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Current and projected future risks of freshwater fish invasions in China

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Biological invasions are a primary threat to global biodiversity, supporting mounting calls for the development of early-warning systems to manage existing and emerging invaders. Here, we evaluated the geographical pattern of invasion risks of currently established and potentially emerging nonnative freshwater fishes in China by jointly considering the threats of introduction and establishment under climate change. Introduction threats were estimated according to proxies of human activities and propagule pressure for two primary pathways (aquaculture or ornamental). Establishment threats for 51 current and 64 potential invaders (based on whether having established or not self-sustaining populations) were assessed using an ensemble of species distribution models under current (1960–1990) and future [2041–2060 (2050s) and 2061–2080 (2070s)] climate scenarios. Geographical patterns of invasion risk were then assessed by overlaying the threats of introduction and establishment for each species group both in present-day and in the future. We found that eastern China displayed the highest threat of introduction. By contrast, southeastern and northwestern regions were identified as the most suitable for the establishment of both current and potential invaders. Under a changing climate, 83 out of 115 species displayed an increase in habitat suitability, resulting in an overall increase of 4.8% by 2050s and 7.1% by 2070s in the extent of suitable habitat for nonnative freshwater fishes. Taken together, invasion risk was found to be highest in southeastern China and lowest in the Tibet Plateau. Our research highlights the importance of assessing invasion risk by integrating the threats associated with the introduction and establishment stages. In particular, our findings revealed convergent patterns of invasion risk between current and potential nonnative freshwater fishes under climate change. Geographic patterns in hotspots of existing and emerging invasions provide critical insights to guide the allocation of resources to monitor and control existing and emerging invasions in China.

Keywords: emerging invasions, establishment threat, introduction pathway, invasion risk, nonnative species, species distribution models

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Introduction

Human activities have led to unprecedented rates of nonnative species introductions, causing significant ecological and evolutionary impacts and posing profound threat to national economies and human welfare (Early et al. 2016, Reid et al. 2019). Developing effective strategies to avoid or reduce the impacts of nonnative species is thus considered fundamental in national-level policies that seek to conserve biodiversity and ecosystem functioning in the future (O'Donnell et al. 2012, Early et al. 2016). Recent decades have witnessed mounting efforts to establish evidence-based regulations to limit species invasions (McGeoch et al. 2016). Given that the prevention of potential invaders is well-recognized as more effective than the eradication of established species, assessing the invasion risk of nonnative species in new areas has become a critical focus of invasion management (Lodge et al. 2006, Carboni et al. 2018). Early-warning systems are now considered among the most promising approaches to nonnative species management, thus facilitating the cost–effective management with limited resources (Hulme 2009).

Understanding what determines successful transition of species through the stages of the invasion continuum is important for targeted management of existing and emerging invasions (Olden et al. 2011, McGeoch et al. 2016). Of the many factors responsible for invasion risk of nonnative species, the introduction pathways (which describe how species are introduced, intentionally or unintentionally, to a new location) and environmental suitability in the recipient ecosystem are paramount (Larson and Olden 2012, Carboni et al. 2018, Cassey et al. 2018). Moreover, ongoing climate change is expected to relax or set the constraints limiting the distributions of nonnative species, leading to remarkable differences between current and future patterns of invasion risk (Rahel and Olden 2008, Walther et al. 2009). Accurate evaluation of invasion risk requires the dual consideration of the threat of dominant introduction pathways and the likelihood of establishment under current and projected future climates.

Species distribution models (SDMs) have emerged as a promising tool to quantify the geographical patterns of invasion risk both now and in the future (Yates et al. 2018). SDMs have been extensively used for predicting environmental suitability of nonnative species in new areas (Olden et al. 2011, Larson and Olden 2012) or under future climates (Li et al. 2016, Dullinger et al. 2017), with important implications for environmental policy and biodiversity management. However, previous research identified 'invasion hotspots' by focusing solely on the habitat suitability of nonnative species in introduced ranges (O'Donnell et al. 2012, Bellard et al. 2013). Although such analyses provide valuable information on the threat of establishment, their value to guide local conservation efforts is more limited because few introduction opportunities may exist in highly suitable areas (McGeoch et al. 2016).

Developing economies often face shortages in financial resources to manage biological invasions, even though these regions may face increasing invasion risks in the future (Early et al. 2016). For example, with intensifying economic development and anthropogenic activities, biological invasions are threatening China's biodiversity with unparalleled magnitude (Liu et al. 2003, 2017a, Lin et al. 2015). As part of the convention on biological diversity (CBD), China has established an ambitious plan to control biological invasions in the next decades [China National Biodiversity Conservation Strategy and Action Plan (2011–2030)], including the objective to 'Improve capacity of early warning, emergency response and monitoring of invasive alien species' (Action 23). Achieving this goal necessitates an integrative assessment of invasion risk of both currently established and potentially emerging nonnative species at a national scale.

