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esa ECOSPHERE

Major drivers of invasion risks throughout the world

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Abstract. In this paper, we investigate how climate, land use, habitat characteristics, and socioeconomic activities contribute to predict the current potential distributions of the "100 among the world's worst invasive alien species". We calculated the predictive power of each of the 41 variables for the 95 species including a large number of plants, vertebrates and invertebrates. We then calibrated the species distribution models with a set of appropriate variables for each invasive alien species to predict the potential distribution of these species and identify the major regions of origin of the invasive alien species. We found that climate variables were primarily predictors of the distribution of the global invaders studied. In addition, the habitat characteristics were also important predictors following by the socioeconomic variables such as the nearest distance to airports, seaports and human population density. We show that the potential areas at the highest risk of invasions from these species are located in Western Europe, Eastern United States, Central America, the eastern coast of Australia, and some Indonesian islands. We argue that these potential hotspots of invasions should be monitored in priority to prevent new invasions from these species. This study provides evidence of the importance of considering both habitat characteristics, socioeconomic and climate change factors for the current and future predictions of biological invasions.

Key words: invasive species; socioeconomic; spatial risk.

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Introduction

Increasing trade and tourism associated with globalization and the expansion of the human population have facilitated the intentional and unintentional movements of species outside their natural boundaries (Levine and D'Antonio 2003, Hulme 2009). For example, the risk of biological invasions in marine environments caused by worldwide shipping movements (through with discharge of ballast water and hull fouling organisms) is increasing globally (Seebens et al. 2013). Consequently, many alien species have been introduced into new regions and of them, a small proportion have become invasive (Jeschke and Strayer 2005). Invasive alien species (IAS) have serious impacts not only on native biodiversity, but also on the economy and human health (Vilà et al. 2010, Simberloff et al. 2012). Recently, the number of IAS has drastically increased around the world, particularly in Europe (Waage et al. 2008, Hulme 2009, Butchart et al.

2010), China (Xu et al. 2012), New Zealand, Australia, South Africa and North America (Levine and D'Antonio 2003, Aukema et al. 2010, Leadley et al. 2014), despite a significant increase in the number of national and international IAS policy plans (Butchart et al. 2010). For these reasons, better anticipation of the spread of IAS and mitigation of their effects have become major challenges for conservation. In particular, we need to understand their basic requirements to survive, establish and spread, and to use this information to assess invasion risks.

Climatic similarity with the native region is considered an essential requirement for successful invasions (Thuiller et al. 2005, Ficetola et al. 2007, Gallien et al. 2010), but other abiotic factors can also play an important role. For instance, the propagule pressure is one of the key drivers of successful introduction of IAS (Hulme 2009). As a result, presence of IAS strongly depends on socioeconomic activities (Pysek et al. 2010, Essl et al. 2011) especially transport and tourism that are directly associated with the pathways of introduction (e.g., ornamental trade and tourism, Hulme 2009), or the intensity of anthropogenic disturbance (Hulme 2009, Pysek et al. 2010, Spear et al. 2013, Dalmazzone and Giaccaria 2014). For instance, sea-ports – a classic symbol of trade and economic development – are important gateways for IAS. The effects of land-use factors are also known as important drivers of IAS (Chytrý et al. 2012, Mattingly and Orrock 2013). Overall, previous studies have shown an important influence of climatic, human (i.e., demography and wealth) and habitat factors (i.e., biotic resistance by native taxa) in explaining the distribution of specific IAS (Chiron et al. 2009, Pysek et al. 2010, Spear et al. 2013). There is, however, no consensus regarding their relative importance and no study has taken into account all four categories of factors (climate, land-use, habitat characteristics and socioeconomic) (Pysek et al. 2010). In addition, most of the few studies that have explored the role of habitat characteristics and socioeconomic factors in biological invasions have focused on single species (e.g., Argentine ants, *Linepithema humile*: Roura-Pascual et al. 2011) or a few taxonomic groups within a particular region (e.g., Europe [Chiron et al. 2009, Pysek et al. 2010], or North Western Europe [Gallardo et al. 2015], or Great Britain [Gallardo and Aldridge 2013]). Understanding which factors are correlated with IAS distribution should be done for a large number of taxonomic groups at a global scale using a large set of predictors. The identification of situations associated with high risks of invasion requires taking into account the main drivers that explain their current distribution. Consequently, this work will help to identify where we should focus our attention to prevent invasions.

In this paper, we investigate the main drivers related to climate, land use, habitat characteristics and socioeconomic variables, which predict the current distributions of 95 out of the 100 among the world's worst IAS (Lowe et al. 2000) including a large number of plants, invertebrates and mammals in terrestrial ecosystems. Then, based on species distribution models and these main drivers, we predict the areas of greatest invasion risks for these IAS worldwide (excluding native ranges) and identify the main regions of origin of these IAS.

