eco-friendly pesticides, synthetic chemicals (Rhoda et al., 2019), chemical baits such as metaldehyde and several local methods such as the use of kerosene, coffee powder (Nair et al., 1968; Raut and Ghose, 1984; Panigrahi and Raut, 1994; Nelson 2012) were also tried with decent success in managing this species. Plant-based pesticides like *Phytolacca dodecandra, Thevetia peruviana* (Raut and Barker, 2002) and *Annona glabra* (Prasad et al., 2004) were found to be effective against this pest. Using invasive species to make products as a control measure has been used in some invasive plant species in Southern India (Uma Shaanker et al., 2010) with considerable success. A similar kind of approach for *L. fulica* should be considered. For example, *L. fulica*, with nearly 60 percent protein in the soft tissues (Creswell and Kompiang, 1981), can be used as fish and poultry feed (Creswell and Kompiang, 1981; Diarra et al., 2015; Diomandé et al. 2008). These studies have shown a significant increase in the growth of poultry when fed with snail meal in combination with other feeds (Creswell and Kompiang, 1981; Diarra et al., 2015; Diomandé et al., 2008). Thus, there is a high potential of using *L. fulica*, which will have threefold benefits a) controlling the snail menace, b) reducing the cost of poultry feed and increasing growth and c) livelihoods of the poor people who can be employed for collection and processing. Later is particularly important in the under-developed or developing countries where a large section of the society is under the poverty line. The citizen science approach has been used extensively in the early detection of introduced species (e.g., Mohapatra and Aravind, 2021). This will help detect the species when the population is small, which can help in designing appropriate control measures by the concerned department. The early detection and eradication should ideally be taken up at a much smaller scale like district (county) or taluka. A national-level long-term programme for managing this species should be devised for each country. Also, the further introduction should be banned. There is a big pet market for *L. fulica* in a country like India (Aravind Personal Observation). This market demand encourages pet owners to breed, distribute, and often release into the wild. This needs to be addressed on a priority basis by either educating the concerned stakeholders or bringing in policy/law banning the breeding and selling of this species.

5. Conclusions

In conclusion, niche expansion and climate niche shifts of *L. fulica* suggest that the snail could adapt to novel environmental conditions generated due to climate change despite having low haplotype diversity across the introduced range. Furthermore, adaptation to novel climatic conditions increases its capacity for invasion in the absence of predators, pathogens or competitors, leading to expansion in population and distribution ranges and finally, modelling tools such as ENM in combination with data from the citizen science approach used in our study help in making decisions to prioritise areas for management of this invasive species and conservation of endemic species against the risk of invasion by *L. fulica*.

Declarations

Author contributions: NAA conceived the idea and got funding and manuscript writing. BBM and P.B. performed data collection and statistical analysis. All three authors contributed to the manuscript.

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DATA AVAILABILITY STATEMENT

Data used here was downloaded from www.gbif.org, www.inaturalist.org, www.indiabiodiversity.org and Sarma et al. 2015.

DECLARATION OF INTERESTS

 The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

1. Gomes C, Sousa R, Mendes T, Borges R, Vilares P, Vasconcelos V et al (2016) Low Genetic Diversity and High Invasion Success of Corbicula fluminea (Bivalvia, Corbiculidae) (Müller, 1774) in Portugal. PLoS ONE 11(7):e0158108. https://doi.org/10.1371/journal.pone.0158108
2. Yang QQ, Liu SW, He C, Yu XP (2018) Distribution and the origin of invasive apple snails, Pomacea canaliculata and P. maculata (Gastropoda: Ampullariidae) in China. Sci Rep 8:1185
3. Vijayan K, Suganthasakthivel R, Sajeev TV, Soora PS, Naggs F, Wade CM (2020) Genetic variation in the Giant African Snail Lissachatina fulica (Bowdich, 1822) in its invasive ranges of Asia and West Africa. Biol J Linn Soc 131:973–985
4. http://www.gbif.org (2017) *Achatina fulica* (Férussac, 1821) in GBIF Secretariat. GBIF Backbone Taxonomy. Checklist dataset https://doi.org/10.15468/39omei accessed via GBIF.org on 2019-01-09
5. Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP (2015) spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38:541–545. https://doi.org/10.1111/ecog.01132
6. Ahamed R, Khuroo A, Charles B, Hamid M, Rashid I, Aravind NA (2019) Global distribution modelling, invasion risk assessment and niche shift patterns of Ox-eye Daisy (*Leucanthemum vulgare*) under climate change. Sci Rep 9:11395. https://doi.org/10.1038/s41598-019-47859-1
7. Atwater DZ, Ervine C, Barney JN (2018) Climatic niche shifts are common in introduced plants. Nat Ecol Evol 2:34–43