Species invasions are the leading threat to freshwater ecosystems (Reid et al. 2019). Extensive species introductions have triggered remarkable changes in fish community structure, including the homogenization of historically-isolated species pools at national (Rahel 2000), continental (Olden et al. 2008) and global (Villéger et al. 2011) scales. This is particularly true in China, where accelerating aquaculture practices and trade activities (Lin et al. 2015, Xiong et al. 2015) have resulted in widespread establishment of nonnative fishes and fundamental changes in biodiversity (Liu et al. 2017a). To address gaps in scientific knowledge and support policy initiatives, this study aimed to reveal current and future geographical patterns of invasion risk for freshwater fishes in China. We assessed invasion risk posed by current and potential nonnative fish species by considering both the threats from introduction (i.e. human-induced releases and escape in the wild, both intentional and unintentional) and establishment (i.e. environmental suitability) under current and projected future climates. We focused specifically on invaders through aquaculture and ornamental pet trade, which are the two most important pathways of nonnative fish introductions in China (Xiong et al. 2015). We hope this study will help inform the development of proactive strategies to monitor the transportation, arrival and spread of problematic species.

Material and methods

Species status and occurrence records

We assembled the list of the nonnative freshwater fish species that have been introduced in China from abroad (i.e. historically absent from China's hydrographic basins) and classified each species according to the primary introduction pathway and establishment status based on the comprehensive compilation of Xiong et al. (2015). More specifically, we considered species introduced through aquaculture production and ornamental pet trade, and classified species as 1) 'current invaders' if self-sustaining populations were established in the wild, and 2) 'potential invaders' if present in the country but not established in the wild (see Xiong et al. 2015 for more details). To increase the realism of the pool of potential invaders, we further reduced the list of 442 fish species to only those that have established populations outside of their native ranges (293 species) according to the list provided in Liu et al. (2017b). Note that here we used a biogeographically-based definition of invaders, as opposed to an impact-based criterion (Valéry et al. 2008), and thus did not intend to characterize any impact associated with biological invasions on the functioning of recipient communities/ecosystems.

We compiled occurrence records for each species from 1) the Global Biodiversity Information Facility (GBIF; available at <www.gbif.org>), 2) FishBase (available at <www.fishbase.org>) and 3) published records collected from the literature (see Supplementary material Appendix 1 Table A1 including species origin). Importantly, we compiled occurrences across both native and nonnative ranges to account for potential non-equilibrium environmental conditions in the new range (Guisan and Thuiller 2005) or potential shifts in climatic niche (Broennimann and Guisan 2008), which can both impair the performance of SDMs. To avoid imbalance and sampling biases in spatial coverage (Dormann et al. 2007), we further supplemented our datasets with occurrences derived from the International Union for Conservation of Nature range maps (IUCN 2014). Although subject to approximation, expert-based range maps provide a reasonably accurate source of information for the distribution of species with deficient occurrence data at a global scale (Fourcade 2016). This was confirmed by the improvement in model performance observed when incorporating this additional set of occurrences to our initial dataset (Supplementary material Appendix 1 Table A2).

All occurrences were carefully examined to eliminate records with likely erroneous coordinates (e.g. by comparing the country where the coordinates fell versus the 'country' field in GBIF) as well as records that did not overlap with the presence of water. To do so, the distribution of fresh waters was delineated according to multiple data sources: 1) hydrological maps of SHuttle Elevation Derivatives at multiple Scales (HydroSHEDS; Lehner et al. 2008), 2) Global Lakes and Wetlands Database dataset (Lehner and Döll 2004) and 3) HYDRO1k (U.S. Geological Survey 2000). To reduce the influence of potential sampling bias, we geographically filtered all occurrences at a resolution of 2.5 arc-minutes (ca 4.7 km at the equator), by randomly choosing for each species one occurrence per grid cell. This allowed to level the degree of spatial aggregation in species occurrences at a biologically relevant scale (i.e. the median parent–offspring dispersal distance for riverine fishes is ~6 km; Comte and Olden 2018). Finally, we only kept species with sufficient data to calibrate the SDMs (Wisz et al. 2008), using a threshold of 30 occurrences as suggested by van Proosdij et al. (2016). This resulted in a final selection of 39 current aquaculture species, 12 current ornamental species, 21 potential aquaculture species and 43 potential ornamental species (Supplementary material Appendix 1 Table A1). The origin of these species is diverse with North America contributing the greatest number of current invaders (41%), and Asia (27%), North America (23%) and South America (22%) demonstrating the most potential invaders.

