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# Global drivers of the conservation–invasion paradox

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## Abstract
The conservation–invasion paradox (CIP) refers to a long-term phenomenon wherein species threatened in their native range can sustain viable populations when introduced to other regions. Understanding the drivers of CIP is helpful for conserving threatened species and managing invasive species, which is unfortunately still lacking. We compiled a global data set of 1071 introduction events, including 960 CIP events (successful establishment of threatened species outside its native range) and 111 non-CIP events (unsuccessful establishment of threatened species outside its native range after introduction), involving 174 terrestrial vertebrates. We then tested the relative importance of various predictors at the location, event, and species levels with generalized linear mixed models and model averaging. Successful CIP events occurred across taxonomic groups and biogeographic realms, especially for the mammal group in the Palearctic and Australia. Locations of successful CIP events had fewer native threat factors, especially less climate warming in invaded regions. The probability of a successful CIP event was highest when species introduction efforts were great and there were more local congeners and fewer natural enemies. These results can inform threatened species ex situ conservation and non-native invasive species mitigation.

**KEYWORDS**
biodiversity conservation, biological invasion, invasion success, propagule pressure, threatened species

## INTRODUCTION

When threatened species are introduced into new regions, they may or may not establish themselves. Successful establishment defines the conservation–invasion paradox (CIP) (Figure 1) (Gibson & Yong, 2017; Lees & Bell, 2008). There have been a series of studies on the CIP that focused primarily on 3 aspects. First, they report on the widespread nature of the phenomenon across taxa and geographic regions, for example, common spadefoot toad (*Pelobates fuscus*) in the Netherlands (Koster et al., 2022), wattle-necked soft-shell turtle (*Palea steindachneri*) in Hawaii (United States) (Marchetti & Engstrom, 2016), yellow-crested cockatoo (*Cacatua sulphurea*) in Hong Kong and Singapore (Gibson & Yong, 2017), and banteng (*Bos javanicus*) in Australia (Bradshaw et al., 2006). The CIP has also been observed in plants (Adams, 2008; Rogers et al., 2005),

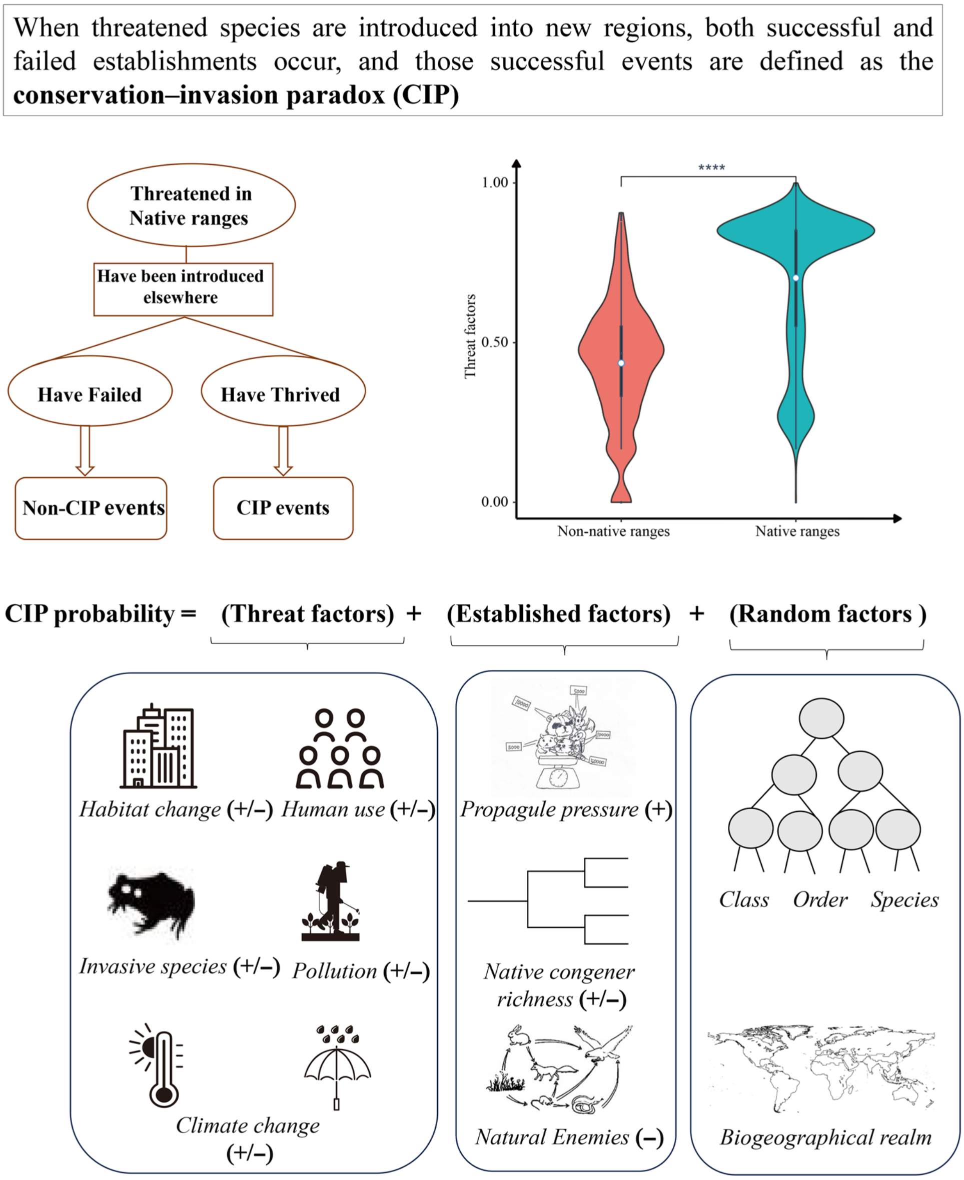


**FIGURE 1** A theoretical and analytic framework clarifying conservation–invasion paradox (CIP) events and potential influencing factors. Positive and negative symbols indicate the hypothesized effect each factor has on the likelihood of a successful CIP event. Silhouettes were free access from iSlide (https://www.islide.cc) and PhyloPic (https://www.phylopic.org/).