Materials and Methods

Species data

IAS data.—The IUCN list of "100 of the world's worst invasive alien species" was created in 2000 by the Invasive Species Specialist Group, a global network of invasion biology experts, with inputs from a wider community of practitioners and scientists (Lowe et al. 2000). This list initially included three micro-organisms, five macro-fungi, four aquatic plants, 30 terrestrial plants, nine aquatic invertebrates, 17 terrestrial invertebrates, three amphibians, eight fishes, three birds, two reptiles and 14 mammals (Lowe et al. 2000). The Rinderpest virus was recently removed from the list, because it has been eradicated, and was replaced by a new species, the Giant salvinia, *Salvinia molesta* (Luque et al. 2013). As recommended by Gallien et al. (2010), we made an extensive search for records of distribution data for the 99 species from both the native and invaded ranges (Bellard et al. 2013). We first collected current distribution data from a variety of online databases (i.e., GBIF, CABI, OBIS, LifeMapper, IUCN and Aquamap). When necessary, we contacted experts to acquire additional data from references and personal communications (GPS data points, information about the real distribution of species

and taxonomy issues to avoid commission errors; see Table S1 for records information). We also removed records corresponding to building or greenhouse presence. Finally, we collected on average 3850 records per species with a minimum of 46 records for the least documented species. Four species were excluded for species distribution modeling because of insufficient numbers of records (<30 occurrences) (i.e., *Asterias amurensis*, *Corbula amurensis*, *Eleutherodactylus coqui*, and *Morella faya*). We therefore performed the species distribution models on 95 IAS. Then, we checked whether the occurrence data corresponded to native or invaded areas, using the Invasive Species Specialist Group (ISSG) and Invasive Species Compedium (CABI) databases. We were able to collect the information about native countries for 87 IAS using these two databases (access July 2014). As a result, Figs 3 and 4 were built for 87 IAS.

Explanatory factors

Four major types of explanatory factors were considered: climatic, land-use, habitat characteristics, and socioeconomic variables, totaling 41 variables (Table S2).

Climatic variables

Climatic data at 0.5 degree resolution (averaged from 1950 to 2000) originated from the Worldclim database (Hijmans et al. 2005). We used the set of 19 bioclimatic variables related to temperature and precipitation. These variables provide a combination of means, extremes and seasonality that are known to influence species distribution (Root et al. 2003). In the case of freshwater species, many studies have revealed strong correlations between spatial patterns and terrestrial climatic variables, and have used species distributions models to successfully predict the distribution of fishes (McNyset 2005) and mussels (Drake & Bossenbroek 2004).

Land-use variables

Land-use and land cover variables were simulated by the Globio3 land model at a 0.5 degree resolution (Alkemade et al. 2009). We reclassified them into 11 land cover type variables by grouping some of them together to only consider major category of land use (Bellard et al. 2013). These land-use variables consisted of the proportion of the grid cell covered by tree cover, regularly flooded tree cover, habitat mosaic, burnt tree cover, shrub cover, herbaceous cover, cultivated and managed areas, bare areas, water areas including lakes, reservoirs and rivers, snow and ice, and artificial surfaces and associated areas.

Habitat characteristics variables

For every grid cell of 0.167°, we calculated species richness derived from the IUCN database for mammals, amphibians, reptiles (IUCN 2013), and from Birdlife International and Nature Serve (2011) for birds. Individual maps for each group were created (i.e., mammals, reptiles, birds, and amphibians) and all groups were also summed together. These species richness variables might be interpreted as a proxy for testing the biotic resistance to IAS: the richer the habitat, the more difficult it could be to invade it (Roura-Pascual et al. 2011 but see Stohlgren et al. 2003, Jeschke and Strayer 2005). We also used the net primary productivity (NPP), which is defined as the net flux of carbon from the atmosphere into green plants per grid cell (Kucharik et al. 2000). We measured habitat heterogeneity with two different surrogates: a Shannon coefficient that represents the diversity of habitat using the land-use variables in each grid cell and the altitudinal variation coefficient for each grid cell (CV SRTM).

Socioeconomic variables as proxy for propagule pressure

Nowadays, several factors are used in the literature as surrogates of propagule pressure, such as economic development and human population density (Pysek et al. 2010, Roura-Pascual et al. 2011, Gallardo and Aldridge 2013). Indeed, many studies have been highlighted that the relationship between the establishment of a novel species and the number of propagules arriving at a given location is one of the key drivers in the establishment of a species (Lockwood et al. 2009, Bacon et al. 2014). For example, many authors have described the role of sea-ports as facilitators of marine invasions (Seebens et al. 2013). In addition, human population density has also been identified as one

of the main predictors of alien species richness at continental scale (e.g., Europe: Pysek et al. 2010).