Climate data

We obtained the data of 19 bioclimatic variables describing current (1960–1990) and future climatic conditions for mid- (2041–2060; hereafter 2050s) and end-century (2061–2080; hereafter 2070s) at the worldwide scale from WorldClim at a 2.5 arc-minutes resolution (Supplementary material Appendix 1 Table A3, Hijmans et al. 2005). Future climate scenarios were based on the Representative Concentration Pathway (RCP) 8.5 ('business as usual') according to a multi-model ensemble based on four Global Circulation Models (GCMs; HadGEM2-CC, MPI-ESM-LR, MIROC-ESM and CCSM4) that had demonstrated good performance in China (Chen and Frauenfeld 2014). Climate projections were averaged across the four GCMs because evidence points to the better performance of multi-model ensemble mean compared to individual GCMs (Jiang et al. 2016). To avoid problems of variable collinearity in subsequent analyses and ensure good performance of SDMs, we used a Principal Component Analysis (PCA) to decrease collinearity between the predictors following Petitpierre et al. (2017). We performed a PCA using the full set of 19 variables under current climate scenario (Supplementary material Appendix 1 Table A3). The six variables corresponding to the first six components of the PCA were then used as new composite predictors to calibrate the SDMs (Supplementary material Appendix 1 Table A4). The composite predictors for each future climate scenario (2050s or 2070s) were then obtained by projecting the corresponding bioclimatic variables into the multi-dimensional PCA climatic space. The PCA was only performed for grid cells overlapping with the presence of water (using the same procedure than for species records, see above).

Species distribution models

Algorithms

To take into account the strengths and weaknesses of individual models, we used an ensemble modeling approach (Araújo and New 2007) based on two regression-based (Generalized Linear Model and General Additive Model) and three machine-learning (Generalized Boosting Model, Random Forest and MaxEnt) models in the 'BIOMOD' platform (Thuiller et al. 2009) in R (R Development Core Team 2016). These five techniques have been demonstrated utility in their capacity to model complex relationships and display strong transferability in novel conditions (Elith et al. 2006, Heikkinen et al. 2012).

Environmental filtering

To further minimize the effect of sampling bias, we performed an environmental filtering of the occurrence datasets (Varela et al. 2014). For each species, we constructed a two-dimensional space defined by the first two axes of a

PCA based on the 19 bioclimatic variables associated with the presence records. We then divided this climatic space into 100×100 grid cells and randomly selected one occurrence per grid cell. Although arbitrary, the choice of the resolution and dimensionality was dictated by a compromise between biological meaningfulness, data interpretability and technical feasibility (Broennimann et al. 2012). We repeated this procedure 20 times to generate 20 presence datasets for each species.

Pseudo-absences

Following the recommendations of Barbet-Massin et al. (2012), the number of pseudo-absences was set to 10 000 for the regression-based models and MaxEnt, and equal to the number of presences for the two other machine-learning methods. As pseudo-absences generated from large geographic areas can reduce model performance, we created minimum area convex polygons encompassing the most concentrated regions of presences and randomly selected the pseudo-absences as any cell falling from 10 to 200 km away from the presences within these polygons (following VanDerWal et al. 2009). Similar to the selection of occurrences, the models were trained using pseudo-absences selected across both native and nonnatives ranges to improve model performance as shown by Mainali et al. (2015). We repeated this procedure for each presence dataset to generate 20 corresponding pseudo-absence datasets for each species.

Model performance

The performance of each model was evaluated using a repeated five times split-sampling approach, i.e. the model was calibrated using 80% of the data and evaluated using the remaining 20%. Model performance was evaluated using two well-established metrics: the area under the ROC curve (AUC; Fielding and Bell 1997) and the true skill statistics (TSS; Allouche et al. 2006). Overall, individual models showed a good to very good performance for all species, with a mean AUC value of 0.90 ($\pm$0.02 SD) and TSS value of 0.73 ($\pm$0.04 SD). In addition, we found similar model performances between native (mean TSS = 0.85 ± 0.04 SD) and introduced (mean TSS = 0.80 ± 0.04 SD) ranges (paired t-test, $t = 0.13$, $df = 48$, $p = 0.89$), indicating a good transferability of the models (see also Supplementary material Appendix 1 Table A2).

Assessing invasion risk

Introduction threat

The number of potential releases and escapes through aquaculture was described using a combination of local aquaculture production and water accumulation along the upstream–downstream gradient (Gozlan 2008). Aquaculture production was obtained at the administrative (i.e. province) scale, which is the lowest spatial resolution available in China (Bureau of Fisheries, Ministry of Agriculture 2016). Data were then downscaled following the method of Early et al. (2016) by weighting the aquaculture production values per administrative unit by the human population density in a given grid cell (Fu et al. 2014). Water accumulation, describing the yield of water in each cell, was quantified as the number of cells containing fresh water upstream of the focal cell and was extracted from HydroSHEDS at a 2.5 arc-minutes resolution (Lehner et al. 2008). These two surrogates of introduction were then combined into a single layer describing the introduction threat for aquaculture species after log-transforming and scaling the original variables between zero and one. The introduction of ornamental species is tightly linked to the economic development level (Gozlan 2008, Early et al. 2016). We therefore used a gridded layer of the Gross Domestic Product (GDP; Huang et al. 2014 at 30 arc-seconds resolution) aggregated at a 2.5 arc-minutes resolution as a proxy of propagule pressure for ornamental species after log-transforming the original values and scaling the values between zero and one.

