Risks of biological invasion on the Belt and Road

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Summary

China's Belt and Road Initiative (BRI) is an unprecedented global development program that involves nearly half of the world's countries [1]. It will not only have economic and political influences, but also may generate multiple environmental challenges, and is a focus of considerable academic and public concerns [2-6]. The Chinese Government expects BRI to be a sustainable development, paying equal attention to economic development and environmental conservation [7]. However, BRI's high expenditure on infrastructure construction, by accelerating trade and transportation, is likely to promote alien species invasions [5], one of the primary anthropogenic threats to global biodiversity [8]. BRI countries may have different susceptibilities to invasive species due to different financial and response capacities [9]. Moreover, these countries overlap 27/35 recognized global biodiversity hotspots [10]. Identifying those areas with high invasion risks, and species with high invasive potentials within BRI countries, therefore, is of vital importance for the sustainable implementation of the BRI, and the development of early, economical, and effective biosecurity strategies [11]. In response, we present here a comprehensive study to evaluate invasion risks by alien vertebrates within BRI. We identified a total of 14 invasion hotspots, the majority of which fall along the six proposed BRI Economic Corridors, with the proportion of grid cells in invasion hotspots 1.6 times higher than other regions. Based on our results, we recommend the initiation of a project targeting

early prevention, strict surveillance, rapid response and effective control of alien species in BRI countries to ensure that this development is sustainable.

Key words: biological invasions, Belt and Road Initiative, developing world, habitat suitability, introduction risk, species distribution model, sustainable development

Results and Discussion

The BRI currently includes more than 120 countries linked by six proposed land-based Economic Corridors between core cities and key ports, along traditional international transport routes, to strengthen connectivity and cooperation between BRI countries (Figure 1). We provide grid-based estimates of current invasion risks for 816 global established alien terrestrial vertebrates across four taxa (98 amphibians, 177 reptiles, 391 birds and 150 mammals, Data S1), for a total of 37,430 grid cells at a resolution of 0.5 ° across BRI countries, based on risk analyses of species introduction and establishment [9], which are two main stages of the invasion process [12].

Introduction risks among BRI regions

We first quantified introduction risks based on spatial data on trade, air passenger numbers, cargo volumes to airports, and cargo volumes to shipping ports (“introduction vectors”) across BRI countries. As trade and transport data are only available at the country level, we applied the “introduction epicentre” framework [9] to quantify the introduction risk for each grid cell across 121 BRI countries with available introduction data. We ranked all grid cells and defined areas of high introduction risk as those grid cells with the top 10% highest values for each of the four introduction vectors, and determined the high overall introduction areas according to the highest level posed by any one vector [9].

Our analyses showed that 14.6% of grid cells from 90.9% (110/121) BRI countries have high overall introduction risks (Figure 2A), most of which (42.4%) are at risk from all four vectors simultaneously (Figure S1). Of particular concern, the proportion of grid cells with high introduction risk on the six BRI economic corridors (defined as a 1° buffer zones around each corridor, Figure 1) is 2.5 times higher than other regions (Chi-square test, $\chi^2 = 575.67$, $P < 0.001$).

Habitat suitability among BRI regions

We then quantified habitat suitability using species distribution modelling (SDM) for the 816 alien terrestrial vertebrates in our analysis. SDM is widely used as a powerful tool to quantify habitat suitability in a new location for an alien species [13], as a further fundamental factor determining their establishment [14]. SDMs fit correlative models to species distribution and environmental niches from native and invaded ranges, and then identify the most suitable habitat for the study area [13]. We performed the SDM analysis based on climate variables alone, and then with the addition of habitat variables, including vegetation and water resources, as proxies of species' requirements for food, reproduction, and biotic interactions [15]. We projected suitable environments for each alien species using an ensemble of five SDM algorithms including generalized additive models (GAM), boosted regression trees (BRT), classification tree analysis (CTA), multiple adaptive regression splines (MARS) and random forest (RF), which are powerful methods for predicting habitat suitability of species under climate change, or as alien species [16].

For all SDMs, two measures evaluating predictive power (the area under a receiver operating characteristic curve, AUC, and the true skill statistic, TSS) revealed good model performance when we used climate variables alone (mean ± S.E., AUC: 0.939 ± 0.00048; TSS: 0.828 ± 0.00094; Figure S2), and when we used climate and habitat variables together (AUC: 0.935 ± 0.00049; TSS: 0.824 ± 0.00098; Figure S2). SDM predictions show that 67.8% (82/121) of BRI countries have high climatic suitability (defined as those grid cells with the top 10% highest species richness) for the 816 alien terrestrial vertebrate species (Figure 2B). As with introduction risk, areas with high habitat suitability are also concentrated on the six BRI corridors. The predicted richness of alien terrestrial vertebrates for grid cells on these economic corridors is approximately 1.1 times higher than other regions (Kruskal-Wallis test, $\chi^2 = 479.01$, $P < 0.001$).

Combined invasion hotspots among BRI regions

Finally, we determined combined invasion hotspots by overlapping areas with high introduction risk and areas with high climatic suitability. We identified a total of 14 combined invasion hotspots covering 68 BRI countries (Figure 3), which primarily include (1) Caribbean islands, (2) central America, (3) southern America areas mainly in central Chile, (4) northern Africa areas including northwest Morocco, northeast Tunisia and northern Algeria, (5) some scattered areas in west Africa including southern Ghana, northern Nigeria, northern Togo, western Cameroon, western Gabon and northern Cote d'Ivoire, (6) some scattered areas in east Africa including central Ethiopia, northern Tanzania and central Kenya, (7) south-eastern coastal areas of South Africa and south Mozambique, (8) south-eastern European areas including Malta, southeast Slovenia, northern Croatia, central Bosnia and Herzegovina, southern Montenegro, central and northern Serbia, central and southern Greece, western Albania and the northern Caucasus regions of Russia, (9) western Asian and eastern European areas including central to west Turkey, southeast Azerbaijan, Lebanon and western Syria, (10) southern Asian areas including Bangladesh, northeast India, Sri Lanka and northern Pakistan, (11) eastern Asian areas including southern part of South Korea, southeast and southwest China, (12) southeast Asian areas including Brunei, Vietnam, southern Thailand, Malaysia, Singapore, Philippines, and the Indonesian island of Java, (13) south Pacific island countries including Fiji and Samoa, and (14) northern and scattered south-central parts of New

Zealand. These invasion hotspots are also mainly located on the six proposed economic corridors, although there are some scattered areas outside these corridors (Figure 3). The proportion of grid cells with combined invasion hotspots is 1.6 times higher on corridors than on non-corridor grid cells (Chi-square test, $\chi^2 = 41.43$, $P < 0.001$).