Here, we used three socioeconomic variables that are likely to mimic propagule pressure: human population density per km^2, distance to the nearest airport and distance to the nearest seaport.

Species Distribution Model Projections

Modeling process

For each species, we used seven species distribution models, within the "biomod2" package (Thuiller et al. 2009). These models are: Generalized Linear Model, Generalized Boosting Trees, Multivariate Adaptive Regression Splines, Random Forest, Flexible Discriminant Analysis, Classification Tree Analyses (see Thuiller et al. 2009 for details about these six modeling techniques) and Maximum entropy (see Elith et al. 2011 for Maximum entropy details). Three sets of pseudo-absences (PAs) were generated by selecting from 1000 to 10 000 random points across the world, according to the number of occurrences N (if $N \leq 1000$ then 1000 PAs were selected, otherwise 10 000 PAs were selected), as recommended by Barbet-Massin et al. (2012), and equal weightings were given to presences and PAs.

We computed response curves for each variable based on the evaluation strip method proposed by Elith et al. (2005). Specifically, this function enables to plot the probability of presence of the species to specific variables. When evaluating the response for a given variable, the values of other variables remain constant to the average values over the known location of the species. The response curves of each species are fitted by the GAM function based on all response curves from the three pseudo-absences runs and the seven models.

Relative importance of the variables to predict the distribution range

Because our modeling protocol is based on various modeling techniques with various criteria, the predictive power of each variable is difficult to assess and compare between models. Therefore, we applied a method that assesses the importance of each variable independently of the modeling technique. This procedure, called the "variable importance" procedure in "biomod2" (Thuiller et al. 2009), includes several steps. First, the model is calibrated with all the variables. Second, a standard prediction is made on the basis of all the variables. Third, the values of the assessed variables are randomized, and a new prediction is made with the randomized variable. Finally, the correlation between the standard prediction and the prediction with the randomized variable is calculated. If the correlation is high, then the assessed variable contributes poorly to the prediction; and the predictive power of the variable is therefore low. Conversely, if the correlation is low, then the predictive power of the variable is high. For each of the variables, this randomization procedure was computed five times per calibrated model, resulting in 45 randomization tests per variable and per species.

Variable selection

Because all the 41 variables are not relevant to predict the current distribution of these IAS, we identified variables that were not intercorrelated and that significantly predicted the current distribution of the given species, using a protocol adapted from Leroy et al. (2014) (Appendix S1 for details). We identified groups of intercorrelated variables using a hierarchical ascendant classification with a distance metric based on Pearson's correlation coefficient at a threshold of 0.7 (Dormann et al. 2007). This resulted in 28 "correlation groups" (Appendix Fig. A1). Then, we identified the variable with highest variable importance value for each group of intercorrelated variables and each species. We did that operation for the 7 algorithms. Finally, we only kept variables that were considered to be important predictors (i.e., highest variable importance value) by at least 50% of the algorithms. This method has the advantage of selecting a subset of variables that are relevant for each species.

Evaluating model performance

We evaluated the predictive performance of each model using a repeated split sampling approach in which models were calibrated with over 80% of the data and evaluated over the remaining 20%. This procedure was repeated three times. We used two different statistical

metrics: True Skill Statistics (Allouche et al. 2006) and the Area Under the receiver operating characteristic Curve (AUC) (Fielding and Bell 1997). AUC values do range from 0.5 to 1 (for models with perfect predictive ability), and AUC above 0.8 are considered to have "good" discrimination abilities (Swets 1988), although it has been recently criticized because of its dependence on parameters such as the prevalence and the spatial extent to which models are carried out (Lobo et al. 2008). Therefore, we also used True Skill Statistics (TSS) that accounts for both sensitivity (i.e., correctly predicted presences/[correctly predicted presences + predicted absences]) and specificity (i.e., correctly predicted absences/[correctly predicted absences + predicted presences]). TSS ranges from −1 to +1, where +1 indicates perfect agreement, and values of zero or less represent a performance no better than random (Allouche et al. 2006). All calibrated models performed very well on the data sets tested here with a mean TSS value of 0.81 and a mean AUC value of 0.95 across the different species (Appendix Fig. A2). This ensured that the interpretations of our results were consistent for all species.