Establishment threat

Calibrated models were used to project the current and future environmental suitability of the 115 nonnative fish species across China's fresh waters. With 20 calibration datasets and five modeling algorithms, we obtained 500 different sets of predicted probabilities of presence for each species and each time horizon, which were subsequently combined using a weighted average approach based on the TSS values of the individual models (after excluding models with TSS < 0.6; Marmion et al. 2009). For each grid cell, we then quantified the overall threat of establishment as the sum of the probabilities of presence across all species, separately for each species group and climate scenario (Scherrer et al. 2017). To identify species-specific establishment threat, we calculated the extent of suitable habitat as the sum of the area of individual grid cells weighted by the probabilities of occurrence and expressed species establishment threat as a percentage of the total area covered by China's fresh waters (6.865×10^6 km^2).

Invasion risk

Geographical patterns of invasion risk were assessed separately for aquaculture and ornamental species by overlaying the threats of introduction and establishment across all grid cells. To do so, cells in each layer were classified into relative categories according to the following percentiles of the respective threats: very high (80–100%), high (60–80%), medium (40–60%), low (20–40%) and very low (0–20%). Areas with higher threats of both introduction and establishment were then identified as displaying a higher risk of invasion (i.e. invasion hotspots; Liu et al. 2019). We focused on the relative invasion risk to take into account the unavoidable uncertainty surrounding predictions of nonnative richness patterns at large spatial scale (Seebens 2019).

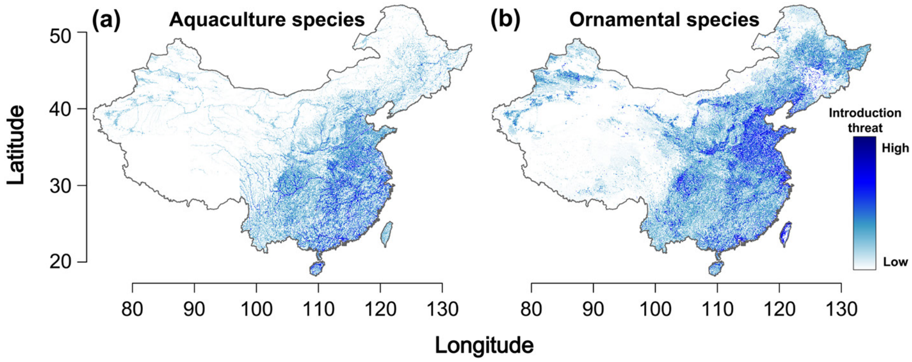

Figure 1. Geographical patterns of introduction threat for (a) aquaculture and (b) ornamental species. The color gradient represents the magnitude of introduction threat estimated according to aquaculture production and water accumulation for aquaculture species and according to Gross Domestic Product for ornamental species.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.63g03p8> (Liu et al. 2019) and Figshare (<https://doi.org/10.6084/m9.figshare.9751934>).

Results

Introduction threat showed marked spatial patterns across China. Eastern regions displayed the highest threats for both aquaculture and ornamental species, whereas northwestern China displayed a higher threat to aquaculture species (Fig. 1). By contrast, southeastern and northwestern China were identified as being the most susceptible to the establishment of nonnative fishes, irrespective of establishment status (current or potential) (Fig. 2a–d). The establishment threat was also particularly high in the northeastern for current aquaculture and potential ornamental species. The Tibet Plateau was predicted to be the least susceptible, especially to potential ornamental species.

Establishment threat was predicted to increase in most areas under both 2050s and 2070s climate scenarios (in 74.6% and 72.4% of grid cells respectively; Fig. 2e–l, Table 1). Under the 2050s scenario, the areas displaying increased susceptibility to nonnative species establishment were widely distributed in