Some areas are predicted to have lower habitat suitability but higher risk of alien species introduction. A biosecurity plan to prevent alien invasions needs to prioritise these areas because aliens may be able to establish in these suboptimal habitats when propagule pressure (the number of individuals introduced into a region) is high [17]. Such areas mainly include some southeast European areas in Austria, Czech Republic, Hungary, Slovakia, Lithuania, Romania, Bulgaria, central Serbia, northeast Croatia, and central Azerbaijan; western Asian and eastern European areas such as Bahrain, Kuwait, Qatar, east Turkey, Oman, United Arab Emirates and Israel; some African regions in Djibouti and Cape Verde; and Asian countries including northern India, central and north Thailand, central to northern parts of South Korea, and most of central and eastern China (Figure 2A; Figure 3).

There are also areas with suitable habitats for the alien species in our analysis, but low introduction risk. These areas should also be monitored closely as most are located in global biodiversity hotspots, and the deleterious impacts of alien species that do arrive in such regions can be high. These areas mainly include the Himalayas, Madagascar, Seychelles, central Bolivia in the tropical Andes, northern South America including eastern Venezuela, Guyana and southern Suriname, some African regions including the Succulent Karoo, Guinean forests of West Africa, Coastal forests of eastern Africa, the Sundaland areas in Kalimantan, Sumatra, and Sulawesi, Papua New Guinea, and central to southern New Zealand (Figure 2B; Figure 3).

Sensitivity of analyses to data and modeling uncertainty

To test the sensitivity of our results to data and modelling uncertainties, we re-conducted all our analyses using only data on the value of the live terrestrial vertebrate trade, using projections based on analogous and non-analogous climates together, incorporating climate plus habitat predictors into SDMs, and using different thresholds (i.e., the top 20% and 25%) to define high introduction risk and high habitat suitability. We obtained similar results under all these trade, climate, model and threshold scenarios, indicating that our results are robust to data uncertainty (Figure S3).

Nevertheless, we acknowledge that there are other uncertainties inherent in all predictive studies. For example, although we restricted our study species to those occupying more than 15 grid cells in order to minimize the potential influence of small occurrence numbers on SDM performance [18, 19], it is still not possible fully to eliminate issues of extrapolation in SDMs. In addition, although we did not detect an obvious signal of variable collinearity (based on a 0.75 cut-off that has been used in previous large-scale studies modelling climatic effects on alien species distributions; e.g., [20]; Table S1), we cannot completely eliminate issues of multi-collinearity among our climate variables. Finally, since the BRI started only five years ago, it is not yet possible to evaluate its impacts on invasions. Interestingly, the predicted higher invasion risk in economic corridor regions than non-corridor regions implies that invasion risk may increase considerably in the future. Our analyses are the best possible in the circumstances, but could be improved in the future by including long-term trade and transportation prediction data, when they become available.

Our study provides the first step in assessing introduction risk and habitat suitability for alien terrestrial vertebrates within the BRI region, and has clear management implications. We propose tiered biosecurity precautions to reduce introduction and secondary spread, rigorous quarantine and surveillance protocols, and rapid response and effective control of alien species during the implementation of the BRI among partner countries.

Those areas identified as combined invasion hotspots (Figure 3) should be prioritised for the prevention of alien incursions, notably areas within the six planned BRI economic corridors, where we observe both high introduction risk and high habitat suitability for aliens. It is of particular concern that most of the BRI corridors cross several biodiversity hotspots (Figure 1), where we also observe high introduction risk (χ^2 = 1752.01, P < 0.001) and high habitat suitability (χ^2 = 8495.86,

$P < 0.001$), supporting recent concerns that the BRI programme may pose substantial threats to global biodiversity conservation [3,4]. Invasive alien species (IAS) prevention projects could primarily target those species with high habitat suitability for each BRI country in our present study (Data S2). In particular, alien species that have not been detected in a region but have invaded neighbouring regions or the same biogeographic realms should be closely monitored. In addition, emerging IAS that have never been reported elsewhere are on the increase and posing new challenges to biosecurity [21]. BRI countries should be especially vigilant for such species and rapidly communicate such observations in order to implement immediate measures to stop further introductions.

Much of the BRI region faces joint introduction risks from different transport vectors (Figure S1), implying a high likelihood of the ad hoc spread of IAS following arrival in a new region. We thus call for stricter screening for alien wildlife imports from contact commodities, contaminated vehicles and equipment through airports, seaports and along other transportation corridors. In addition, increased biogeographic connectivity as a result of the BRI might facilitate flows of alien species between regions that historically have been poorly connected. Trade origin and circulation data should thus be shared by exporter and importer countries, which can be further applied to trade network analyses to increase the effectiveness of IAS prevention [22].

As many BRI countries have limited economic capacities, we suggest that a special fund should be established to support the operation of proposed biosecurity measures. This fund could be used to enhance research into IAS prevention and eradication techniques, periodical training of volunteers and professionals in taxonomic identification of problematic species, and the collection of species distribution and ecological traits (e.g., life history, diet, parasites, etc.). These data could then be further integrated into GIS-based maps and freely-available online databases with regular maintenance, review, and validation by experts. They could also be shared with resource managers who are interested in the IAS within their areas, and used in scientific research such as SDMs by incorporating finer spatial data to guide further field surveys. It is also essential to organize regular opportunities for communication between scientists, policy makers and public volunteers to share and discuss new knowledge on IAS. It would be particularly helpful to invite international experts from countries outside the BRI region, where the IAS of concern are native or have become invasive, who are familiar with the species distributions, traits, impacts, introduction pathways and eradication approaches, and who can provide constructive recommendations for IAS detection and control.

Despite these environmental challenges, the BRI may also provide opportunities for participating countries to pay greater attention to ecological and environmental conservation during development [3, 4]. For example, while it remains a subject of debate, the Chinese government has been calling for the BRI to be "green, healthy, intelligent and peaceful" and for all recipient countries to "deepen cooperation in environmental protection, intensify ecological preservation and build a green Silk

Road” [10]. As the convenor of this mega-project, we hope China will take this opportunity by working together with participating countries to make BRI not only one of trade and economic development, but also one of sustainable development inclusive of, and beneficial to, the natural environment. Adopting the alien species prevention and management suggestions proposed here would be an important step along that road.