insects (Gibson & Yong, 2017), and fish (Crain & Moyle, 2011; Marková et al., 2020). Second, they describe the introduction pathway of threatened species to new ranges (Gibson & Yong, 2017). There are deliberate and accidental introductions (Lees & Bell, 2008), including through commercial wildlife trade (e.g., caged birds), hunting (e.g., ungulate introduction for game hunting) (Gibson & Yong, 2017; Marchetti & Engstrom, 2016), and ex situ conservation (Bradshaw et al., 2006; Marchetti & Engstrom, 2016). Third, they explore the possible conservation implications for species threatened by the CIP (Gibson & Yong, 2017; Lees & Bell, 2008; Marchetti & Engstrom, 2016). Despite these efforts, a global picture of CIP events across taxonomic groups is still lacking, and the factors driving such events remain poorly understood. Filling this knowledge gap may help conservation of threatened species and management of invasive species.

Based on what is known about conservation and invasion, several potential factors may explain the CIP. Native threat factors may be absent or greatly reduced in new ranges. For example, the European rabbit (*Oryctolagus cuniculus*) thrives in Australia by escaping hunting, habitat degradation, rabbit calicivirus, Myxoma virus, and natural enemies (Jaksic & Soriguer, 1981; Lees & Bell, 2008). The Burmese python (*Python bivittatus*), a large and endangered snake in Asia due to trade and habitat loss (Stuart et al., 2012), has established populations in Florida (USA), where native threat factors are not present, that have caused severe declines in small mammal populations (Dorcas et al., 2012; McCleery et al., 2015). However, reduced threat factors may not always promote a species' establishment when it is introduced to a new range. For example, land-use change usually facilitates invasions by affecting native species and opening ecological niches for non-native species (Huenneke, 1992), but this may not occur for threatened species that are sensitive to anthropogenic disturbances in their native range. The situation is similar for pollution and climate change threats. Although some studies suggest that pollution (Crooks et al., 2011) and climate change (Bellard et al., 2013; Gu et al., 2023) can promote species invasions, threatened species in particular may have low phenotypic plasticity or adaptation potential to pollution and climate change.

Sympatric invasive species may cause some species to be threatened in their native ranges and to fail to establish in non-native ranges, but the invasion meltdown hypothesis predicts that non-native species established earlier may promote secondary invasions (Simberloff & Holle, 1999). Threatened species exploited by humans may be particularly unlikely to establish, whereas high volumes of anthropogenic introduction can increase propagule pressure and thus establishment, especially for those deliberately introduced for human use (García-Díaz et al., 2015). For example, the richness of established non-native species is closely related to human population density (Dawson et al., 2017). Native threat factors may be overcome by high propagule pressure from multiple introduction events or from a large number of introduced individuals (Lockwood et al., 2009). For instance, European rabbits failed to spread in Australia over 70 years of continuous introductions until a key genetic type emerged from 24 rabbits introduced in 1959 (Alves et al., 2022). Furthermore, habitat presence, as indicated by the richness of congeners and presence of natural enemies, may also determine the occurrence of CIP events (Redding et al., 2019; Sakai et al., 2001; Stockwell et al., 2003). However, the relative importance of these factors for CIP events has not been examined.

We compiled a global database of threatened terrestrial vertebrate introduction events in which both successful (i.e., CIP event) and unsuccessful (non-CIP event) establishment occurred outside their native ranges. We focused on terrestrial vertebrates because they have relatively clear introduction histories and information is available on distributions for non-native amphibians and reptiles (Capinha et al., 2017, 2020; Kraus, 2009; Liu et al., 2014), birds (Dyer et al., 2017; Redding et al., 2019), and mammals (Biancolini et al., 2021; Capellini et al., 2015; Long, 2003). We then compared the intensities of threat factors identified by the International Union for Conservation of Nature (IUCN) (habitat change, human use, climate change, pollution, invasive species, and pathogens, such as chytrid fungus [*Batrachochytrium dendrobatidis*] [IPBES, 2019]) between native and non-native ranges for each CIP event. We hypothesized that the intensity of threat factors in CIP events is low. We also explored potential factors that may influence the occurrence of CIP events, including IUCN threat factors and other important factors affecting success of non-native species invasion, such as propagule pressure (Liu et al., 2014; Lockwood et al., 2009), richness of native congeners (Tingley et al., 2011), number of natural enemies (Keane, 2002), and richness of other non-native species (Redding et al., 2019). To examine these factors, we used model averaging with generalized linear mixed models. We aimed to answer the following 3 questions: How prevalent are CIPs across taxa and geographic regions globally, to what extent have native threats been alleviated in non-native ranges for CIPs, and what are the relative effects of location-, event-, and species-level factors in explaining CIPs? Based on our findings, we devised recommendations for threatened species conservation and invasive species mitigation.

# METHODS

## CIP and non-CIP event occurrence

Because one species may be introduced to multiple locations, we defined CIPs and non-CIPs at the event level as successful or failed establishment events of threatened species in different regions, respectively (Appendix S1). We categorized the threatened terrestrial vertebrates based on the IUCN Red List of Threatened Species (https://www.iucnredlist.org/, accessed 30 November 2021), which classifies them as vulnerable (VU), endangered (EN), or critically endangered (CR). We then determined the establishment status (successful or failed) of these species in non-native ranges based on widely used databases across taxa. For non-native amphibians and reptiles, we used a compendium of 2142 introduction events involving 676 non-native reptiles and amphibians (Kraus, 2009) and the literature from the last decade (Capinha et al., 2017, 2020; Liu et al., 2019, 2021). For non-native birds, we obtained data from the Global Avian Invasions Atlas (GAVIA), a spatial and temporal data set with 27,723 distribution records and establishment statuses for 971 non-native birds worldwide (Dyer et al., 2017; Redding et al., 2019). For non-native mammals, we integrated and cross-checked 4 main sources: Long (2003), Capellini et al. (2015), Lundgren et al. (2017), and Biancolini et al. (2021). Because the exact time when the species was threatened in its native range was not available, we did not verify whether the endangerment of the species in its native ranges occurred before the species was introduced into other regions.