8. Beaumont LJ, Pitman A, Perkins S, Zimmermann NE, Yoccoz NG, Thuiller W (2011) Impacts of climate change on the world's most exceptional ecoregions. *Proceedings of National Academy of Sciences*, 108, 2306–2311. https://doi.org/10.1073/pnas.1007217108
9. Bellard C, Genovesi P, Jeschke JM (2016) Global patterns in threats to vertebrates by biological invasions. *Proceedings of Royal Society B- Biological Sciences*, 283, http://doi.org/10.1098/rspb.2015.2454
10. Bellard C, Thuiller W, Leroy B, Genovesi P, Bakkenes M, Courchamp F (2013) Will climate change promote future invasions? Glob Change Biol 19:3740–3748. https://doi.org/10.1111/gcb.12344
11. Bequaert JC (1950) Studies in the Achatininae, a group of African Land Snails. Bull Museum Comp Zool 105:1–216
12. Bernie D (2010) Temperature implications from the IPCC 5th assessment Representative Concentration Pathways (RCP). Work stream 2, Report 11 of the AVOID programme (AV/WS2/D1/R11).
13. Boria RA, Olson LE, Goodman SM, Anderson RP (2014) Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecol Model 275:73–77
14. Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG, Thuiller W, Fortin M-J, Randin C, Zimmermann NE, Graham CH, Guisan A (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. Glob Ecol Biogeogr 21:481–497
15. Broennimann O, Guisan A (2008) Predicting current and future biological invasions: both native and invaded ranges matter. Biol Lett 4:585–589
16. Broennimann O, Treier UA, Müller-Schärer H, Thuiller W, Peterson AT, Guisan A (2007) Evidence of climatic niche shift during biological invasion. Ecol Lett 10:701–709
17. Datta A, Schweiger O, Kühn I (2019) Niche expansion of the invasive plant species Ageratina adenophora despite evolutionary constraints. J Biogeogr 46:1306–1315
18. Davis CJ, Butler GC Jr (1964) Introduced Enemies of the Giant African Snail, *Achatina fulica* Bowdich, in Hawaii (Pulmonata: Achatinidae). *Proceedings Hawaiian Entomological Society*, 18, 377–389
19. Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM (2011) Beyond predictions: Biodiversity conservation in a changing climate. Science 332:53–58. https://doi.org/10.1126/science.1200303
20. Di Cola V, Broennimann O, Petitpierre B, Breiner FT, D'Amen M, Randin C, Engler R, Pottier J, Dorothea PD, Dubuis A, Pellissier L, Mateo RG, Hordijk W, Salamin N, Guisan A (2016) ecospat: an R package to support spatial analyses and modelling of species niches and distributions. Ecography 40:774–787
21. Dietz H, Edwards PJ (2006) Recognition that causal processes change during plant invasion helps explain conflicts in the evidence. Ecology 87:1359–1367
22. Dillon ME, Wang G, Huey RB (2010) Global metabolic impacts of recent climate warming. Nature 467:704–706

23. Dreyer JBB, Higuchi P, Carolina silva A (2019) *Ligustrum lucidum* W. t. Aiton (broad-leaf privet) demonstrates climatic niche shifts during global-scale invasion. Sci Rep 9:3813. https://doi.org/10.1038/s41598-019-40531-8
24. Edelaar P, Roques S, Hobson EA, Gonçalves da Silva A, Avery ML, Russello MA, Senar JC, Wright TF, Carrete M, Tella JL (2015) Shared genetic diversity across the global invasive range of the monk parakeet suggests a common restricted geographic origin and the possibility of convergent selection. Mol Ecol 24:2164–
25. Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. Annu Rev Ecol Evol Syst 40:677–697
26. Fernandes AM, Wink M, Sardelli C, Aleixo A (2014) Multiple speciation across the Andes and throughout Amazonia: the case of the spot-backed antbird species complex (*Hylophylax naevius/Hylophylax naevioides*). J Biogeogr 41:1094–1104
27. Fitzpatrick MC, Hargrove WW (2009) The projection of species distribution models and the problem of non-analog climate. Biodivers Conserv 18:2255. https://doi.org/10.1007/s10531-009-9584-8
28. Fontanilla IKC, Sta. Maria IMP, Garcia JRM, Ghate H, Naggs F, Wade CM (2014) Restricted Genetic Variation in Populations of *Achatina (Lissachatina) fulica* outside of East Africa and the Indian Ocean Islands Points to the Indian Ocean Islands as the Earliest Known Common Source. PLoS ONE 9(9):e105151. https://doi.org/10.1371/journal.pone.0105151
29. Fourcade Y, Engler JO, Rödder D, Secondi J (2014) Mapping Species Distributions with MAXENT Using a Geographically Biased Sample of Presence Data: A Performance Assessment of Methods for Correcting Sampling Bias. PLoS ONE 9:e97122. https://doi.org/10.1371/journal.pone.0097122
30. Gallagher RV, Beaumount LJ, Hughes L, Leishman MR (2010) Evidence for climatic niche and biome shifts between native and novel ranges in plant species introduced to Australia. J Ecol 98:1126–1136
31. Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD (2010) A framework for community interactions under climate change. Trends in Ecology and Evolution 25:325–331. https://doi.org/10.1016/j.tree.2010.03.002
32. Goncalves E, Herrera I, Duarte M, Bustamante RO, Lampo M, Velásquez G, Sharma GP, García-Rangel S (2014) Global invasion of *Lantana camara*: Has the climatic niche been conserved across continents? PLoS ONE 9(10):e111468. https://doi.org/10.1371/journal.pone.0111468
33. Gregoric DEG, Núñez V, Vogler R, Rumi R (2011) Invasion of the Argentinean Paranense Rainforest by the Giant African Snail *Achatina fulica*. Am Malacological Bull 29:135–137
34. Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AI, Regan TJ, Brotons L, McDonald-Madden E, Mantyka-Pringle C, Martin TG, Rhodes JR, Maggini R, Setterfield SA, Elith J, Schwartz MW, Wintle BA, Broennimann O, Austin M, Ferrier S, Kearney MR, Possingham HP, Buckley YM (2013) Predicting species distributions for conservation decisions. Ecol Lett 16:1424–1435. https://doi.org/10.1111/ele.12189