Ensemble modeling approach

Robust forecasts of the distribution of species were built using an ensemble forecast approach that accounts for the variability between the seven species distribution models and provides the central tendency (Araújo and New 2007), only keeping the projections for which the evaluation of the model estimated by TSS were higher than 0.6. Because of the potential problems raised by Lobo et al. (2008) on the use of AUC as a measure of model performance, we used TSS for the final consensus distributions. The final current consensus distributions were obtained by calculating the weighted mean proportional to their TSS evaluation of the distribution for each species (Marmion et al. 2009). Then, we transformed the probability maps obtained from the ensemble projections into binary suitable/non-suitable maps per species, using the threshold, which maximised the TSS, as proposed by Allouche et al. (2006). This ensured the most accurate predictions since it is based on both sensitivity and specificity (Jiménez-Valverde and Lobo 2007). We also took uncertainties of the modeling process into account by discounting variations between modeling techniques, pseudo-absences runs, and cross validations runs in estimates of environmental suitability (Kujala et al. 2013). We exhaustively projected the range of possible outcomes on the basis of our modeling process (7 modeling techniques × 3 pseudo-absence runs × 3 cross-validation runs = 63 projections of environmental suitability per species). From all these projections, we calculated the weighted average probability of occurrence of each pixel (with weights proportional to the TSS evaluation per model), from which we subtracted the weighted standard deviation following Kujala et al. (2013). As a result, pixels with a strong disagreement among model projections (i.e., with a high standard deviation among projections) receive a lower probability of occurrence than pixels with a strong agreement (i.e., with a low standard deviation). This procedure allows us to map regions of high suitability with low model uncertainties by excluding regions of high uncertainties.

Evaluation of major fluxes of IAS among countries

We established fluxes of species from their native to potential invaded areas for the 87 IAS for which information about the native countries was available. To this aim, we calculated the number of times each country received IAS and the number of times each country was the origin of the invasion (i.e., number of IAS that were native from that country). Therefore, we were able to identify the fluxes between native and invaded countries. In order to simplify the map, we classify countries into 13 regions (North America, Central America, South America, Western Europe, Northern Africa, Central Africa, South Africa region, Middle East, Central Asia, Russia, China, South East Asia, Ocean islands and Australia). In addition, we only represent the most relevant fluxes between countries by keeping the fluxes higher than the 50 percentile of all fluxes.

Results

Drivers of IAS distribution

Overall, an average of nine variables was selected per species. Socioeconomic variables