Native and non-native range information for birds was obtained from the BirdLife International & NatureServe geodatabase (http://datazone.birdlife.org/species/requestdis, accessed January 2022), the GAVIA database, and updated references (Dyer et al., 2017; Redding et al., 2019). We collected native and non-native range information for mammals from the IUCN database and global non-native mammal species data sets (Biancolini et al., 2021; Capellini et al., 2015; Long, 2003; Lundgren et al., 2017). In addition to the range maps, we also collected literature from recent years (Appendix S2). We determined the native ranges of amphibians based on IUCN spatial range maps (https://www.iucnredlist.org/resources/spatial-data-download) and recent updates for global reptiles (Roll et al., 2017). Because amphibians and reptiles lack range maps for non-native ranges, the distribution data of non-native amphibians and reptiles were obtained mainly from databases, including Global Biodiversity Information

Facility (http://www.gbif.org/), iNaturalist (https://www.inaturalist.org/), Biodiversity Information Serving Our Nation (https://bison.usgs.gov/), iDigBio (https://www.idigbio.org/), and Atlas of Living Australia (http://www.ala.org.au/), and from recently published articles (Appendix S2). We then used the CoordinateCleaner R package to remove erroneous records, such as those in a nation's capital and those without precise coordinates (Zizka et al., 2019). We excluded samples that lacked precise native or non-native range data (Kraus, 2009; Liu et al., 2021). For some records that provided only descriptions of the sample locations, we inferred geographic coordinates with Google Maps tools (http://maps.google.com/maps).

## Native threat factor collection

According to the IUCN Red List (https://www.iucnredlist.org/), there are 12 threat mechanisms that can be grouped into 5 major categories (IPBES, 2019): habitat change (residential and commercial development, agriculture and aquaculture, energy production and mining, transportation and service corridors, natural system modifications, geological events), human use (biological resource use, human intrusions and disturbance), invasive species (invasive and other problematic species, including pathogens), climate change (including extreme weather), and pollution. The number of species affected by each threat factor is in Appendix S3. We extracted all variables at a spatial resolution of 0.5° grids, which is a common resolution for global studies used to balance the analysis accuracy and calculation efficiency (Early et al., 2016; Liu et al., 2019).

We quantified habitat change based on anthropogenic land-use change (ALUC). We obtained global land-use data from the Anthromes 2 data set (Anthropogenic Biomes 2, accessed 17 October 17) in ESRI GRID format (Ellis et al., 2010). We used the 1900 and 2000 data to calculate the temporal changes in land use and computed the percentage of grids that changed to a more anthropogenically influenced type for each grid with the reclassify and raster functions in ArcGIS Pro (Zhang et al., 2022).

Because detailed data on human use of wildlife, such as human hunting pressure, are not available at the global scale, we used population density as a surrogate for human use. The mean human population density in each species' range was extracted from the Socioeconomic Data and Applications Center (http://sedac.ciesin.columbia.edu/gpw, accessed January 2022) after resampling at a 0.5° resolution with bilinear interpolation (Phillips et al., 2006).

We quantified the invasive species factor by calculating the number of other established non-native terrestrial vertebrates within the range of the introduced species. Considering that not all established non-native species have serious negative effects, we used the invasive species that threaten native biodiversity and natural ecosystems from the Global Invasive Species Database (GISD) (https://www.iucngisd.org/gisd/) (Pagad et al., 2015). Specifically, the frog chytrid fungus *B. dendrobatidis* was grouped in this category, considering its potential Asian origin and spread through the global amphibian trade (Fisher & Garner, 2020; Liu et al., 2013; O'Hanlon et al., 2018).

We used 2 temperature and precipitation variables: monthly mean temperature change (TEMP) and monthly average precipitation variation (PRE) (from the University of East Anglia Climate Research Unit [https://sites.uea.ac.uk/cru/, accessed December 2023]) (Harris et al., 2013). We extracted temperature and precipitation values for all grids occupied by each event and calculated temperature and precipitation slopes from 1970 to 2000 to reflect the trend of temperature and precipitation changes (Zhang et al., 2022).

To examine the pollution factor, we collected pesticide use data (POL) corresponding to the distributional ranges of each species from the Rivers in Crisis database (http://www.riverthreat.net/data.html, accessed July 2022) (Vörösmarty et al., 2010). The CIP and non-CIP event occurrences were spatially joined using ArcGIS Pro 2.5.0 with the pesticide layers. For each event, we used the zonal statistics tool to calculate the pesticide averages in each grid at a resolution of 0.5°.

## Potential factors explaining CIP

The occurrence of CIP events may depend not only on whether the native threat factors were reduced in non-native ranges, but also on those factors that can influence establishment after introduction. Therefore, we investigated 3 major important factors that potentially influence the establishment of vertebrate species when they are introduced to new ranges: propagule pressure, native congener richness, and natural enemies.