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Author Contributions

YL and XLIU designed the study; XL, XLIU, TS, CH and YL collected the data; XLIU, XL and YL analysed the data; XLIU, TMB and YL wrote the manuscript.

Declaration of Interests

The authors declare no competing interests.

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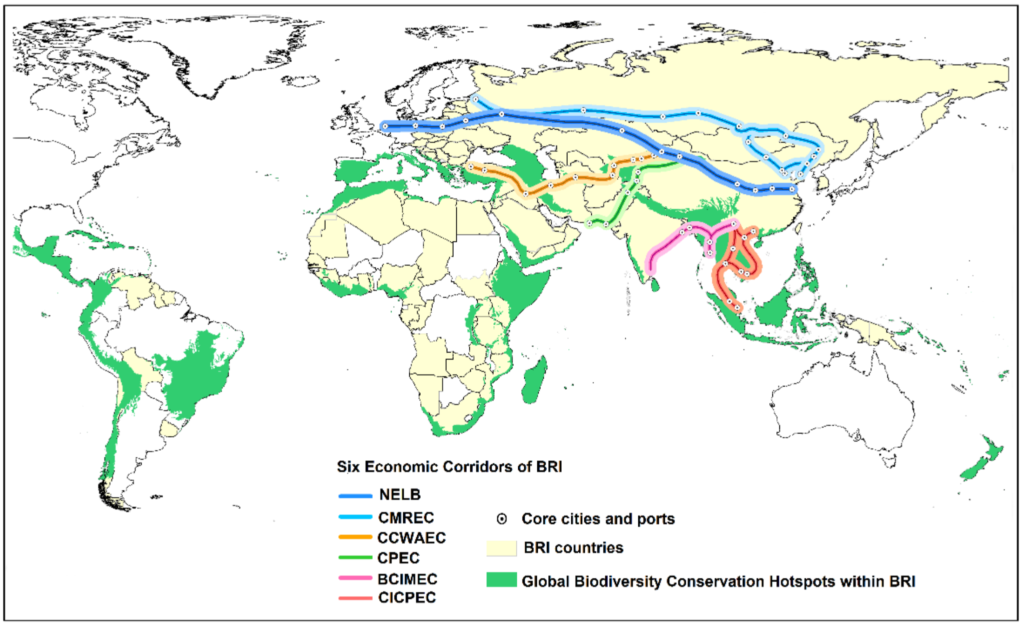
Figure Legends

Figure 1. Location of the 123 BRI countries and six land-based proposed Economic Corridors linking core cities and key ports along traditional international transport routes.



The list of 123 BRI countries is based on the Chinese Belt and Road government website (https://www.yidaiyilu.gov.cn/, last accessed on December 5, 2018). South Sudan and Niue are excluded from data analyses as their trade, airport and seaport data are not available. The location of 6 proposed Economic Corridors are based on National Administration of Surveying, Mapping and Geoinformation of China (http://bzdt.nasg.gov.cn/jsp/browseMap.jsp?picId=%274o28b0625501ad13015501ad2bfc0083%27). NELB: New Eurasian Land Bridge; CMREC: China-Mongolia-Russia Economic Corridor; CCWAEC: China-Central and West Asia Economic Corridor; CPEC: China-Pakistan Economic Corridor; BCIMEC: Bangladesh-China-India-Myanmar Economic Corridor; CICPEC: China-Indo-China Peninsula Economic Corridor.

Figure 2. BRI areas with (A) high introduction risk, and (B) high habitat suitability based on predicted alien terrestrial vertebrate species richness.

See Figure S1 for relative contributions of each single introduction vector and different vector combinations to overall introduction risk. See Data S2 for projected distributions of the 816 alien terrestrial vertebrate species in each BRI country.