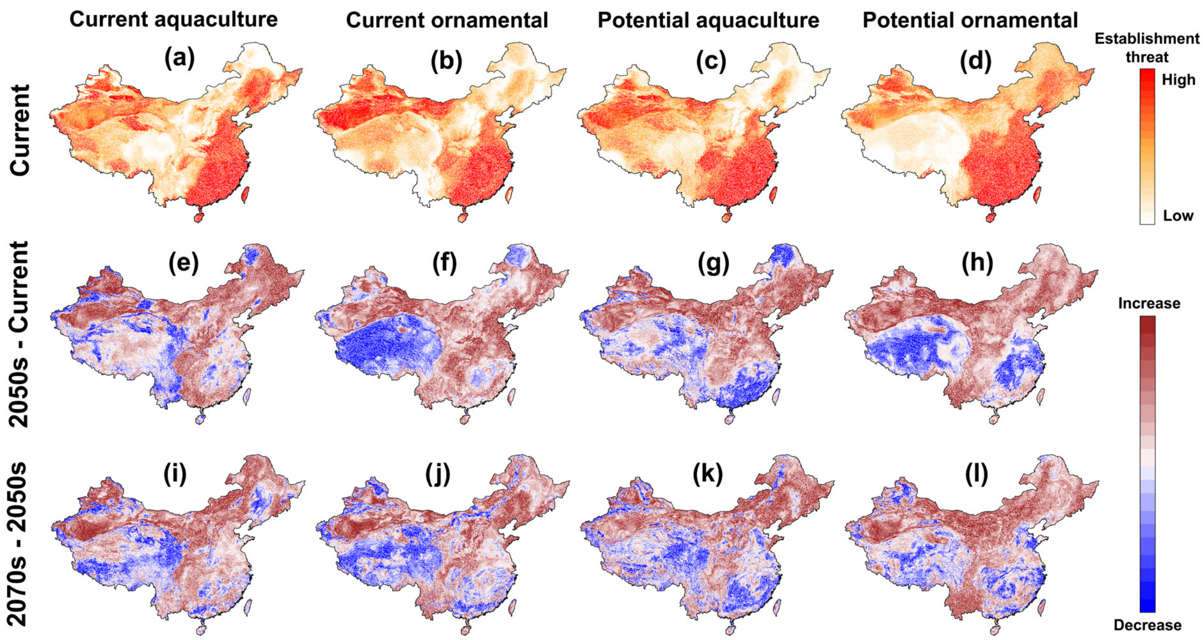

Figure 2. Establishment threat under current climatic conditions and changes in establishment threat assessed between two consecutive time periods (mid-panels: 2050s – current; bottom panels: 2070s–2050s) according to introduction pathways and establishment status: (a, e, i) current aquaculture species, (b, f, j) current ornamental species, (c, g, k) potential aquaculture species and (d, h, l) potential ornamental species. Color gradients represent the variables broken into their respective percentile classes for the magnitude of establishment threat and the changes between scenarios.

Table 1. The percentage (%) of cells with increased environmental suitability and species with increased establishment threat between two consecutive time periods (2050s–current and 2070s–2050s). Species are clustered into four groups based on introduction pathways and establishment status: current aquaculture species, current ornamental species, potential aquaculture species, potential ornamental species.

Group	Percentage of cells		Percentage of species	
	2050s–current	2070s–2050s	2050s–current	2070s–2050s
Current aquaculture	78.66	73.72	76.92	76.92
Current ornamental	70.54	68.35	58.33	58.33
Potential aquaculture	74.26	69.25	57.14	71.43
Potential ornamental	74.76	78.12	79.07	72.09

northern China (Fig. 2e–h), whereas western Tibet showed a decreased in establishment threat to ornamental species (Fig. 2f, h). Under the 2070s scenario, the north was predicted to experience a lower increase in establishment threat than compared to the 2050s scenario, and the areas displaying a decrease in establishment threat also became more dispersed across the country (Fig. 2i–l). Species-specific establishment threat was generally high, with the current extent of suitable areas of nonnative freshwater fishes representing on average of 34.1% (±12.8 SD) of China' fresh waters (Fig. 3). The extent of suitable habitat was further predicted to increase for most species (83 out of 115) in the future, with an average increase of 4.8% (±8.2 SD) by 2050s, and to continue to increase by an average of 2.3% (±3.9 SD) by 2070s (Fig. 4, Supplementary material Appendix 1 Fig. A1, Table A5).

Remarkable differences in establishment threat were found among species introduced from different continents under the three scenarios, with invaders from North America and South America posing a higher threat (Supplementary material Appendix 1 Table A5). Different species also demonstrated marked differences in current patterns and changes in establishment threat. For instance, the largest extent of current suitable habitat for *Osphronemus goramy* (5.46×10^6 km^2; 79.6% of China's fresh waters) was about 15 times larger than the smallest extent modelled for *Epalzeorhynchos bicolor* (0.368×10^6 km^2; 5.4% of China's fresh waters). Similarly, the largest increases of 42.6% and 21.1% were observed for *Anabas testudineus* under 2050s and 2070s scenarios respectively, whereas the largest decreases were observed for *Labeotropheus fuelleborni* under 2050s scenario (−7.7%) and *Oreochromis mossambicus* under 2070s scenario (−3.6%). However, no significant differences were observed in species-specific establishment threat among the four freshwater fish groups under any of the scenarios considered (Kruskal test, $p > 0.05$, df = 3; Fig. 3).