Propagule pressure is a fundamental factor determining non-native species establishment. It is assumed that the greater the introduction effort (i.e., more introduction events or more individuals in each introduction event), the greater the probability of non-native species establishment (Lockwood et al., 2005; Simberloff, 2009). Because the exact number of individuals involved in each introduction event was generally unavailable, we quantified propagule pressure as the minimum number of independent introduction numbers (NOI) available for each introduction event (Tingley et al., 2011) based on an extensive literature search in Google Scholar (https://scholar.google.com/) (keywords "*species* + *location*," which included species common name, scientific name or synonym, and the name of the location where the introduction event occurred) (Appendix S4). There were cases for which there was no information on the exact number of introduction events. For example, some studies describe only the introduction events qualitatively as "some," "occasional," "a few," "several," "many", "numerous," "frequent," or "common." For these terms, we used different values based on previous studies. Some, occasional, and a few were a minimum of 2. Several was 3. Many, numerous, frequent, and common were 4 (Kraus, 2009; Tingley et al., 2011). Some studies did not report either exact numbers or qualitative information. We treated these cases as a single introduction event based on the approach by Kraus (2009).

The preadaptation hypothesis proposes that introduced species may have a greater probability of establishment in regions where they are closely related phylogenetically to native species (i.e., where congeners are native) because these species may have similar environmental requirements (Darwin's, 1859). Conversely, the naturalization hypothesis suggests that the non-native congener may face greater competition pressure from natives and thus may have a lower probability of establishment (Tingley et al., 2011). We counted the number of sympatric native congeners in a genus (CONG) by overlaying IUCN GIS range maps for each terrestrial vertebrate species (Liu et al., 2014).

The enemy release hypothesis suggests that the absence of enemies in non-native ranges is important for the invasion success of non-native species (Enders et al., 2020; Schulz et al., 2019). Given that species interactions in nature are complex and it is impossible to construct detailed food webs for each site at the global scale (Brose et al., 2019), we applied a relatively coarse but general approach by assuming that species at higher trophic levels can be regarded as potential predators or natural enemies, following previous studies (Fornoff et al., 2021). We considered natural enemies as those species at a higher level on the food chain than the invading species. We identified natural enemies for each CIP event by overlaying the invading species distribution where the CIP event occurs with the IUCN GIS range maps for global amphibians, reptiles (Roll et al., 2017), and terrestrial mammals (http://www.iucnredlist.org/, accessed November 2021), and as well as accessing the geographic database of the International Bird Union (http://datazone.birdlife.org/species/requestdis, accessed on January 2022) for birds, and then filtering these higher trophic-level species.

## Data analyses

To test whether there were fewer native threats associated with CIP events in new locations relative to native locations, we compared differences habitat change, human use, pollution, temperature and precipitation change, and threats from other invasive species between the native and non-native ranges based on the 2-tailed Wilcoxon signed rank test. We used the rstatix package in R (Kassambara, 2020) to conduct this analysis.

We then explored the factors influencing the occurrence of CIP events (i.e., 1, CIP event; 0, non-CIP event) by integrating 9 predictor variables, including the 6 native threat factors and the other 3 potential factors related to non-native species establishment. To improve normality, we $\log_{10}$-transformed the number of introductions before analyses and transformed human use, richness of other exotic species, and number of natural enemies to $\log_{10}(x+1)$. Before analyses, we scaled 9 predictor variables to a mean value of 0 and a unit variance of 1 (Redding et al., 2019). These 9 variables did not show high multicollinearity (Spearman correlation coefficient, $r < 0.7$) (Appendix S5) (James et al., 2015). We used generalized linear mixed-effects models (GLMMs) with a binomial distribution and logit link to investigate the effect of the 9 predictors on the occurrence of CIP events. To account for geographic and taxonomic pseudoreplication of samples, we treated the invaded biogeographical realm, class, order, and species identity as random effects and the 9 predictor variables as fixed effects. The biogeographical realms were the Palearctic, Australian, Nearctic, Sino-Japanese, Panamanian, Oceania, Oriental, Afrotropical, Neotropical, Madagascan, and Saharo-Arabian (Holt et al., 2013). To control for the potential influence of the dominant sample size of CIP events compared with non-CIP events on our results, we assigned sample weights inversely proportional to the class frequency into GLMMs (Cui et al., 2019; Wang et al., 2017). We constructed 511 ($2^9 - 1 = 511$ models) GLMMs and ranked each model with Akaike's information criterion corrected for small sample sizes (AICc) (Burnham & Anderson, 2004). Then, we applied a model averaging approach to determine the relative importance of each predictor variable with the glmer function in the lme4 package (Lee & Grimm, 2018) and the dredge and model.avg functions in the MuMIn package (Barton & Barton, 2015). We conducted all the analyses in R 2.15.2 (R Core Team, 2019).

European rabbit introductions accounted for a large proportion of our data set (527 out of 1071). We therefore performed sensitivity analyses by removing the rabbit samples and repeating all analyses to test whether our results were affected by the outlier rabbit samples.

# RESULTS

There were 960 CIP events (89.6%) and 111 non-CIP events (10.4%) among the 1071 introduction events. The CIP events included 17 amphibian events, 59 reptile events, 79 bird events, and 805 mammal events (Figure 2). The number of CIP events varied among biogeographical realms. The most occurred in the Palearctic (520 events, 30 species), followed by the Australian (146 events, 31 species), Nearctic (117 events, 60 species), Oriental (104 events, 36 species), Oceania (72 events, 29 species), Neotropical (36 events, 12 species), Panamanian (23 events, 16 species), Afrotropical (19 events, 9 species), Saharo-Arabian (15 events, 7 species), Sino-Japanese (11 events, 4 species), and Madagascan (8 events, 5 species) (Figure 2).

Among the 960 CIP events, 667 had less ALUC in invaded ranges than in native ranges, 772 events had less human use (HSE), 651 events had lower numbers of invasive non-native species (INS), 520 events had less pollution (POL), 520 events had less monthly average precipitation variation (PRE), and 572 events had less monthly mean temperature change (TEMP; Appendix S6). Some species may be affected by multiple factors simultaneously. Further analyses indeed revealed a reduction in native threat factors in non-native ranges for CIP events along ALUC (2-tailed Wilcoxon signed-rank test: $n = 960$, $p < 0.001$) (Figure 3a) (HSE: $n = 960$, $p < 0.001$ [Figure 3b]; INS: $n = 960$, $p < 0.001$ [Figure 3c]; POL: $n = 960$, $p < 0.001$ [Figure 3d]; TEMP: $n = 960$, $p < 0.001$ [Figure 3e]; PRE: $n = 960$, $p < 0.001$ [Figure 3F]).