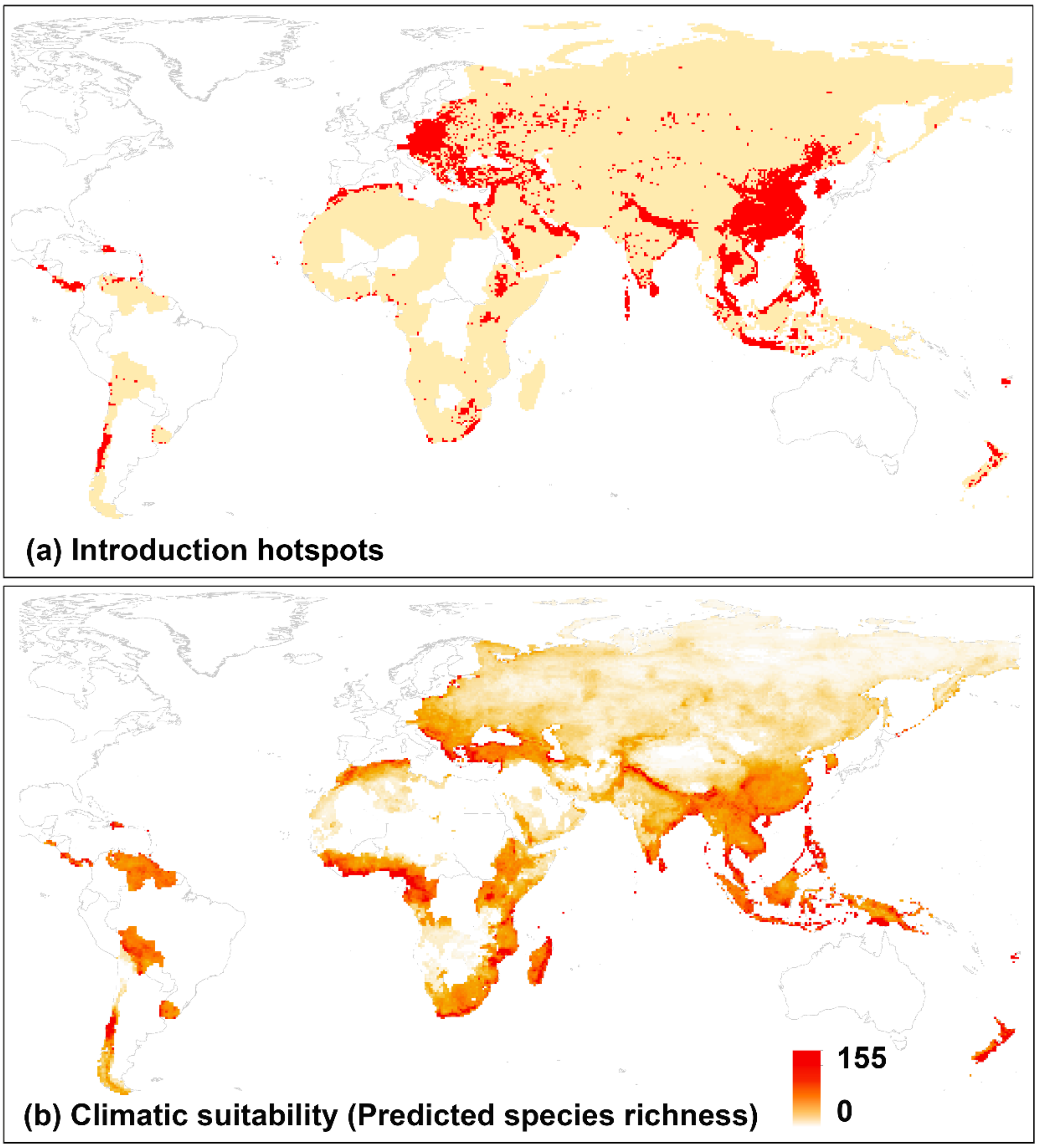
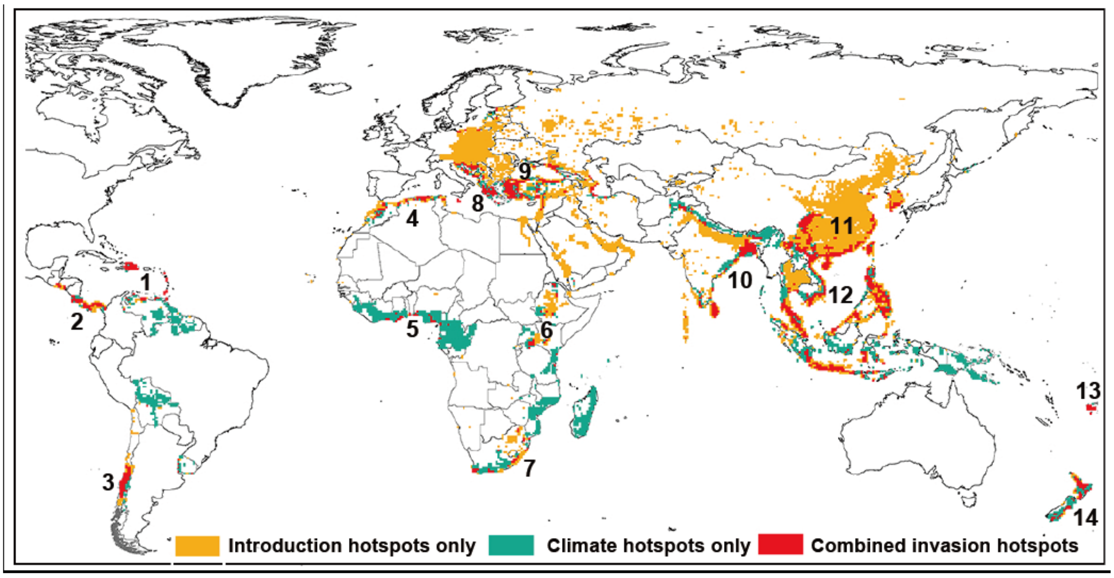


Figure 3. Locations of the 14 overall invasion hotspots with both high introduction risk and high habitat suitability among BRI countries.

The number relates to the 14 invasion hotspots described in the main text. See Figure S3 for further details of invasion hotspots under different prediction scenarios.



STAR METHODS

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Yiming Li (liym@ioz.ac.cn).

METHOD DETAILS

Quantifying introduction risk

Preventing species introduction is considered to be the most effective strategy for IAS management as eradicating aliens following establishment is at best costly and at worst impossible [23]. Introduction risk may be quantified by the value of trade and the capacity of different introduction vectors [9]. Trade can not only represent the probability of intentional and accidental alien species introductions as stowaways, contaminants, pests and pathogens with international commodities [24], but also can act as a proxy for propagule pressure, which is a key determinant of population establishment after introduction [17]. In addition to trade, the probability of species introduction is also correlated with the quantity of various transport vectors such as air passenger numbers, and air and sea cargo volumes [9]. We therefore assess the role of four main introduction vectors (trade value, air passenger numbers, air cargo volume, sea cargo volume) on the introduction risk of exotic terrestrial vertebrates.

As trade and transport data are only available at the country, airport or seaport level, we apply a framework termed as the "introduction epicentre" [9] to quantify the introduction risk for grid cells at a resolution of 0.5° for the BRI region. This method assumes that although there may be a higher likelihood of animals escaping in areas where airports and seaports are located, the spatial distribution of introduction risk is mainly dependent on the final destinations of traded goods and arriving passengers, and therefore is associated with the distribution of local human population density [9, 25]. To achieve this, per capita values of import trade, air passenger numbers, air cargo volumes and sea cargo volumes were first calculated by dividing the total quantity of each introduction vector by total human population size for each BRI country, and then calculating the introduction epicentre by multiplying the per capita value by the human population density of each grid cell [9]. The grid cell resolution of 0.5° here is widely used and is a reasonable resolution at which biosecurity and management decisions can be practically made at large spatial scales [9, 16].