By overlaying threats of introduction and establishment, we identified southeastern China as a hotspot of invasion for all freshwater fish groups (Fig. 5, Supplementary material Appendix 1 Fig. A2, A3). However, other regions showed contrasted patterns of invasion risk among species groups. For example, northwestern China displayed the highest risk of invasion from both current and potential aquaculture species, but was predicted to be less vulnerable to ornamental species. Similarly, northeastern regions were expected to face high risks of invasion, but only from current aquaculture and potential ornamental species. By contrast, the Tibet Plateau

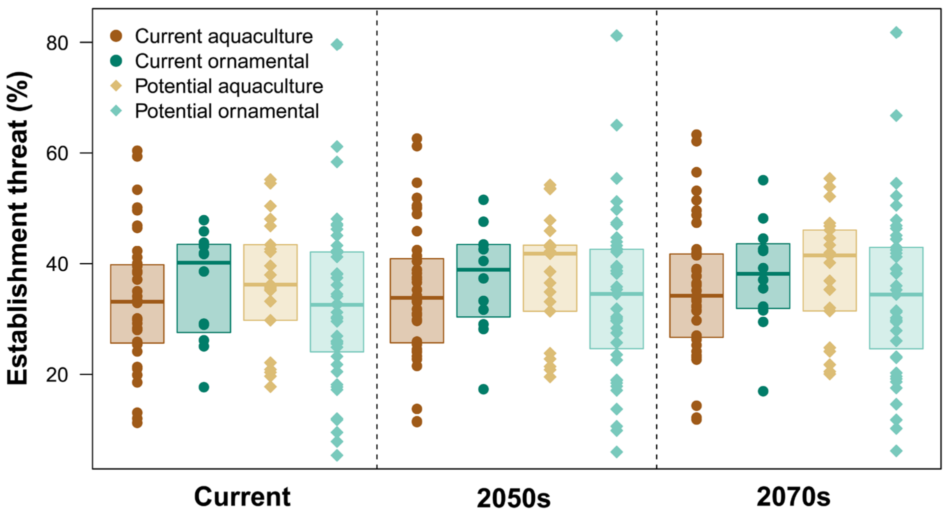

Figure 3. Species-specific establishment threat expressed as the percentage (%) of China's fresh waters predicted to be suitable for the nonnative freshwater fish species under current and future (2050s and 2070s) climate scenarios. Species are clustered into four groups based on introduction pathways and establishment status: current aquaculture species, current ornamental species, potential aquaculture species, potential ornamental species.

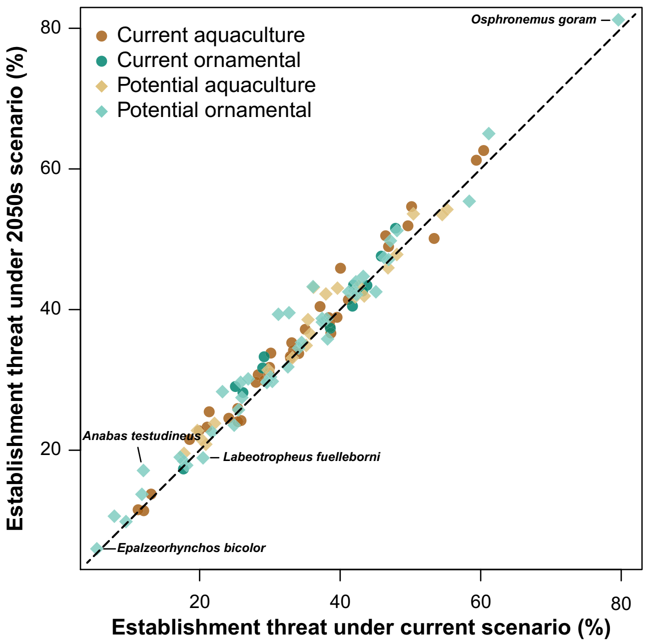

Figure 4. Comparison of species-specific establishment threat under current and 2050s climatic scenarios. Establishment threat is expressed as the percentage (%) of China's fresh waters predicted to be suitable for the species. Species are clustered into four groups based on introduction pathways and establishment status: current aquaculture species, current ornamental species, potential aquaculture species, potential ornamental species. Points located above the 1:1 line indicate species displaying an increase in establishment threat under 2050s climate change scenario, and points below the 1:1 line indicate species displaying a decrease in establishment threat.

and neighboring regions (e.g. Sichuan Province) showed a lower overall risk for all species groups both in present-day and in the future.