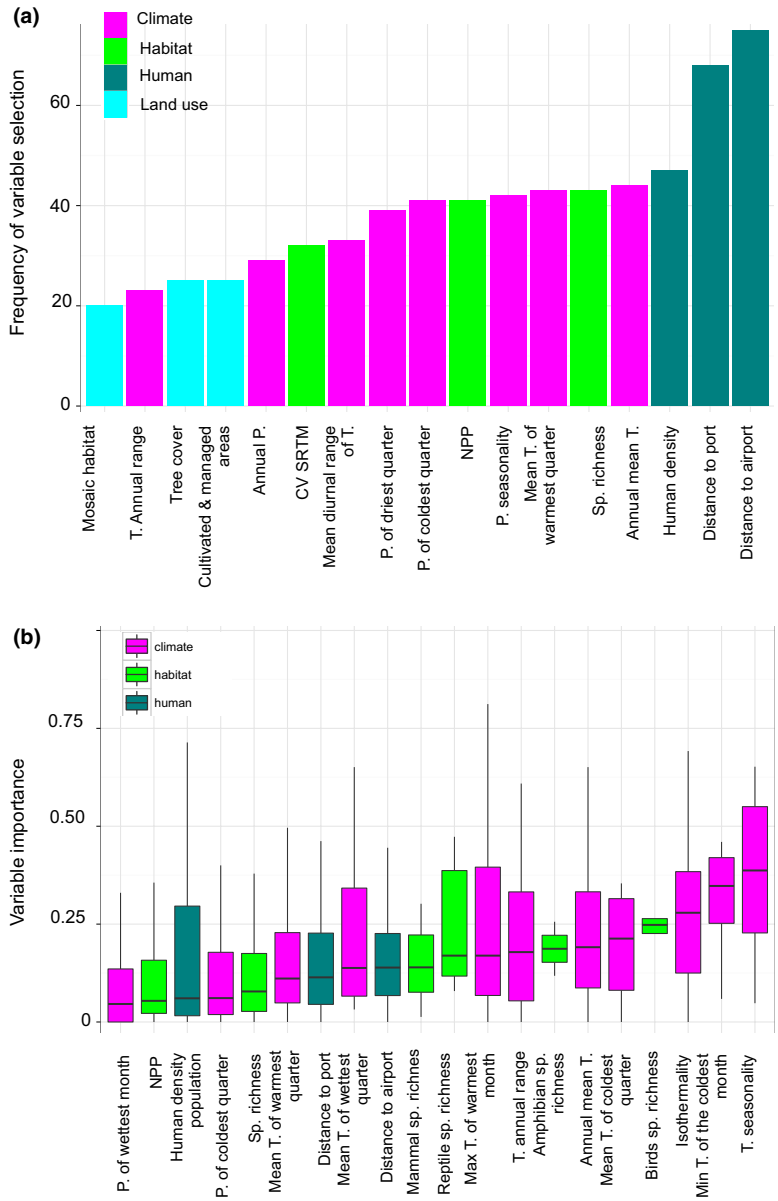

Fig. 1. (a) Frequency of selected variables of climate, habitat characteristics, socioeconomic and land use variables. Only the variables that were selected at least 20 times for the 95 species are shown here. P., precipitation; T., temperature; sp., species; NPP, net primary productivity; CV SRTM, elevational variation coefficient. (b) Boxplot of variable importance ordered by the median importance for climate, habitat characteristics, socioeconomic, and land use variables.

(i.e., distance to the nearest airport, distance to the nearest seaport, and human population density) were the most selected variables, since they were selected for 47 species out of the 95 (Fig. 1A). The second most often selected variables were those related to temperature (i.e., mean annual temperature and mean temperature of the warmest quarter, 43 IAS) and habitat characteristics (i.e, species richness and Net Primary Productivity [43 and 41 species, respectively, Appendix Fig. A3]). Overall, cultivated and managed

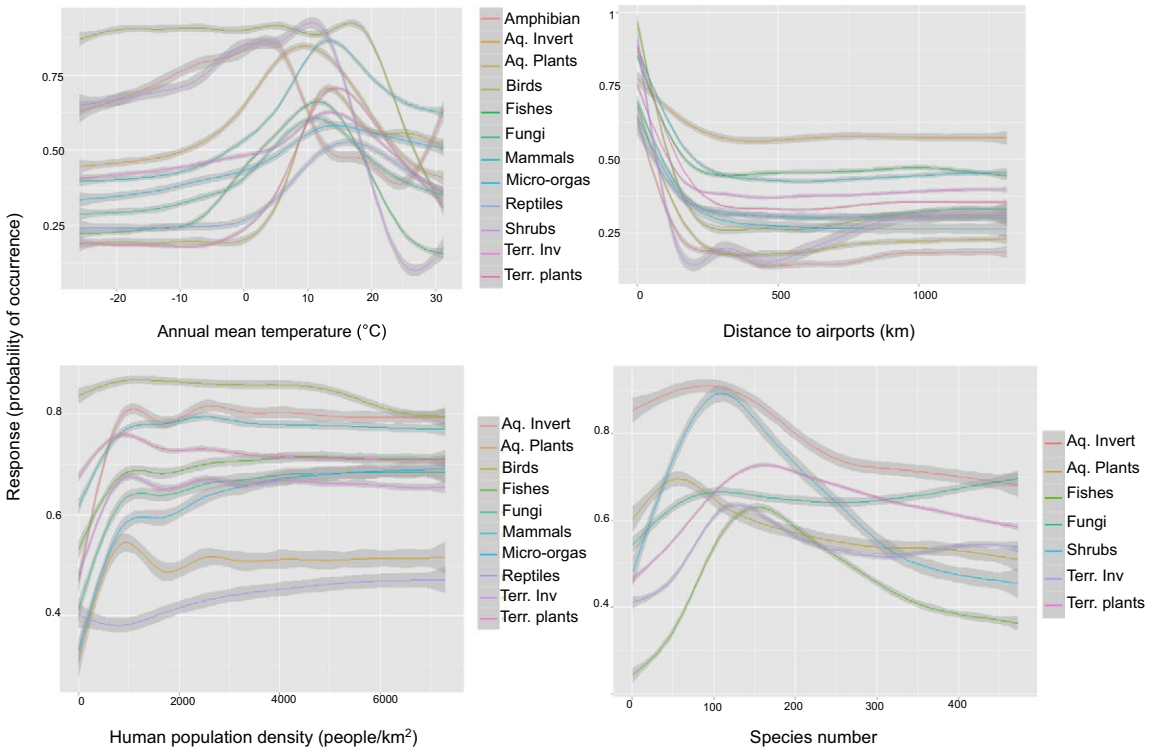

Fig. 2. Predicted responses of the invasive alien taxa to four environmental predictor variables. Solid lines: fitted GAM function based on all response curves from the three Pseudos-absences runs and seven modeling techniques. Gray areas represent 95% confidence intervals.

areas and tree cover were the most selected land-use variables (25 species). We observed that frequencies of selected variables differ across the taxonomic groups (Appendix Fig. A3). For example, nearest distance to seaports was the most selected variable for aquatic invertebrates and plants, and fishes, while nearest distance to airports was the most selected variable for terrestrial plants and invertebrates. The human population density variable was also highly selected for terrestrial plants and invertebrates compared to other taxonomic groups. We also observed that species richness, Net primary productivity and tree cover were highly selected to predict the current distribution of terrestrial plants. The mammal species richness was the most selected variable to predict the current distribution of the invasive mammals studied here. Moreover, the cultivated areas variable was also highly selected to predict the distribution of terrestrial invertebrates.