The trade data were collected as the mean annual U.S. dollar value of all goods imported from the years 2007-2016 for each country (except Timor-Leste, Palestine, Somali, and Chad, for which trade data are not available) from the United Nations Commodity Trade Statistics database (Comtrade; http://comtrade.un.org, accessed on December 5, 2018). Previous studies suggest that the pet trade may be more pervasive for terrestrial vertebrates [26]. We detected a highly significant correlation between overall trade and live terrestrial vertebrate trade after excluding farm livestock

(Spearman correlation coefficient $r = 0.769$, $P < 0.001$). Therefore, we present analyses using overall trade in the main text as it not only can reflect deliberate trade, but also can capture unintentional introductions such as illegal trade, which is increasingly regarded as an important introduction pathway for alien vertebrates [27]; we present analysis based on the live terrestrial vertebrate trade in the supporting material (Figure S3). The average annual total human population data from the years 2007 to 2016 for each country were obtained from the World Bank Open Data (https://data.worldbank.org/indicator/SP.POP.TOTL, accessed on March 21, 2018). Human population density data from the year 2015 at 0.5 °resolution were obtained from the Gridded Population of the World (GPW, v4) database from the Socioeconomic Data and Applications Center in NASA's Earth Observing System Data and Information System (EOSDIS) hosted by CIESIN at Columbia University (http://sedac.ciesin.columbia.edu/data/collection/gpw-v4, accessed on May 8, 2018). We calculated the average annual total number of air passengers (unit: million passenger-km), volume of air cargo (unit: million ton-km) and volume of sea cargo (unit: TEU, 20 foot equivalent units) from the years 2007-2016, for each country (except Guinea, Djibouti, Burundi, Grenada, and Dominica for which air passenger data are not available, Guinea, Djibouti, and Burundi for which air cargo data are not available, and Bolivia, Cape Verde, Chad, Burundi, Rwanda, Seychelles, Somalia, Uganda, Zambia and Zimbabwe for which sea cargo data are not available) from the World Bank Open Data (see Key Resources Table, accessed on December 5, 2018).

The air passenger and cargo data were based not only on international airports, but also included domestic airports as species can be secondarily introduced into more regions within a country after arrival, on which the introduction epicentre quantification framework was based [9].

Habitat suitability predictions

Study species and occurrence data

The study species list is based on widely used databases (see Key resource table in STAR methods) on global reptile and amphibian introductions [28] with a recent update [29], the global alien bird invasion database from the Global Avian Invasions Atlas (GAVIA) [30], which is a comprehensive database on establishment status and spatial distributions of global bird invasions, and a global alien mammal species dataset [31] and a recent update [32]. We only used data for those resident species that have established populations in non-native ranges [12]. Furthermore, we excluded species without exact native range information, species re-introduced into their native range, species released within their native ranges, species experimentally introduced to small islets, and data that represented questionable introductions without robust evidence. We obtained native and alien range information for amphibians and reptiles from the International Union for Conservation of Nature (IUCN, www.IUCN.org, accessed on Januray 12, 2018), the Global Invasive Species Database (GISD, http://www.iucngisd.org/gisd/, accessed on January 13, 2018), and the global reptile and amphibian introduction dataset [28, 29]. The native and alien range information for non-native bird species was obtained from the BirdLife International & NatureServe geodatabase (BLINS, available at http://datazone.birdlife.org/species/requestdis, accessed on January 12, 2018) describing the presence, origin and breeding seasonality of bird species around the world, and the GAVIA database [30]. We collected native and alien range information for invasive mammal species from the IUCN database, and the global alien mammal species dataset [31].

Occurrence data on alien terrestrial vertebrates (amphibians, reptiles, birds and mammals) established worldwide in both their native and invaded ranges were collected from a variety of databases (see Key resource table in STAR methods) and an intensive review of published references (Data S1). For those comprehensive geodatabases providing species spatial distributions such as BLINS and GAVIA for birds, we obtained occurrence data by digitizing breeding bird distribution maps at a 0.5 °resolution for further SDM analyses [16]. We paid particular attention to reviewing relevant references to collect supplementary occurrence data for those species distribute in undeveloped and developing BRI territories such as China, which may be underestimated in the public database (Data S1). Most of our collected records have explicit geographic coordinates. For a small fraction of records with only a text description of the sampling locations, we inferred geographic coordinates using mapping tools including Google Maps (http://maps.google.com), Global Gazetteer (Falling Rain Genomics, Palo Alto, USA) and MapQuest (MapQuest Inc., Denver, USA). We carefully checked geographic and taxonomic accuracy for each species and excluded those species without exact native range information or precise occurrence data based on validations of different authority databases across taxa (amphibians and reptiles: [28, 29], birds: BLINS and GAVIA dataset [30], and mammals: [31, 32]), and those locations occupied by migratory species during non-breeding seasons. For analyses, we used only those species occurring in more than 15 grid cells because some algorithms in SDMs may have a limited ability to cope with species with low occurrence data [18, 19, 33]. These criteria resulted in a total of 816 species including 98 amphibians, 177 reptiles, 391 birds and 150 mammals.

Environmental predictor variables

Climate is one fundamental factor explaining species distributions and is widely used in predicting species potential distributions. Nevertheless, habitat factors may also directly and indirectly affect species distributions by influencing food availability, reproduction and biotic interactions. Therefore, we used two sets of environmental predictor variables. First, we used climatic factors alone based on different climate predictors representing the known physiological constraints for different taxa. For amphibians and reptiles, we used a total of eight temperature and precipitation variables: annual average temperature and precipitation, seasonal temperature and precipitation, the minimum temperate of the coldest month, the highest temperature of the warmest month, and the precipitation of the wettest and the driest quarters [34]. For birds, we used six bioclimatic variables: temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, precipitation of wettest month, precipitation of the driest month and precipitation seasonality [16, 35, 36]. For mammals, we used a total of 10 bioclimatic variables based on previous studies of mammal species distribution modelling at large spatial scales [37]: annual mean temperature, mean temperature of the wettest quarter, mean temperature of the driest quarter, mean temperature of the warmest quarter, mean temperature of the coldest quarter, annual precipitation, precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter, and precipitation of coldest quarter. These climatic variables were obtained from the WorldClim database [38] and were rescaled to the 0.5° resolution using a bilinear function, which is considered more realistic than the simpler nearest-neighbour method [39]. Pairwise Pearson rank correlation analyses showed that the coefficients of these climatic predictors for each taxon were all < 0.75 (Table S1), a cutoff frequently used for evaluating climatic collinearity in modelling climate effects on alien species large-scale distribution patterns (e.g., [20]), indicating that these selected predictor variables lack significant multi-collinearity problems.