Model averaging analyses based on GLMMs showed that all 9 predictors were included in the 8 best models (i.e., $\Delta$AICc $< 2$)

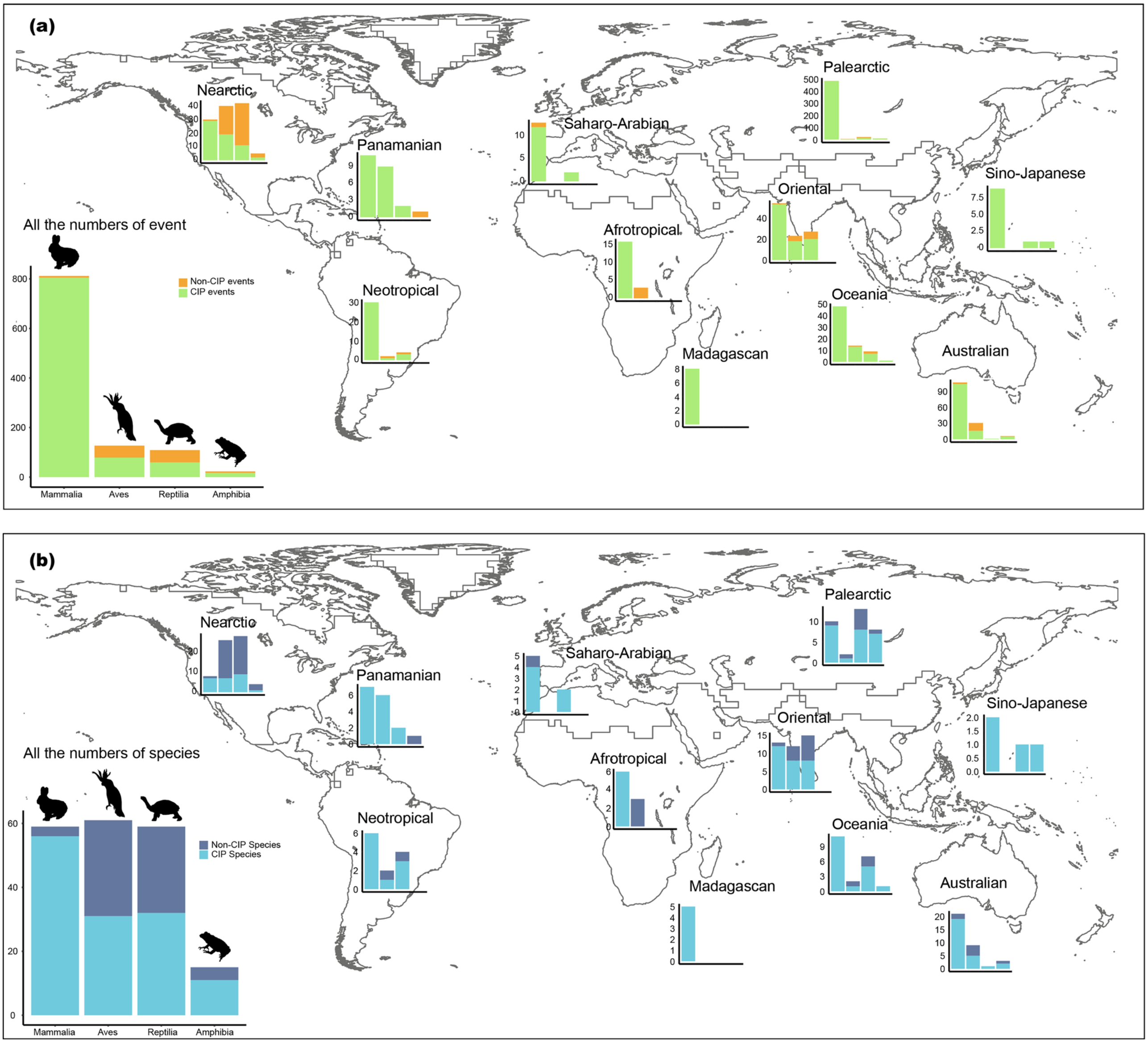


**FIGURE 2** The geographic distribution of conservation–invasion paradox (CIP) events and non-CIP events across taxonomic groups and biogeographical realms at the (a) event level and (b) species level. Silhouettes were free access from PhyloPic (https://www.phylopic.org/).

(Table 1), but only number of introductions (NOI), native congener richness (CONG), natural enemy (NE), and TEMP appeared in each of the 8 top models. These 4 factors also had the highest relative importance values among all the variables (NOI, 1.0; CONG, 0.99; NE, 0.98; TEMP, 0.88). The probability of CIP events increased with NOI (estimate [SE] = 18.02 [3.29], $p < 0.001$) and CONG (estimate [SE] = 10.30 [4.14], $p < 0.05$) but decreased with NE (estimate [SE] = −12.81 [5.10], $p < 0.05$) and TEMP (estimate = −6.43 [2.91], $p < 0.05$) (Figure 4), indicating that there was a greater probability of CIP events when species were introduced to areas with greater introduction efforts, greater native congener richness, fewer natural enemies, and lower climate warming. These factors explained a total of 87–89% of the variance in CIP occurrence (Table 1), demonstrating a good model fit. Moreover, after removing the European rabbit samples, the sensitivity analyses based on the remaining 544 events yielded results similar to those of the main analyses (Appendix S7), indicating that our results were robust to data uncertainties caused by sample outliers.