35. Hagenblad J, Hülskötter J, Acharya KP, Brunet J, Chabrerie O, Cousins SAO, Dar PA, Diekmann M, De Frenne P, Hermy M, Jamoneau A, Kolb A, Lemke I, Plue J, Reshi ZA, Graae BJ (2015) Low genetic diversity despite multiple introductions of the invasive plant species *Impatiens glandulifera* in Europe. *BMC Genetics*, 16, 103. https://doi.org/1010.1186/s12863-015-0242-8
36. Holt RD (1990) The microevolutionary consequences of climate change. Trends in Ecology and Evolution 5:311–315
37. Hulme M (2014) Why we should disagree about climate change. In: Fiona C, Neilson B (eds) Climate Change and Museum Futures. Routledge, pp 9–15. https://doi.org/10.4324/9780203752975
38. Hulme PE (2017) Climate change and biological invasions: evidence, expectations, and response options. Biol Rev 92:1297–1313. https://doi.org/10.1111/brv.12282
39. Ihlow F, Secondi CJ, Herrel J, Rebelo A, Measey R, Lillo GJ, De Villiers F, Vogt AF, Busschere S, Backeljau C, Rödder D (2016) Impacts of climate change on the global invasion potential of the African clawed frog *Xenopus laevis*. PLoS ONE 11(6):e0154869. https://doi.org/10.1371/journal.pone.0154869
40. IUCN Works (2016), Jan 15 Invasive species. Retrieved from https://www.iucn.org/theme/species/our-work/invasive-species
41. Joshi M, Charles B, Ravikanth G, Aravind NA (2017) Assigning conservation value and identifying hotspots of endemic rattan diversity in the Western Ghats, India. Plant Divers 39:263–272. https://doi.org/10.1016/j.pld.2017.08.002
42. Kramer-Schadt S, Niedballa J, Pilgrim JD, Schröder B, Lindenborn J, Reinfelder V, Stillfried M, Heckmann I, Scharf AK, Augeri DM, Cheyne SM, Hearn AJ, Ross J, Macdonald DW, Mathai J, Eaton J, Marshall AJ, Semiadi G, Rustam R, Bernard H, Alfred R, Samejima H, Duckworth JW, Breitenmoser-Wuersten C, Belant JL, Hofer H, Wilting A (2013) The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions*, 19, 1366–1379
43. Kumar S, Graham J, West AM, Evangelista PH (2014) Using district-level occurrences in MaxEnt for predicting the invasion potential of an exotic insect pest in India. *Computer in Electronics and Agriculture*, 103, 55–62
44. Lauzeral C, Leprieur F, Beauchard O, Duron Q, Oberdorff T, Brosse S (2011) Identifying climatic niche shifts using coarse-grained occurrence data: A test with non-native freshwater fish. Glob Ecol Biogeogr 20:407–414. https://doi.org/10.1111/j.1466-8238.2010.00611.x
45. Lopez JLB, Estrada E, Romero CE, Me´ndez U, Rodrıguez S, Goyenechea JJM, Castillo Ceron JM (2017) Evidence of niche shift and invasion potential of *Lithobates catesbeianus* in the habitat of Mexican endemic frogs. PLoS ONE 12(9):e0185086. https://doi.org/10.1371/journal.pone.0185086
46. Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the World's Worst Invasive Alien Species. Published by The Invasive Species Specialist Group ISSG. https://doi.org/10.1614/WT-04-126.1
47. McMahon SM, Harrison SP, Armbruster WS, Bartlein PJ, Beale CM, Edwards ME, Kattge J, Midgley G, Morin X, Prentice C (2011) Improving assessment and modelling of climate change impacts on

global terrestrial biodiversity. Trends in Ecology and Evolution 26:249–259. https://doi.org/10.1016/j.tree.2011.02.012

48. Sean M McMahon1 andy P.Harrison2 W. ScottArmbruster31213 Patrick J.Bartlein4 Colin M. Beale5 Mary E.Edwards6 Jens Kattge7 GuyMidgley8 XavierMorin910I. Colin Prentice211
49. Mead AR (1961) The giant African snail: a problem in economic malacology. Chicago, University of Chicago Press
50. Mead AR (1979) Pulmonates volume 2B. Economic malacology with particular reference to *Achatina fulica*. Academic Press, London
51. Medley KA (2010) Niche shifts during the global invasion of the Asian tiger mosquito, *Aedes albopictus* Skuse (Culicidae), revealed by reciprocal distribution models. Glob Ecol Biogeogr 19:122–133. https://doi.org/10.1111/j.1466-8238.2009.00497.x
52. Moore BA (2005) Alien invasive species: impacts on forests and forestry. A review. Forest Health and Biosecurity Working Paper FBS/8E. Forestry Department, FAO, Rome
53. Moss RH, Edmonds JA, Hibbard KA, Manning MR, Rose SK, van Vuuren DP et al (2010) The next generation of scenarios for climate change research and assessment. Nature 463:747–756
54. Muniappan R (1973) Biological control of the giant African snail. Alafua Agricultural Bulletin 8:13–46
55. NASA Jet Propulsion Laboratory (JPL) (2013) NASA Shuttle Radar Topography Mission Global 3 arc second. Version 3. 6°S, 69°W NASA EOSDIS Land Processes DAAC, USGS Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota (https://lpdaac.usgs.gov), accessed January 1, 2018, at https://doi.org/10.5067/MEaSUREs/SRTM/SRTMGL3.003
56. Ning S, Wei J, Feng J (2017) Predicting the current potential and future worldwide distribution of the onion maggot, *Delia antiqua* using maximum entropy ecological niche modeling. PLoS ONE 12(2):e0171190. doi:10.1371/journal.pone.0171190
57. Parmesan C, Possingham HP, Thomas CD (2008) Assisted colonisation and rapid climate change. Science 321:345–346
58. Pearman B, Randin CF, Broennimann O, Vittoz P, Van der Knaap WO, Engler R, Lay GL, Zimmermann NE, Guisan A (2008) Prediction of plant species distributions across six millennia. Ecol Lett 11:357–369
59. Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J Biogeogr 34:102–117
60. Pereira HM, Leadley PW, Proenca V, Alkemade R, Scharlemann JPW, Fernandez-Manjarres JF et al (2010) Scenarios for global biodiversity in the 21st century. Science 330:1496–1501
61. Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C, Guisan A (2012) Climatic niche shifts are rare among terrestrial plant invaders. Science 335:1344–1348. https://doi.org/10.1126/science.1215933

62. Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026
63. Phillips SJ, Dudík M, Schapire RE (2004) A maximum entropy approach to species distribution modeling. In Twenty-first international conference on Machine learning - ICML '04. https://doi.org/10.1145/1015330.1015412
64. Pyke CR, Thomas R, Porter RD, Hellmann JJ, Dukes JS, Lodge DM, Chavarria G (2008) Current practices and future opportunities for policy on climate change and invasive species. Conserv Biol 22:585–592. https://doi.org/10.1111/j.1523-1739.2008.00956.x
65. R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/
66. Raut SK, Barker GM (2002) *Achatina fulica* Bowdich and Other Achatinidae as Pests in Tropical Agriculture. In: Raut S, Barker GM (eds) Mollusks as Crop Pest. Landscare Research, Hamilton, New Zealand, pp 55–114
67. Rodda GH, Jarnevich CS, Reed RN (2011) Challenges in identifying sites climatically matched to the native ranges of animal invaders. PLoS ONE 6(2):e14670. doi:10.1371/journal.pone.0014670
68. Roman J, Darling JA (2007) Paradox lost: genetic diversity and the success of aquatic invasions. Trends Ecol Evol 22:454–464
69. Salamin N, Wuest RO, Lavergne S, Thuiller W, Pearman PB (2010) Assessing rapid evolution in a changing environment. Trends Ecol Evol 25:692–698
70. Sarma RR, Munsi M, Aravind NA (2015) Effect of climate change on invasion risk of giant African snail (*Achatina fulica* Férussac, 1821: Achatinidae) in India. PLoS ONE 10(11):e0143724. https://doi.org/10.1371/journal.pone.0143724
71. Schoener TW (1970) Non-synchronous Spatial Overlap of Lizards in Patchy Habitats. Ecology 51:408–418. https://doi.org/10.2307/1935376
72. Schotman CYL (1989) Plant pests of quarantine importance to the Caribbean, vol 21. RLAC-PROVEG, p 80
73. Shabani F, Kumar L (2015) Should species distribution models use only native or exotic records of existence or both? Ecol Inf 29:57–65
74. Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M (2013) Impacts of biological invasions: What is what and the way forward. Trends Ecol Evol 28:58–66
75. Soberón J (2007) Grinnellian and Eltonian niches and geographic distributions of species. Ecol Lett 10:1115–1123
76. Sridhar V, Vinesh LS, Jayashankar M (2014) Mapping the potential distribution of *Achatina fulica* (Bowdich) (Stylommatophora: Achatinidae) in India using CLIMEX, a bioclimatic software. Pest Manage Hortic Ecosyst 20:14–21