As well as climate factors, we also conducted supplementary analyses by including two habitat factors – vegetation and water availability – which are key factors influencing species reproduction and food availability [36] (Figure S3). They may also reflect the quality of microhabitat primary productivity, and are regarded as useful surrogates for biotic interactions, which are recognised to be important in species distribution modelling [15]. For the vegetation variable, we calculated the annual normalized difference vegetation index (NDVI) for each grid cell based on the monthly data covering years of 2001-2005 (http://neo.sci.gsfc.nasa.gov/, accessed on February 4, 2018). NDVI is a remote sensing measurement of earth vegetation coverage closely related to net primary productivity and biomass, and is widely used in macroecology and conservation science when direct measurement of productivity is not available [40]. For water resources, we extracted the open waters from the Global Lakes and Wetlands Database (GLWD, http://www.wwfus.org/science/data.cfm, accessed on August 9, 2017) including lakes, reservoirs, and rivers with areas more than 0.1 km^2, after removing saltwater lakes based on the information from the Saline Lakes Database (http://lakes.chebucto.org/saline1.html). We derived a raster dataset for SDMs by calculating the percentage area of open water within each 0.5° grid cell.

Habitat suitability prediction

Species distribution models (SDMs) are a commonly used and powerful tool to identify suitable habitats for potential invaders [13]. We predicted suitable habitats of the 816 alien terrestrial vertebrates by applying an ensemble of five different algorithms that have been widely used and demonstrated to have good performance in SDMs [16, 41]: generalized additive models (GAM), boosted regression trees (BRT), classification tree analysis (CTA), multiple adaptive regression splines (MARS) and random forest (RF). We conducted model analyses in the *biomod2* package in R 3.2.3 using the default settings of each algorithm [42]. These algorithms fit statistical relationships between the species' current native and invaded geographic distributions and the corresponding climatic or climatic plus habitat predictors, with a higher habitat suitability value for a given grid cell indicating a higher relative probability of species' presence.

We developed the SDMs using occurrence data from both species native and invaded ranges in order to avoid underestimating a species' entire occupied niche, because alien terrestrial vertebrates may be able to invade novel realized niches in new ranges [43-45]. SDMs are regarded as quite sensitive to sampling bias in species occurrence data [33]. Thus, we applied a target-group method to minimize potential sampling bias on our results [31]. We used all occurrence data from the Global Biodiversity Information facility (GBIF, http://www.gbif.org) for each taxon as the background data representing available sampling areas to account for the distribution of sampling effort for each taxon across the globe [46]. This approach allows background data having the same sampling bias as the species occurrence data, which has been widely used and shown a good performance to deal with sampling bias issue in SDMs [47]. As there are different sample sizes among taxa, ranging from relatively small range sizes for herpetofauna to wider distributional ranges for mammals and birds, we randomly chose 30,000 background data points for amphibians and reptiles, 70,000 background data for mammals, and 100,000 for birds to run each simulation

[35]. Equal weights were given to presence data and background points (i.e., 50% balancing the weights of presences and background points to a prevalence of 0.5) [13, 35]. We calibrated models and evaluated their performances using 70% of the dataset as training data, and projected onto the remaining 30% as test data. We conducted a fivefold cross-validation of the models using random training data each time. Model performance was measured using two methods: the area under the receiver operating characteristic curves (AUC) and true skill statistic (TSS). AUC values range from 0.5 to 1, with values of 0.7 - 0.9 indicative of good model performance, and values > 0.9 of excellent performance [33]. TSS considers omission and commission errors by summing sensitivity and specificity minus one. It ranges from -1 to 1, with values < 0.4 indicating poor model performance, 0.4 - 0.8 fair to good performance, and > 0.8 excellent performance [48] (Figure S2).

When SDMs are projected to new geographic regions, there are usually non-analogous climates – regions where at least one climatic variable has a value outside its range in the training region – which can lead to uncertainties in model predictions [49]. In order to make conservative predictions and minimize such uncertainties, we restricted our model projections onto those analogous climates that can be sampled by occurrence and background records in both native and invaded ranges. However, we also conducted supplementary analyses by incorporating non-analogous climates (Figure S3).

We applied an ensemble approach to reduce prediction variations by different SDM algorithms [50]. In order to increase model prediction accuracy, we excluded those models with AUC < 0.8 or TSS < 0.6 from the final ensemble prediction [13]. We assigned weights to each model based on their TSS values and constructed ensemble models by calculating the weighted mean of environmental suitability across the predictions [13].

The prediction results based on presence-background SDMs always generated continuous environmental suitability, which are difficult to compare across species. Therefore, we followed previous studies using a threshold maximizing TSS method to convert continuous SDM outputs into species presence (1) and absence (0) predictions, and then estimated the total number of species for each grid cell by summing the resultant presence-absence maps [16].

Identifying combined invasion hotspots

We defined grid cells with the top 10% highest trade value, air passenger numbers, air cargo volumes and sea cargo volumes as high introduction risk areas for each of the four vectors. We then identified areas with overall high introduction risk according to the highest level of risk posed by any one of the vectors assuming that the four vectors are not additive [9]. Regions with high habitat suitability were defined as those grid cells with the top 10% highest projected number of species. We finally investigated the spatial overlap of introduction risk and habitat suitability, and quantified grid cells as combined invasion hotspots when both introduction risk and habitat suitability are high [9]. To avoid uncertainty from the threshold choice in defining high introduction risk and habitat suitability, we also used 20% and 25% cut-offs to assess the consistency of our results (Figure S3).

Data file titles

Data S1. The databases and literatures used for the collection of occurrence data of 816 global alien amphibian, reptile, bird and mammal species. Related to STAR Methods.

Data S2. Projected distributions of 816 global alien terrestrial vertebrate species in 121 BRI countries based on analogous climate variables. Related to Figure 2.