Discussion

Identifying species and areas that face elevated risk of invasion is critical for establishing cost–effective invasion management systems (Early et al. 2016, McGeoch et al. 2016). In this study, we evaluated nation-wide threat for China's fresh waters to currently established and potentially emerging nonnative freshwater fishes, accounting for the threats associated with the introduction and establishment stages. Our results pointed to dramatically greater invasion risk by the middle of the century, resulting from the likely establishment of new invaders together with the predicted spread of most current nonnative fishes under climate change. Southeastern China was identified as the region most susceptible to the dual invasion from aquaculture and ornamental species, whereas northwestern China appeared particularly at risk from aquaculture species.

Our results showed that latent invasion risk from potential nonnative fishes was equal to risks associated with species already established in China. This suggests that without effective prevention of unintentional introductions, the establishment of new nonnative fishes in China's fresh waters are imminent. In this regard, the fact that current and potential invaders show similar spatial patterns of invasion risk suggests that management efforts may have the co-benefit of simultaneously controlling current invaders and preventing potential invaders. For example, the southeastern regions were highly vulnerable to both emerging and existing invasions, implying the possibility of improving management efficiency by concurrently implementing strategies for early detection and prevention of secondary spread.

Our results also revealed notable differences in the geographic pattern of introduction and establishment threats, highlighting the importance of assessing invasion risk by considering introduction pathways and habitat suitability in focal regions. In particular, we reported that northwestern China was predicted to be highly threatened by aquaculture species but less susceptible to ornamental species; a pattern that may be explained by flourishing aquaculture practices and lower GDP (thus lower ornament fish ownership) in this area. For instance, over last three decades, aquaculture production in Xinjiang (main region of the northwest) rapidly increased by ca 41 times (Bureau of Fisheries, Ministry of Agriculture 2016). Some sturgeon and salmon species (e.g. *Acipenser nudiventris* and *Coregonus muksun*) are also widely reared in the cold waters found in the northwest, intensifying the propagule and colonization pressures from aquaculture species (Lin et al. 2015). By contrast, southeastern China demonstrates high invasion risk to aquaculture and ornamental species, reflecting the combination of mild climates, sufficient precipitation, abundant water resources, intensified aquaculture practices and other human activities (Fu et al. 2014, Huang et al. 2014, Bureau of Fisheries, Ministry of Agriculture 2016).

Climate change is predicted to increase invasion risk across China, following an overall increase in habitat suitability for nonnative freshwater fish species in the future. This is consistent with previous findings for other taxonomic groups at broader spatial scales (O'Donnell et al. 2012, Bellard et al. 2013, Dullinger et al. 2017) and supports the notion that climate warming will accelerate the spread of nonnative species by relaxing thermal constraints limiting their distributional ranges (Rahel and Olden 2008, Walther et al. 2009). Increase in establishment threat was especially evident in northeastern China, as expected from the northward spread of nonnative species as climate warms (Rahel and Olden 2008). Nonetheless, climate change was also found to decrease the invasion risk from nonnative species in several regions, most notably in western Tibet. This represents new management opportunities to constrain or reduce local population sizes of nonnative freshwater fishes as climatic conditions become less suitable.

Our study confirms the importance of taking into account climate change projections to improve the effectiveness of management strategies seeking to stop or slow emerging invasions (Walther et al. 2009, Bellard et al. 2013,