77. Strubbe D, Broennimann O, Chiron F, Matthysen E (2013) Niche conservatism in non-native birds in Europe: Niche unfilling rather than niche expansion. Glob Ecol Biogeogr 22:962–970. https://doi.org/10.1111/geb.12050
78. Strubbe D, Jackson H, Groombridge J, Matthysen E (2015) Invasion success of a global avian invader is explained by within-taxon niche structure and association with humans in the native range. Divers Distrib 21:675–681. https://doi.org/10.1111/ddi.12325
79. Swets JA (1988) Measuring the accuracy of diagnostic systems. Science 240:1285–1293
80. Syfert MM, Coomes DA (2013) The Effects of Sampling Bias and Model Complexity on the Predictive Performance of MaxEnt Species Distribution Models. PLoS ONE 8(2):e55158. https://doi.org/10.1371/journal.pone.0055158
81. Thiengo SC, Faraco FA, Salgado NC, Cowie RH, Fernandez MA (2007) Rapid spread of an invasive snail in South America: the giant African snail, *Achatina fulica*, in Brasil. Biol Invasions 9:693–702
82. Tingley R, Vallinoto M, Sequeira F, Kearney MR (2014) Realised niche shift during a global biological invasion. *Proceedings of National Academy of Sciences*, 111, 10233–10238. https://doi.org/10.1073/pnas.1405766111
83. Turner GI (1964) Transmission by snails of the species *Phytophthora* which causes foot tot of *Piper nigrum* L. in Sarawak. Nature 202:1133
84. Turner GI (1967) Snail transmission of the species of *Phytopthora* with special reference to foot rot in *Piper nigrum*. Mycol Res 50:251–258
85. Veloz SD (2009) Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. J Biogeogr 36:2290–2299
86. Verbruggen H, Tyberghein L, Belton GS, Mineur F, Jueterbock A, Hoarau G, Gurgel CFD, De Clerck O (2013) Improving Transferability of Introduced Species' Distribution Models: New Tools to Forecast the Spread of a Highly Invasive Seaweed. PLoS ONE 8(6):e68337. https://doi.org/10.1371/journal.pone.0068337
87. Vogler RE, Beltramino AA, Sede MM, Gutiérrez Gregoric DE, Núñez V, Rumi A (2013) The giant African snail, Achatina fulica (Gastropoda: Achatinidae): Using bioclimatic models to identify South American areas susceptible to invasion. Am Malacological Bull 31:39–50
88. Walther GR, Roques A, Hulme PE, Sykes MT, Pysek P, Kühn I, Zobel M, Bacher S, Botta-Dukát Z, Bugmann H, Czúcz B, Dauber J, Hickler T, Jarosík V, Kenis M, Klotz S, Minchin D, Moora M, Nentwig W, Ott J, Panov VE, Reineking B, Robinet C, Semenchenko V, Solarz W, Thuiller W, Vilà M, Vohland K, Settele J (2009) Alien species in a warmer world: risks and opportunities. Trends in Ecology and Evolution 24:686–693
89. Wan JZ, Wang CJ, Tan JF, Yu FH (2017) Climatic niche divergence and habitat suitability of eight alien invasive weeds in China under climate change. Ecol Evol 7:1541–1552. https://doi.org/10.1002/ece3.2684
90. Wan JZ, Wang CJ, Yu FH (2016) Impacts of the spatial scale of climate data on the modeled distribution probabilities of invasive tree species throughout the world. Ecol Inf 36:42–49

91. Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conserveatism: Quantitative approaches to niche evolution. Evolution 62:2868–2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x
92. Wei J, Zhang H, Zhao W, Zhao Q (2017) Niche shifts and the potential distribution of *Phenacoccus solenopsis* (Hemiptera: Pseudococcidae) under climate change. PLoS ONE 12(7):e0180913. doi:10.1371/journal.pone.0180913
93. Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Davies TJ, Grytnes J, Harrison SP, Hawkins BA, Holt RD, McCain CM, Stephens PR (2010) Niche conservatism as an emerging principle in ecology and conservation biology. Ecol Lett 13:1310–1324. https://doi.org/10.1111/j.1461-0248.2010.01515.x
94. Wiens JJ, Graham CH (2005) Niche Conservatism. Integrating evolution, ecology, and conservation biology. Annu Rev Ecol Evol Syst 36:519–539. doi:10.1146/annurev.ecolsys.36.102803.095431
95. Lira-Noriega A, Soberón J, Peterson T, Falconi A, Contreras-Díaz M, Martínez-Meyer RG, Barve E, Barve N (2020) ntbox: an R package with graphical user interface for modeling and evaluating multidimensional ecological niches. Methods Ecol Evol 11:1199–1206. doi:10.1111/2041-210X.13452. https://github.com/luismurao/ntbox
96. Hagenblad J, Hülskötter J, Acharya KP, Brunet J, Chabrerie O, Cousins SA, Dar PA, Diekmann M, De Frenne P, Hermy M, Jamoneau A (2015) Low genetic diversity despite multiple introductions of the invasive plant species Impatiens glandulifera in Europe. BMC Genet 16(1):103–105
97. Roda A, Millar JG, Jacobsen C, Veasey R, Fujimoto L, Hara A et al (2019) A new synthetic lure for management of the invasive giant African snail, Lissachatina fulica. PLoS ONE 14(10):e0224270. https://doi.org/10.1371/journal.pone.0224270
98. Creswell DC, Kompiang IP (1981) Studies on Snail Meal as a Protein Source for Chickens: 1. Chemical Composition, Metabolizable Energy, and Feeding Value for Broilers. Metabolism and Nutrition 60:1854–1860
99. NAIR MRGK, JACOB A (1968) Use of metaldehyde as duts and sprays to control the giant African snail Achatina fulica Bowdich. Indian j entomol 30:58–60
100. PANIGRAHI A, RAUT SK (1994) Thevetia peruviana (Family; Apocynaceae) in the control of slug and snail pests. Mem Inst Oswaldo Cruz 89:247–250
101. RAUT SG, GOSHE KC (1984) Pestiferous land snails of India. Zoological Survey of India N° 11. Bani Press, Calcuta, p 151
102. Nelson S (2012) Injuries Caused by the Giant African Snail to Papaya. Miscellaneous Pests, June 2012, MP-6, pp. 1–7
103. Uma Shaanker R, Gladwin Joseph NA, Aravind R, Kannan, Ganeshaiah KN (2010) Invasive plants in tropical human dominated landscapes: need for a paradigm shift in their management. In: Perrings C, Mooney H, Williamson M (eds) Bioinvasions and Globalization: Ecology, Economics, Management, and Policy. Oxford University Press, London, pp 202–219