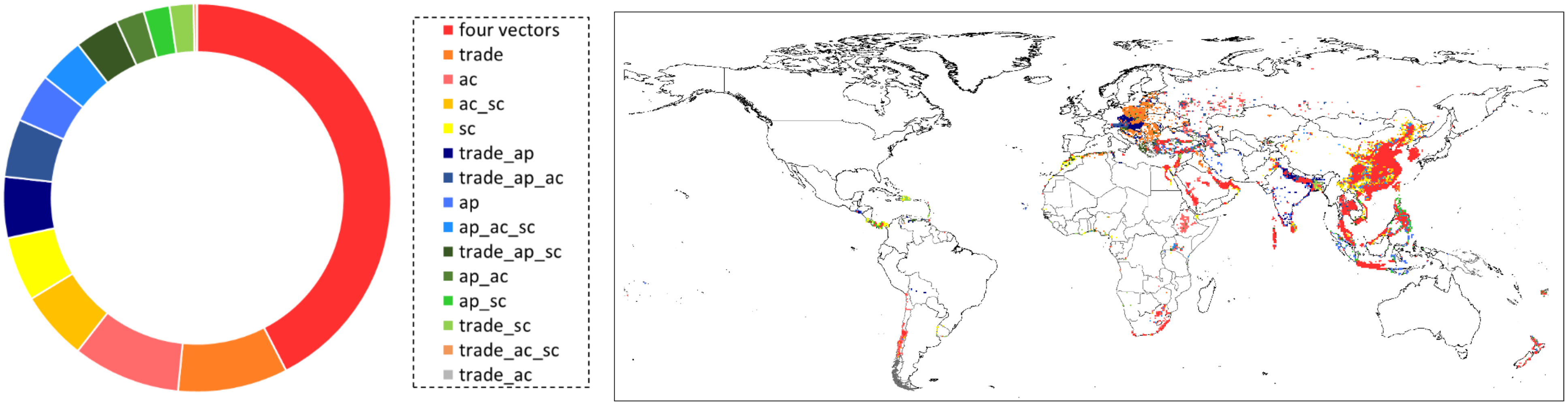


Figure S1. Relative contributions of each single introduction vector and different vector combinations to overall introduction risk and their corresponding geographical locations along BRI countries. Related to Figure 2.

ap: air passenger numbers, ac: air cargo volumes, sc: sea cargo volumes.

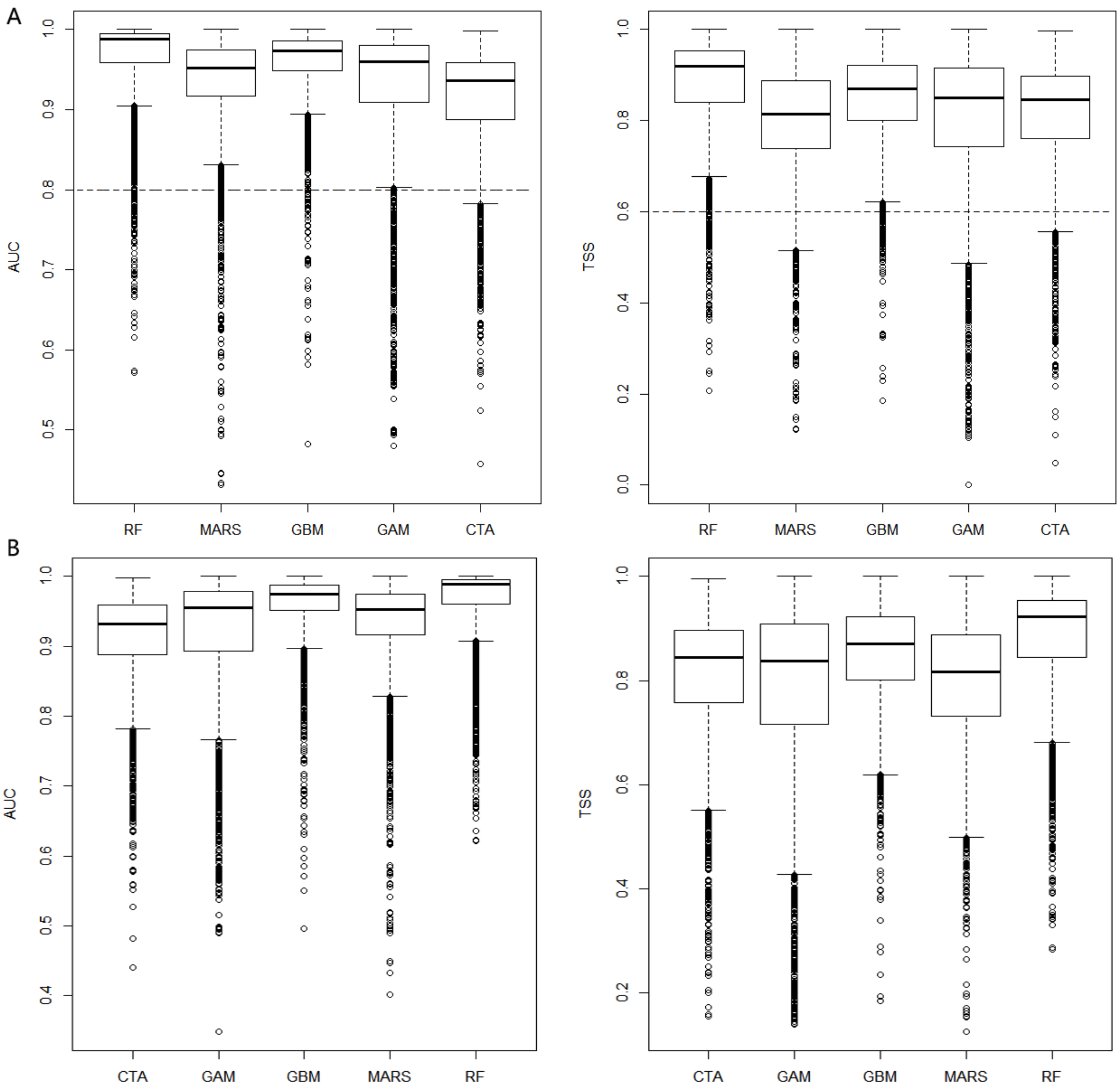


Figure S2. Model performance for all five calibrated models using AUC and TSS based on climate variables only (A) and based on climate and habitat variables together (B). Related to STAR Methods. Dashed lines indicate thresholds used in our ensemble approach. The black line inside the box indicates the median. The bottom and top boarders represent the first and third quartiles. The upper whisker extends from the upper border to the highest value that is within 1.5 times of inter quartile range (distance between the first and third quartiles) from the third quartile. The lower whisker extends from the lower border to the lowest value within 1.5 times of inter quartile range of the first quartile.