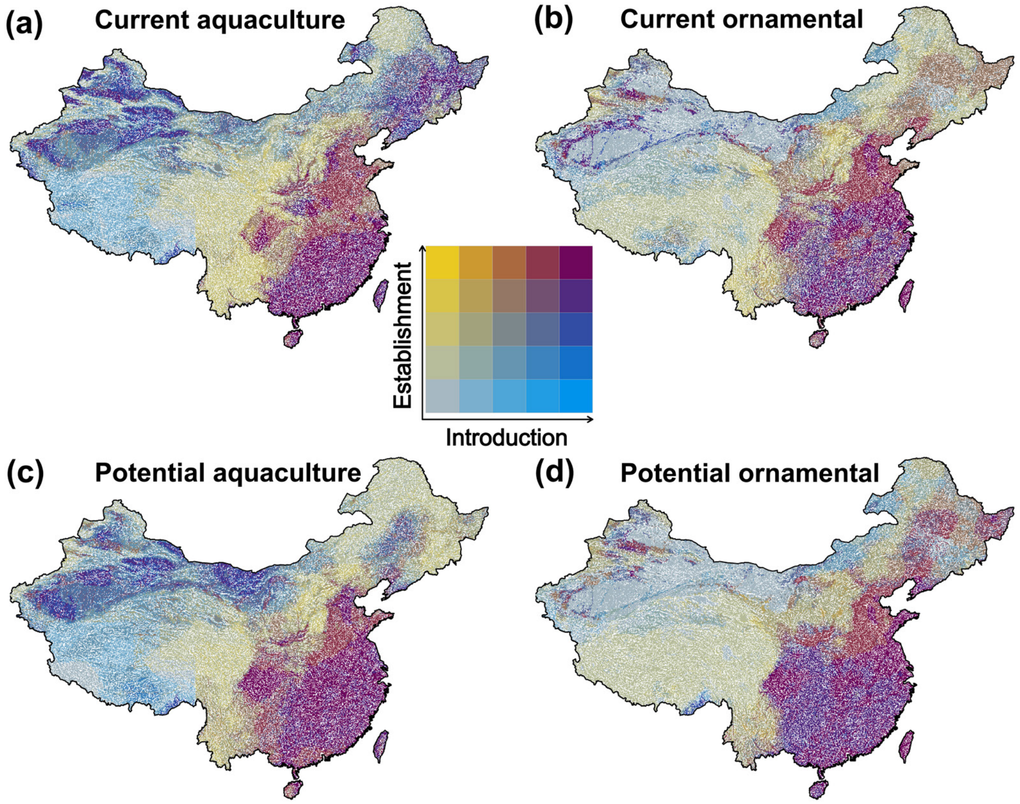

Figure 5. Geographic patterns of invasion risk under future (2050s) climatic conditions defined by overlaying the threats of introduction and establishment for (a) current aquaculture species, (b) current ornamental species, (c) potential aquaculture species and (d) potential ornamental species. Color gradients represent the variables broken into their respective percentile classes.

Li et al. 2016). The accelerating establishment and spread of nonnative species will undoubtedly continue to homogenize China's freshwater fish fauna and further accentuate the loss of distinctiveness across communities in the future (Liu et al. 2017a). More simplified communities may synchronize local biological responses to environmental disturbances and compromise the potential for resilience to future invasions (Olden et al. 2004, 2008). This, in turn, could facilitate the establishment of other invaders and exacerbate the magnitude of invasion-related impacts ('invasional meltdown'; sensu Simberloff 2006).

Despite providing new insights into the vulnerability of China's freshwater ecosystems to fish invasions, several sources of uncertainty must be acknowledged. First, although climatic conditions across introduced ranges are likely to be the main drivers of establishment (Bellard et al. 2013), biotic (e.g. competition, predation) and other abiotic (e.g. habitat availability) factors in the recipient ecosystems also play important roles in invasion success (Liu et al. 2014). However, the incorporation of fine-scale biological data into national assessments is not possible due to insufficient data. In addition, incorporating variables that represent instream conditions is recommended to calibrate SDMs for freshwater species, but recent research showed that predictions do not fundamentally differ for climate versus instream-based models (McGarvey et al. 2018). Second, despite our efforts to remove any potential sampling biases through careful geographical and environmental filtering of the occurrence records, uneven spatial distribution of collection efforts may have truncated the full range of suitable areas, especially for species for which available data are few and opportunistic (Beck et al. 2014). This can be particularly problematic to select pseudo-absences in regions where nonnative species are actively invading and are by definition not in spatial equilibrium (El-Gabbas and Dormann 2018). Third, we did not consider the fact that changing socio-economic activities may also affect the pathways of introduction in the future (Li et al. 2016). For example, human activities in western China have undergone an apparent growth after the implementation of the 'China's Western Development Strategy' (Schneider & Mertes 2014), which might further intensify the invasion risk in this area. Considering changes in the geography of introduction would undoubtedly generate more accurate predictions of the spatio-temporal patterns of invasion risk.

Likewise, SDMs ignore any transient demographic and dispersal dynamics, including dispersal constraints, movement ability and habitat configuration (Tonkin et al. 2019). Although more precise projections could be obtained by incorporating species' traits related to habitats requirements and movement process (Broennimann and Guisan 2008, Carboni et al. 2018), these data are only available for a few well-studied species, precluding their incorporation in systematic study like ours (O'Donnell et al. 2012). We also considered only the species already present in the country and did not include additional species likely to be introduced from other geographical areas. Although our choice was guided by biological considerations (i.e. propagule pressure increases with proximity to existing populations, Lockwood et al. 2005), invasive species profiling (Howeth et al. 2016) may help to broaden the list of potential invaders in future assessments. Nonetheless, despite the rather restricted set of species considered in our study (115 out of 439 nonnative species compiled by Xiong et al. 2015), the geographic projections of habitat suitability were generally consistent among species groups displaying a large diversity of traits and origins, indicating that our results are likely to be representative of the current and future invasion risk of nonnative freshwater fish species in China.

In conclusion, biosecurity frameworks that integrate risks from species invasions now and in the future provide the greatest opportunity to advance environmental protection strategies. By providing a basis for improved capacity of early warning, emergency response and monitoring of invasive alien species, the results presented here help contribute to China's ongoing challenge to control biological invasions in the coming decades.

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Supplementary material (available online as Appendix ecog-04665 at <www.ecography.org/appendix/ecog-04665>). Appendix 1.