Regarding the predictive power of variables, climatic variables (i.e., temperature seasonality, minimum temperature of the coldest month and isothermality) were the most important predictors, followed by habitat characteristics variables including species richness variable (Fig. 1B). In particular, reptile and bird species richness are among the most important predictors of the two invasive alien reptiles and the three invasive alien birds, respectively (>0.15). Following these, socioeconomic variables such as distance to the nearest airport or distance to the nearest seaport, and human population density were also found as fair contributors to models for the majority of taxonomic groups. In contrast, land use variables did not explain significantly the current distribution of these IAS. However, specific land use variables appear to be fair predictor for some IAS such as tree cover for invasive alien terrestrial plants ($N = 29$), cultivated areas for terrestrial invertebrates ($N = 17$) and mammals ($N = 14$), water bodies for invasive alien fishes ($N = 8$).

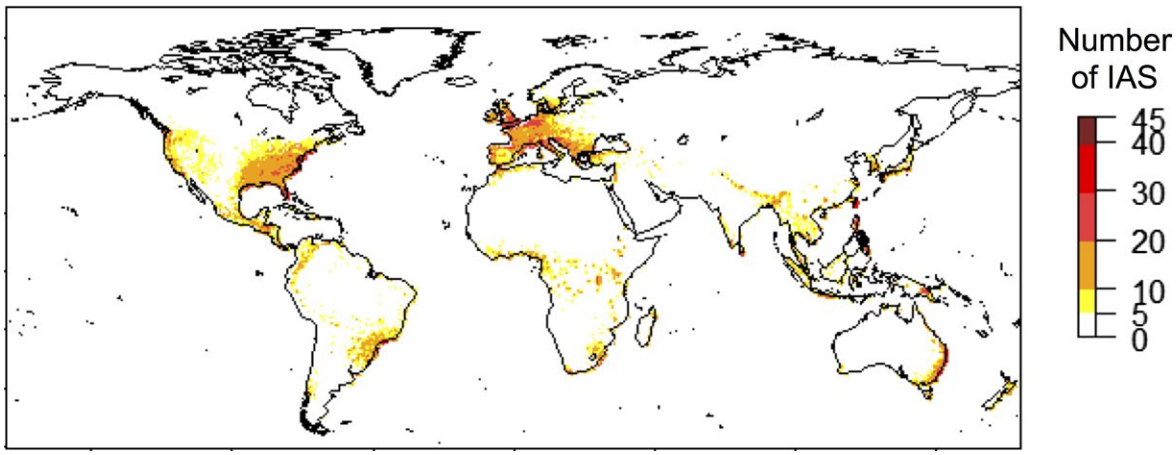

Fig. 3. Map of the potential invasion hotspots (predicted species occurrences across the native range were excluded) using the list of the "100 of the world's worst invasive species". Model uncertainty was discounted (following Kujala et al. 2013) to show solely areas that were predicted to be suitable with certainty (see Materials and Methods for details).

Taxa suitability response to environmental variables

The fitted response curves showed a clear response of the invasive taxa to some of the best environmental predictor variables (Fig. 2). Most of the taxa showed an unimodal response to temperature or precipitation-related variables (Fig. 2 and Appendix Fig. A4, respectively). A strong response was predicted in relation to distance to airports, with a strong increase close to airports (<200 km), especially for terrestrial IAS (Fig. 2). Species response to human population density was also clear, with a rapid increase in the probability of occurrences with increasing human density reaches 2000 at which probability of occurrence levels off, in particular for terrestrial invertebrates (N = 17), plants (N = 29) and mammals (N = 14). The patterns per taxa for species richness were more complex. The probability of occurrence of species was predicted to be low at very low species richness (except for aquatic invertebrates) and then increasing until species richness reached 100–150 species per pixel. Above this value, the probability of occurrences decreased for shrubs, aquatic invertebrates, fishes, terrestrial plants and invertebrates, reptiles, and mammals (see also Appendix Fig. A5). In contrast, the probability of occurrence of the two invasive alien amphibians increased with species richness of amphibians (Appendix Fig. A5).