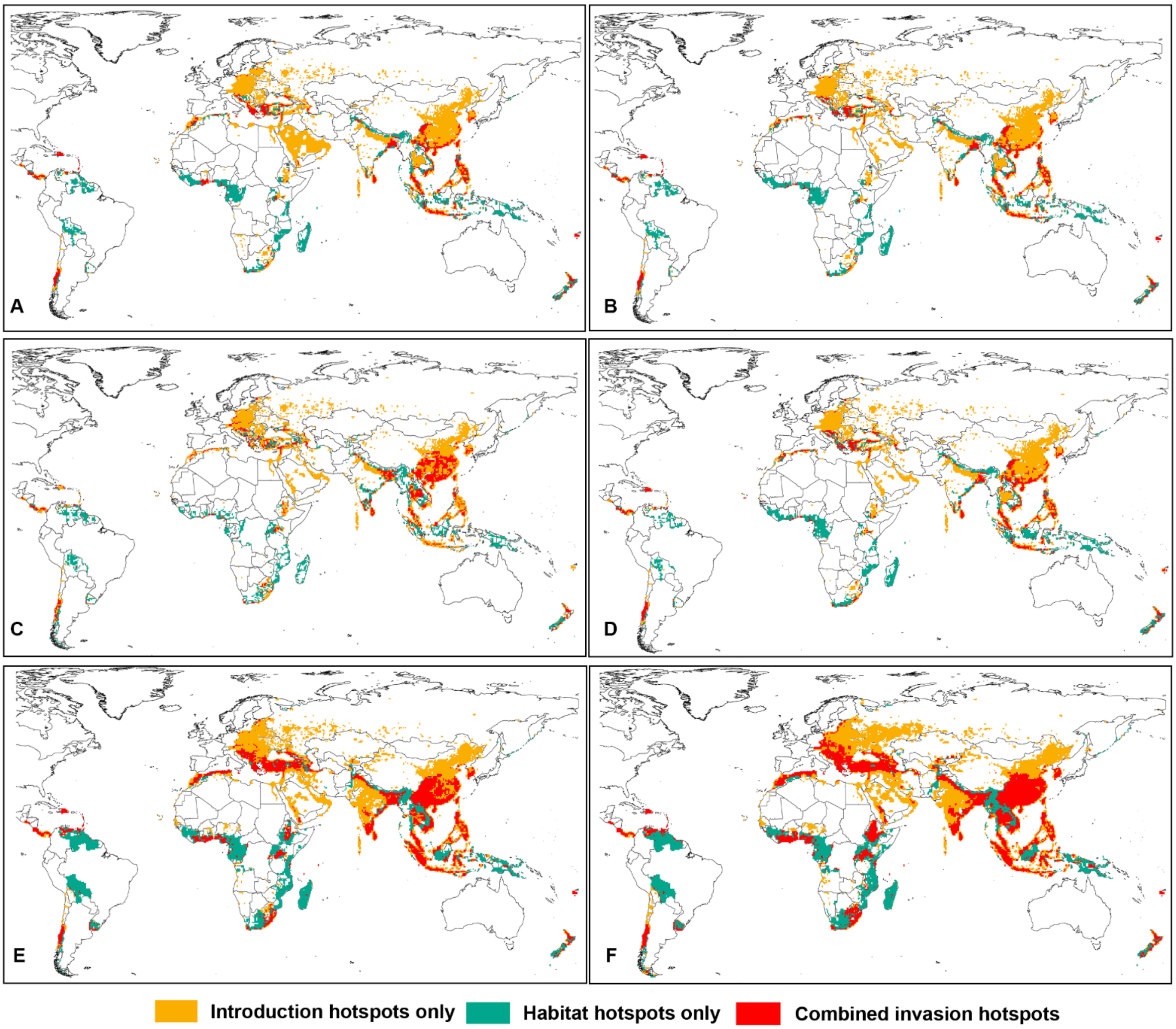


Figure S3. Combined invasion hotspots based on areas with high introduction risks and high habitat suitability under different prediction scenarios. Related to Figure 3.

(A) introduction hotspots using live vertebrate trade; (B) species richness projected using climate only variables when the projections are extrapolated to non-analogue conditions; (C) species richness projected using climate and habitat variables together; (D) species richness projected using climate and habitat variables when the projections are extrapolated to non-analogue conditions; (E) invasion hotspots were defined as the top 20% highest introduction and habitat factors; and (F) invasion hotspots were defined as the top 25% highest introduction and habitat factors.

Amphibian

	bio4	bio5	bio6	bio12	bio15	bio16	bio17
bio1	-0.536	0.725	0.737	0.529	0.508	0.586	0.179
bio4		0.167	-0.870	-0.295	-0.046	-0.338	-0.053
bio5			0.304	0.347	0.566	0.379	0.137
bio6				0.480	0.274	0.524	0.159
bio12					0.180	0.720	0.713
bio15						0.451	-0.368
bio16							0.414

Reptile

	bio4	bio5	bio6	bio12	bio15	bio16	bio17
bio1	-0.203	0.712	0.730	0.502	0.657	0.575	0.169
bio4		0.382	-0.725	-0.255	-0.032	-0.304	-0.025
bio5			0.318	0.298	0.610	0.341	0.115
bio6				0.530	0.416	0.589	0.183
bio12					0.122	0.716	0.740
bio15						0.390	-0.345
bio16							0.444

Bird

	bio5	bio6	bio13	bio14	bio15
bio4	-0.229	-0.736	-0.218	0.180	0.109
bio5		0.653	0.353	-0.117	0.519
bio6			0.407	-0.106	0.164
bio13				0.483	0.288
bio14					-0.457

Mammal

	bio8	bio9	bio10	bio11	bio12	bio16	bio17	bio18	bio19
bio1	0.741	0.746	0.724	0.736	0.404	0.480	0.062	0.328	0.194
bio8		0.461	0.738	0.644	0.311	0.409	0.044	0.461	-0.013
bio9			0.731	0.902	0.325	0.375	0.014	0.109	0.279
bio10				0.763	0.287	0.368	0.018	0.278	0.115
bio11					0.337	0.412	-0.031	0.225	0.128
bio12						0.735	0.732	0.725	0.728
bio16							0.574	0.715	0.621
bio17								0.652	0.714
bio18									0.470

Table S1. Pearson correlation coefficients among climatic predictor variables used for species distribution modeling among different taxa. Related to STAR Methods.

bio1: Annual Mean Temperature, bio4: Temperature Seasonality (standard deviation *100), bio5: Max Temperature of Warmest Month, bio6: Min Temperature of Coldest Month, bio8: Mean Temperature of Wettest Quarter, bio9: Mean Temperature of Driest Quarter, bio10: Mean Temperature of Warmest Quarter, bio11: Mean Temperature of Coldest Quarter, bio12: Annual Precipitation, bio13: Precipitation of Wettest Month, bio14: Precipitation of Driest Month, bio15: Precipitation Seasonality (Coefficient of Variation). bio16: Precipitation of Wettest Quarter, bio17: Precipitation of Driest Quarter, bio18: Precipitation of Warmest Quarter.