# DISCUSSION

This study, to our knowledge, is the first to quantify the potential factors influencing the long-term phenomenon of successful establishment of threatened species in non-native ranges. Consistent with our prediction, we found that native threat factors were less intense in non-native ranges for CIP events. Moreover, high introduction efforts (i.e., propagule pressure), more native

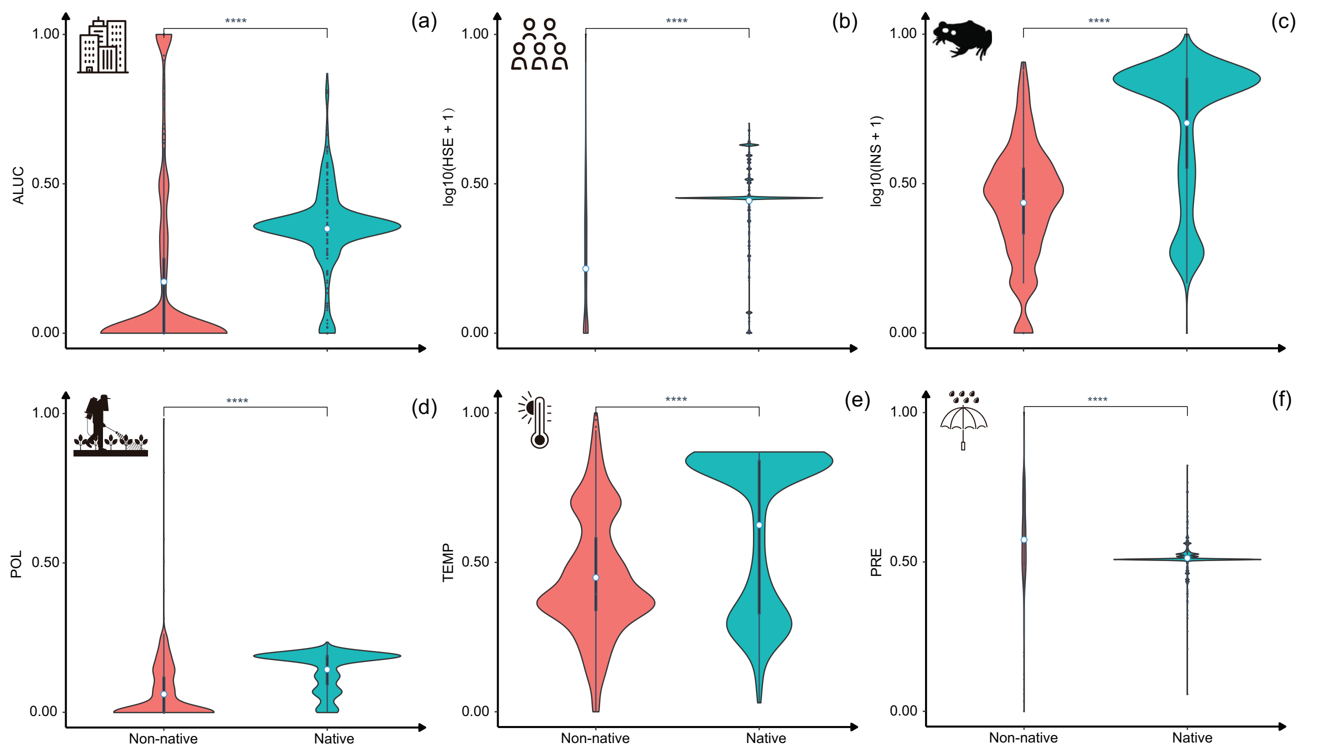


**FIGURE 3** Comparison between native and non-native ranges for conservation–invasion paradox (CIP) events of the 6 threat factors: (a) anthropogenic land-use change (ALUC), (b) human use (HSE), (c) invasive non-native species (INS), (d) pollution (POL), (e) monthly mean temperature change (TEMP), and (f) monthly average precipitation variation (PRE). All predictor variables are standardized with a mean value of 0 and a unit variance of 1. Silhouettes were free access from iSlide (https://www.islide.cc) and PhyloPic (https://www.phylopic.org/).

**TABLE 1** The top generalized linear mixed models[a] (i.e., ΔAICc < 2) used to predict conservation–invasion paradox (CIP) events based on a combination of 9 fixed effect factors[b] and random effects of biogeographical realms and taxonomic identity.[c]

| Variable | Model[d] | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| ALUC | | | + | | | | | |
| CONG | + | + | + | + | + | + | + | + |
| HSE | – | – | – | | | | – | – |
| INS | | | | – | | – | – | – |
| NOI | + | + | + | + | + | + | + | + |
| POL | – | | – | | – | – | | – |
| PRE | – | – | – | – | – | – | – | – |
| NE | – | – | – | – | – | – | – | – |
| TEMP | – | – | – | – | – | – | – | – |
| ΔAICc[e] | 0.00 | 1.06 | 1.11 | 1.13 | 1.26 | 1.38 | 1.42 | 1.43 |
| Akaike weight[f] | 0.09 | 0.06 | 0.05 | 0.05 | 0.05 | 0.05 | 0.05 | 0.05 |
| $R^2$ | 0.89 | 0.88 | 0.89 | 0.87 | 0.89 | 0.89 | 0.87 | 0.89 |

[a]Binomial error structure and a logit link function with conservation–invasion paradox events (yes, 1; no, 0) as the response variable.
[b]Factors: INS, other invasive non-native species; TEMP, monthly mean temperature change; PRE, monthly average precipitation variation; CONG, native congener richness; ALUC, anthropogenic land-use change; HSE, human use; NOI, number of introductions; POL, pollution; NE, natural enemy.
[c]Class, order, species.
[d]Key: +, model contains a variable with positive effect; –, model contains a variable with a negative effect; blank, variable is not in the model. Models ranked in order of increasing ΔAICc.
[e]Akaike information criterion (AIC) difference between each model and the highest ranked model.
[f]Probability that a model is best given the particular set of models considered.