Figures

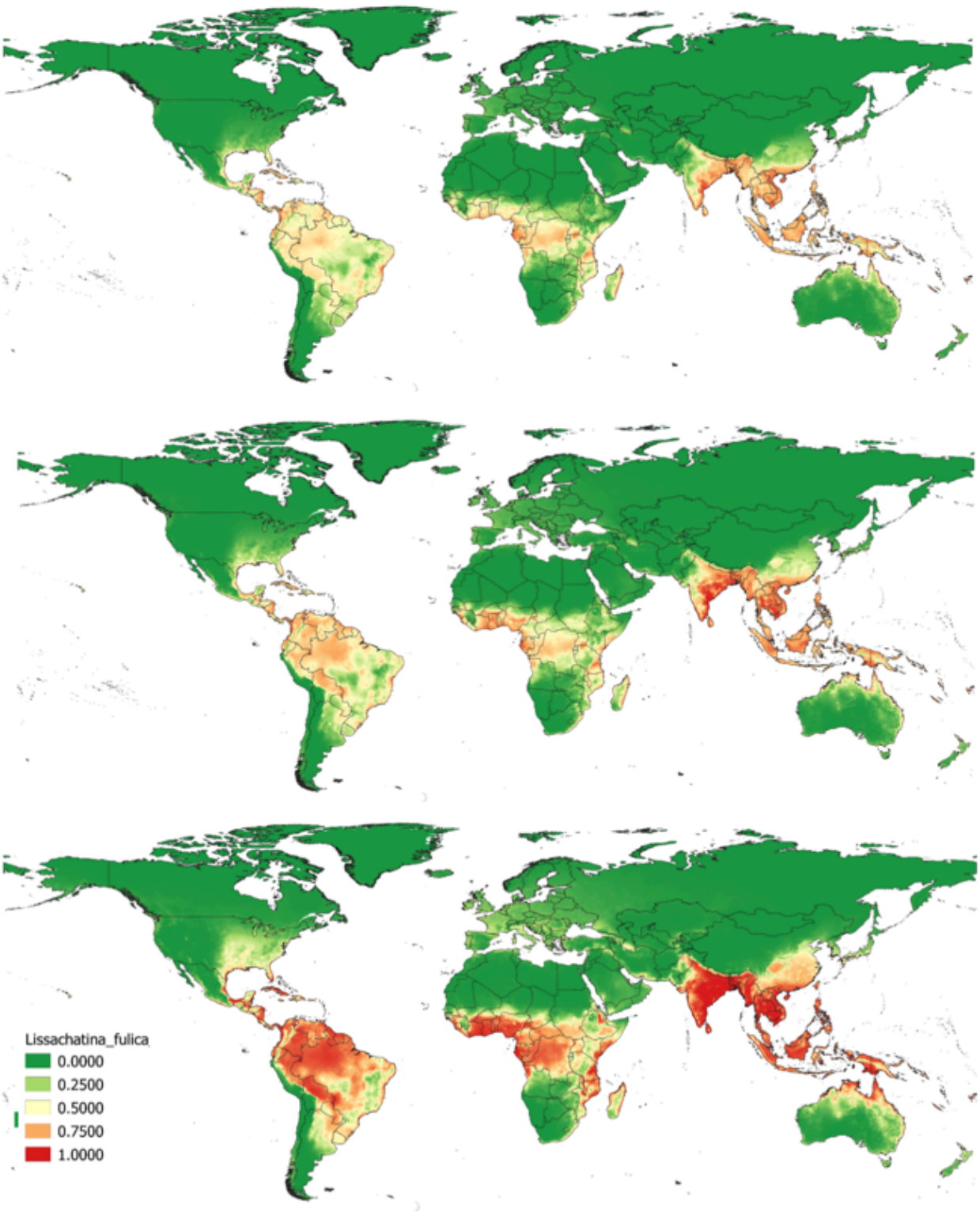


Figure 1

Potential distribution of *L. fulica* under present (A), SSP2.6 (B) and SSP 8.5 (C)