Suitable conditions for IAS

We have predicted the presence of each IAS and then built a map of IAS richness around the world (Fig. 3). Model uncertainty was discounted to focus solely on areas predicted to be suitable with certainty (see Materials and Methods section). Overall, several large regions were predicted to be currently suitable for a high number of IAS (i.e., between 20 and 50 species): Western and Central Europe, the Eastern part of North America, Central America, the east coast of Australia, and some of the Indonesian islands. South America, Central and South Africa were also suitable for a significant number of IAS (i.e., between 5 and 20 species; Fig. 3). In contrast, regions such as Russia, the main part of Asia, and North Africa as well as most of Australia were not predicted to be suitable to these IAS.

We analyzed the native and IAS movements across regions. Most of the fluxes of invasion into Europe were predicted to come from species native to Asia and North-America, especially regarding plants and invertebrates (Fig. 4 and Appendix Fig. A6). The main risk of invasion in Central America was also predicted to originate from Asia, especially India, China, and Indonesian islands (Fig. 4). Regarding North America, most of the invasive risk originates from Asia, Europe and South America. In contrast, most

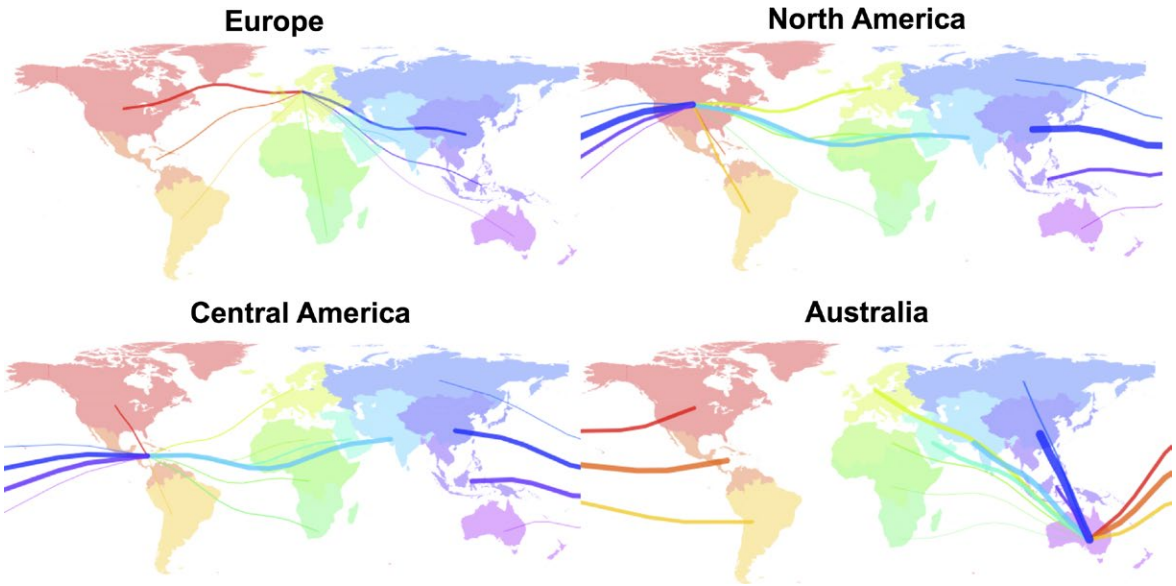

Fig. 4. Map representing the major fluxes of IAS (>0.5 of the total flux in number of IAS, from native regions to the four regions at risk: Europe, North America, Central America and Australia). Width of the line is proportional to the number of IAS contributed by native region. Color of the line depends on the native origin of the species: North America (red), Central America (orange), South America (yellow), Europe (light yellow), North Africa (light green), Central Africa (green), South Africa (dark green), Middle East (light blue), Central Asia (blue), Russia (dark blue), China (dark purple), South East Asia and Ocean islands (purple), and Australia (magenta).

of the risk for Australia originates from species native to Asia and America regarding our sample of IAS. Overall, considering only the major flux (>50% of the total flux in IAS unit) across the different regions, we illustrate that most of these IAS are native to Asia (Appendix Fig. A6). In addition, major fluxes to Europe, Central America and South America mainly originates from areas at similar latitude.

Discussion

We have shown that climate matching and habitat characteristics such as species richness variables – and to a lesser extent socioeconomic factors – were primarily associated with the distribution of the many IAS studied. Despite the inclusion of potential surrogates of disturbed habitats (i.e., land use classes such as cultivated areas), the most important predictors were mainly related to temperature and precipitation. This supports the fact that climate matching between native and invaded regions is an undeniable requirement for successful invasions at a global scale (Thuiller et al. 2005, Ficetola et al. 2007, Gallardo et al. 2015). This result also confirms the importance of using climatic variables in species distribution models to identify the risk of invasions at coarse resolution (but see Pysek et al. 2010). In addition, different climate and temperature variables were selected for each species. This last result shows the importance of selecting appropriate climatic variables for each species.