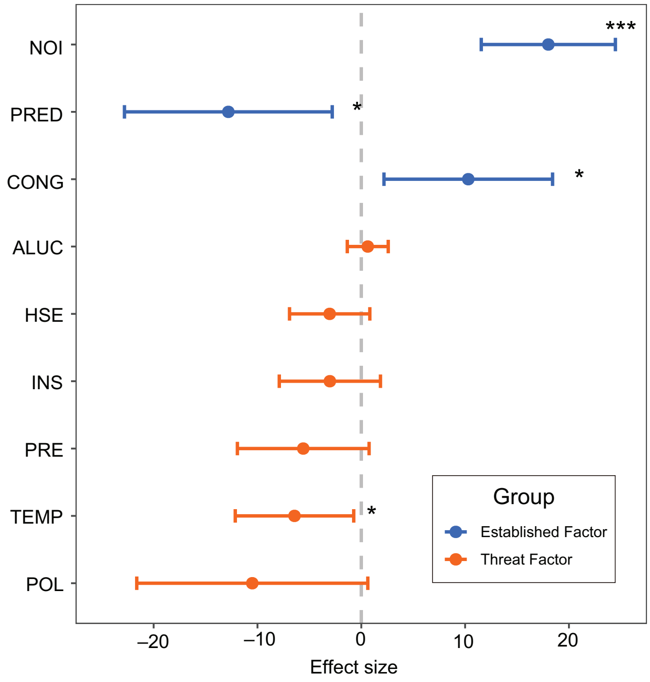


**FIGURE 4** Relative importance of the 9 variables in predicting the occurrence of conservation–invasion paradox (CIP) events according to model averaging analyses based on generalized linear mixed models after accounting for taxonomic and biogeographic nonindependence of the samples (INS, other invasive non-native species; TEMP, monthly mean temperature change; PRE, monthly average precipitation variation; CONG, native congener richness; ALUC, anthropogenic land-use change; HSE, human use; NOI, number of introductions; POL, pollution; NE, natural enemy; whiskers, model-averaged 95% confidence intervals; *$p < 0.05$; ***$p < 0.001$).

congeners, and fewer natural enemies might help threatened species become established in new ranges.

Our results showed that CIP events were indeed more likely to occur when native threat factors were released in new ranges. However, further analyses based on model averaging indicated that there were variations in relative importance of different threat factors in predicting CIP. We found that this was especially important for climate warming because CIP events tended to occur in places where climate warming had less of an effect. This result supported our prediction that threatened species may have low phenotypic plasticity or potential to adapt to climate fluctuation, especially temperature change here, which thus may limit their establishment in the introduced range.

Introduced species may also be more likely to establish in areas with climates similar to their native ranges (Redding et al., 2019), although the role of climatic matches in explaining invasion outcomes is still debated. We therefore conducted supplementary analyses by incorporating climatic similarity into the GLMMs, but we did not find a significant effect on CIP event occurrence (Appendix S8). One potential explanation is that some species may occupy novel realized climatic niches when they arrive in new areas (Tingley et al., 2014).

Our results also supported our initial hypothesis that most native threat factors have complex effects on invasion outcomes when threatened species are introduced into new ranges (Figure 1). For instance, although habitat disturbance and environmental pollution can facilitate non-native species establishment by creating vacant ecological niches (Crooks et al., 2011; Huenneke, 1992), we did not detect a significant role of habitat change or pollution in predicting threatened species establishment elsewhere.

We also did not find a significant effect of the number of other invasive species, demonstrating that the invasion meltdown hypothesis seems unlikely to explain CIP occurrence in our present study. This result was robust when we used the number of all the other recorded established non-native species and when we used only the number of established non-native species introduced earlier based on the First Records database (Seebens et al., 2018) (Appendix S9). All these finding indicated that threatened species might be more sensitive to land-use change, pollution, and invasive species than nonthreatened species, which warrants further investigations.

Previous case studies show that the release of wildlife trade and hunting pressure is crucial in the successful establishment of threatened species in new areas (Gibson & Yong, 2017). We used human population density as a surrogate for human use to quantify the degree of wildlife trade and hunting pressure, which might be one reason we did not find that human use played an important role in CIP occurrence. We suggest that further studies are needed when related data are available at the global scale.

Our findings also demonstrated that some well-known factors, such as high introduction propagule pressure, native congener richness, and few natural enemies, may facilitate the establishment of threatened species in new areas. The important effect of the number of introduction events strongly supported the propagule pressure hypothesis, which is a general theory predicting non-native species establishment (Cassey et al., 2004; Colautti et al., 2006; Lockwood et al., 2009). A high number of introductions and individuals in each introduction event may reduce genetic bottlenecks or demographic stochasticity and increase the population's capacity to adapt to new selection pressures (Ghabooli, 2014). For example, a successful introduction after many rounds of effort ultimately facilitated the invasion of European rabbits in Australia (Alves et al., 2022).

The positive relationship between CIP and native congener richness supports the preadaptation hypothesis, which predicts that the establishment of non-native species is greater in the presence of native congeners (Tingley et al., 2011), especially at large spatial extents (Park et al., 2020). This result was also consistent with previous studies on the positive relationship between the richness of native congeners and the establishment success and spread of non-native amphibians and reptiles at the global scale (Ferreira et al., 2012; Liu et al., 2014; Tingley et al., 2011) and at the continental scale in Europe and North America (Poessel et al., 2012). A greater richness of closely related species might indicate that there is more habitat for introduced non-native species and thus that these species are more likely to become established (Redding et al., 2019).