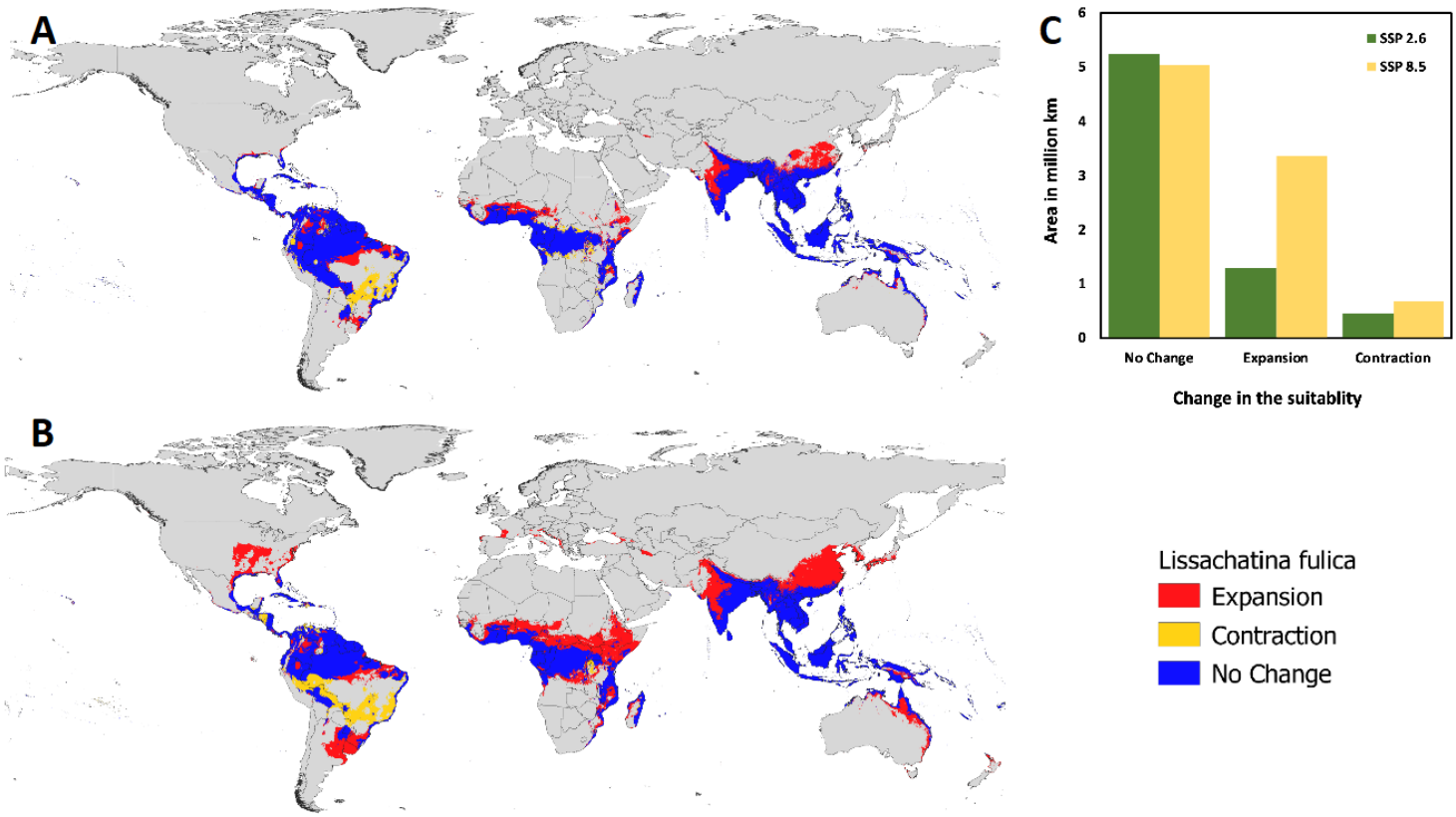


Figure 2

Change in the suitability from current scenario to SSP 2.6 (a) and SSP 8.5 (b). Total area change is in millions of kilometres is given in (c).