The important effect of reduced natural enemies on CIP events corroborated the enemy release hypothesis (Enders et al.,

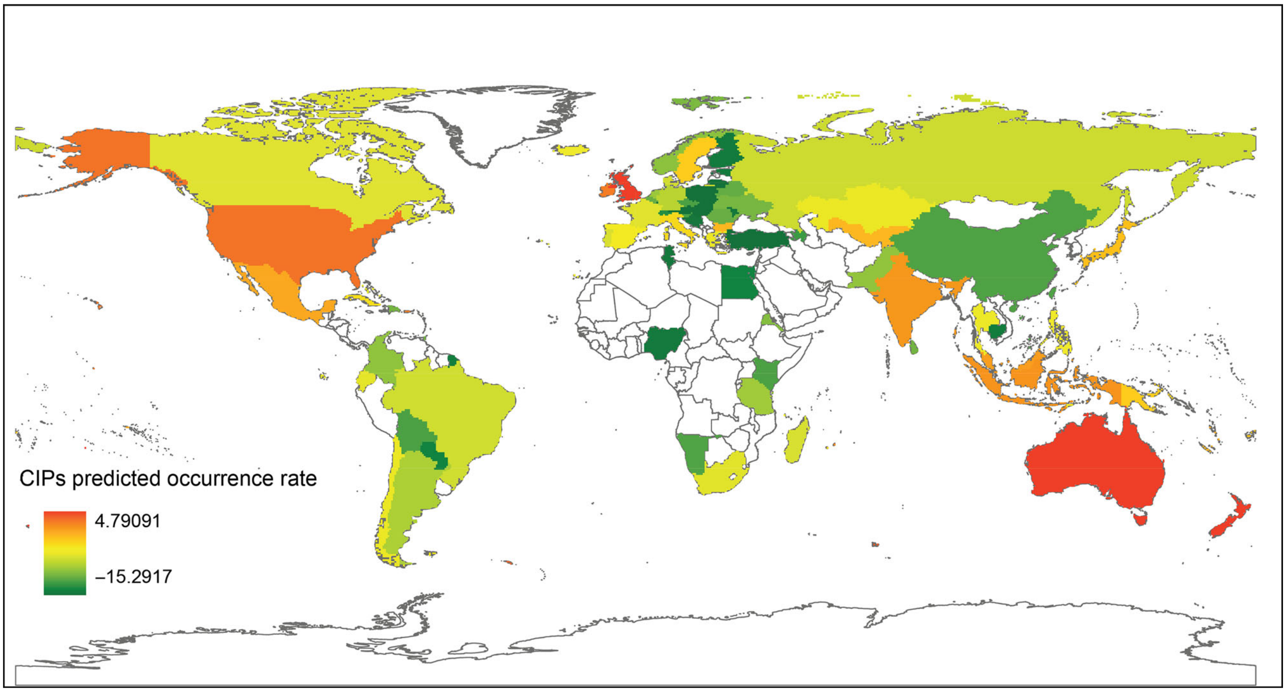


**FIGURE 5** Predicted likelihood of conservation–invasion paradox (CIP) events in each administrative unit at the global scale based on the fitted values and 95% confidence intervals (CIs) for CIP events in each administrative region and the important predictors in the generalized linear mixed models.

2020; Schulz et al., 2019). This result was also consistent with some empirical observations. For example, European rabbits face 24 natural enemies in their original habitat but few in invaded areas, which promotes establishment success (Lees & Bell, 2008).

There were some limitations to our analyses. For example, because sample sizes were limited for each taxon, especially non-native amphibians, and the mammal group was dominated by European rabbit samples, we combined taxa in our main analysis. To test whether there were certain important predictor variables across taxa, we conducted supplementary analyses with birds and reptiles (Appendix S10) and found that although the importance of different factors varied across taxonomic groups, propagule pressure was still one most important factor for predicting establishment. Furthermore, because we were unable to determine the exact time at which each non-native species was established, we could not directly test whether earlier invaders facilitated further establishment. Finally, although we conducted intensive data collection on the occurrence of CIP and non-CIP events, we likely missed local reports in non-English languages (Amano et al., 2021).

Despite the methodological limitations, our findings may provide useful information for threatened species conservation and invasive species mitigation strategies. Reintroducing threatened species to new areas is a classic conservation approach (Li & Pritchard, 2009). However, reintroduced populations may still be affected by their native threat factors if these threats are not removed (Rocha & Bergallo, 2012). For instance, the Arabian oryx (*Oryx leucoryx*) was poached to extinction on the Arabian Peninsula and in the United States after its introduction there. Forty individuals were reintroduced and reestablished in the Arabian Desert, but poaching has again caused the reintroduced population to collapse and negated the decade of reintroduction efforts (Spalton et al., 1999). Our results indicated that the species can be introduced to areas with low or no original threats, especially areas without high temperature fluctuations and natural enemies. Moreover, most introduced species usually start with a small population and can thus be limited by genetic bottlenecks (Birzu et al., 2019) and inbreeding depression (Hofmeister et al., 2021). Our results suggested that number of introductions is critical for sustaining the population establishment of threatened species (Figure 4; Table 1). Multiple introduction events or more individuals at each event can be an important way to overcome the founder effect (Stuart et al., 2023) and increase the probability of population restoration. Using the important predictors we identified, we also generated a prediction map based on the GLMM fitted values and 95% confidence intervals for CIP events in each administrative region (Zhang et al., 2022). This map suggests that CIP events may be more likely to occur in the United Kingdom, New Zealand, Cook Islands, Australia, French Southern Territories, South Georgia, the South Sandwich Islands, the United States, Kiribati, Ireland, and Puerto Rico (Figure 5). However, the potential effects of reintroduced species on other local species and ecosystem functions should be carefully evaluated. It thus needs the combined efforts by conservation biologists and invasion ecologists to collaborate on future reintroduction efforts for threatened species.

## AUTHOR CONTRIBUTIONS

Xuan Liu conceived the study. Xuan Liu and Zhiyong Yuan supervised the project. Xuan Liu and Yanhua Hong designed the study. Yanhua Hong and Xuan Liu collected and analyzed the data. Yanhua Hong, Xuan Liu, and Zhiyong Yuan wrote the manuscript.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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