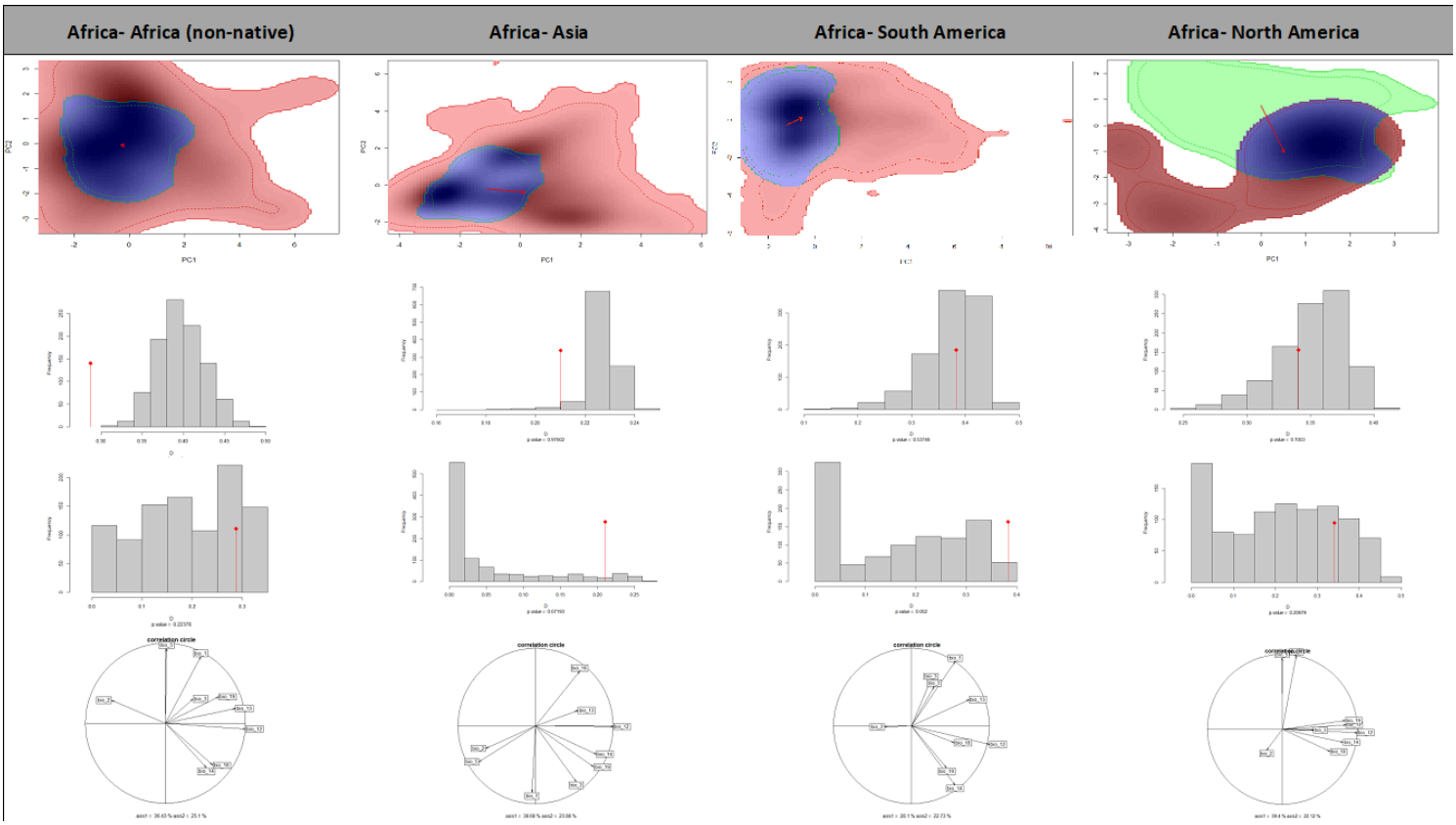


Figure 3

Summary of Niche conservatism test analysis. **(a)** The density of species occurrences in native (Africa) vs introduced regions of the world. The solid and dashed lines show 100% and 50% of the available (background) environment. The blue colour indicates the niche overlap between native and introduced regions; the green colour indicates niche unfilling and the red colour niche expansion. The red arrow indicates the change in the niche centroid between native and Introduced range and centroid shift between native and introduced region, **(b-c)** niche equivalency and similarity tests and **(d)** The correlation circle shows the variable importance along the first two principal axes.

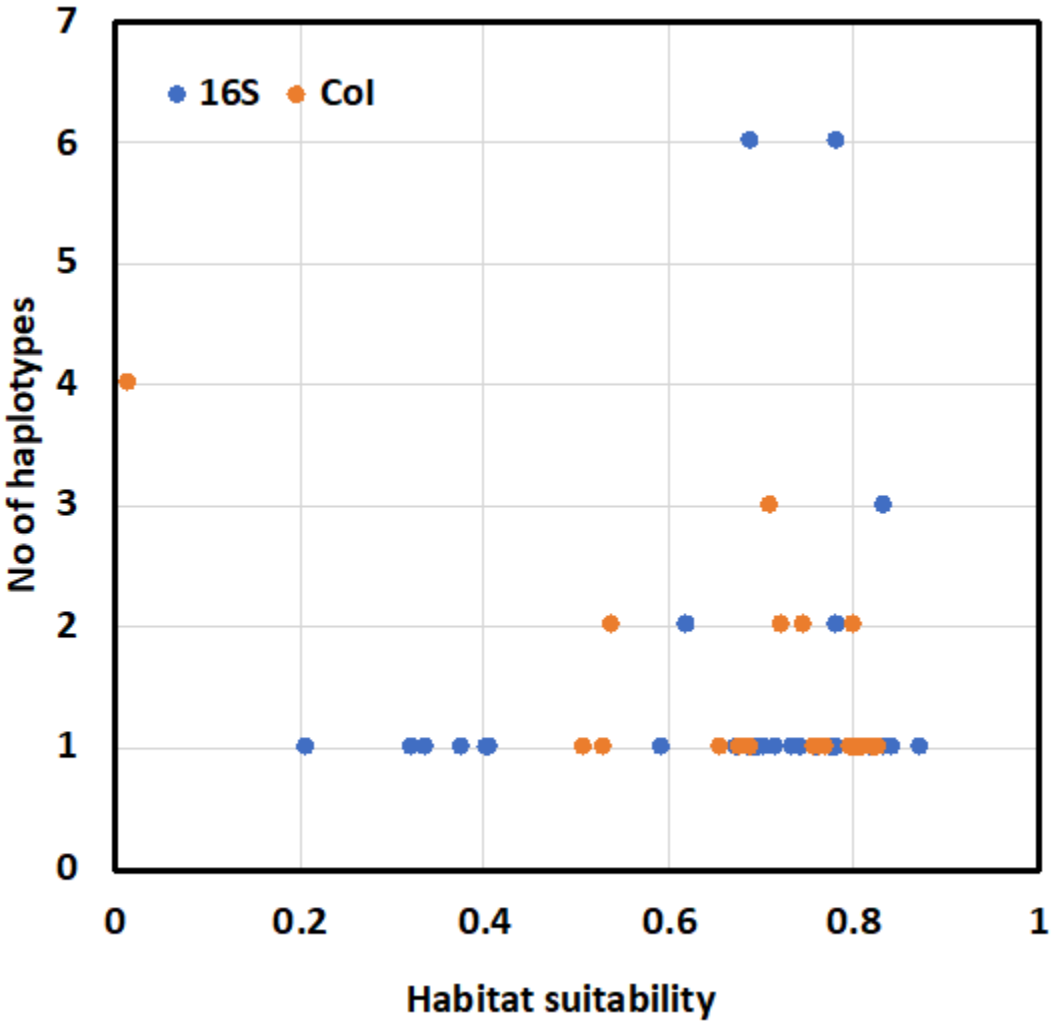


Figure 4

Habitat suitability versus haplotype richness for L. fulica at the global level. The vertical dashed line indicates a 10% training threshold derived from maxent output for the current climatic scenario