We also highlighted the fact that probability of occurrence of IAS increases with species richness to reach a peak at 100–150 native species per pixel. This finding supports the hypothesis that some highly productive ecosystem will promote high species richness for both native and IAS (Stohlgren et al. 2003) at least until they reach a specific value. Another possibility is that these IAS are among the worst invaders because they have mainly invaded protected areas where biodiversity is rich and of high interest for conservation. We could also make the hypothesis that the

conditions that prevent rich biodiversity are also likely to make it difficult for exotic organisms to establish. Above this peak, the probability of occurrence for IAS decreases again, maybe because high biodiversity ecosystems offer more biotic resistance to invaders (Kennedy et al. 2002). In this case, preventing decline of biodiversity should be carefully considered as a way of limiting biological invasions. However, this result has not been supported by previous studies (Stohlgren et al. 2003, Jeschke and Strayer 2005, see also Jeschke 2014). Therefore, it is not possible to establish that the relationship between the presence of these IAS and the native species richness is explained by the biotic resistance hypothesis.

Despite that socioeconomic variables (related to nearest distance to airports, nearest distance to seaports and human population density) were selected as a predictor for more than 40 species (i.e., terrestrial invertebrates, mammals, birds, shrubs, aquatic invertebrates, and fishes), they have relatively less important scores to explain the current distribution of these IAS compared to climate or habitat characteristics variables. The importance of socioeconomic variables can be explained by their relationship with the introduction pathways. For instance, nearest distance to seaports was the most selected predictor for all the aquatic invertebrate species. This result tends to confirm the major role of the release of ballast water by increasing global trade and transport of current invasions worldwide (see also Gallardo and Aldridge 2013, Seebens et al. 2013). Moreover, we also found that nearest distance to airport and human population density (proxy of propagule pressure) were also important predictors for terrestrial invertebrates and plants. This result is consistent with increases in the rate of terrestrial biological invasions that have been linked to the continued expansion of the worldwide airline transportation network (Tatem and Hay 2007, Tatem 2009). Gallardo et al. (2015) also highlighted that factors related to human footprints explained a substantial amount of terrestrial IAS distributions over North Western Europe. Overall, increases in the number and spread of alien species have been strongly associated with substantial increases in the extent and volume of trade and transport, particularly over the last 25 yr (Levine and D'Antonio 2003, Hulme et al. 2009).

Despite the importance of land-use variables to predict IAS presence at small scales (e.g., Roura-Pascual et al. 2011, Chytrý et al. 2012), these variables were on average poor predictor variables in our study. This result was consistent across all the taxonomic groups although some specific variables were revealed as fair predictors. For instance, cultivated and managed areas and tree cover emerged as moderately important predictors for at least 20 species (i.e., they were systematically selected but only predict a low proportion of the current distribution of the species). This could be partially explained by the fact that these variables are mostly important at a local level, while the coarse resolution used in this study is not adequate to capture local factors. Another explanation is that climate strongly influences patterns of land cover and use and so already explains a major part these variables at large spatial scales and coarse resolution (Thuiller et al. 2004).

Furthermore, we produced an invasion risk map of IAS that are among the most dangerous, which both excluded the native range of species, and counted a model with high certainty only. This map therefore shows the areas predicted with certainty to be suitable for a large number of these IAS, and thus provides additional insights into invasion risk evaluation at the world scale. We demonstrated that Western and Central Europe, North and Central America, Eastern Australia and some of the Indonesian islands were predicted to be particularly suitable for these IAS. Some of these regions have already been highlighted as a major hotspot of marine invasion (Molnar et al. 2008). On the positive side, these regions have also been highlighted as the hotspot of IAS research except for Central America (Lowry 2012). As all these regions represent some of the most important trade areas around the world, the former regions are likely to be highly vulnerable to invasions and from a management perspective, the importation of these IAS to these regions should be closely monitored to prevent new introductions. Moreover, we also found some "cold-spots" of invasions regarding these IAS (e.g., Africa, major parts of Asia). However, because these areas suffer of a strong research deficit in biological invasions (Bellard and Jeschke 2015), further monitoring and research programs should be implemented to establish

if our findings reflect true "cold-spots" of invasions or reporting bias.

It should be noted that species distribution models have some limitations. In particular it is relevant to take into account additional drivers of invasions such as biotic interactions or local climatic conditions (Araújo and Luoto 2007, Kharouba et al. 2013, Wisz et al. 2013). In addition, species distribution models assume niche conservatism through space and time. In this case, niche shifts in the invaded range might prevent the capture of the full niche of the species, leading to an underestimation of the potential species area (Tingley et al. 2014). The difference in the residence time between these IAS is also likely to influence the results, since recent arrivals are less likely to fulfill their niche. However, it was not possible to take this into account at the world scale because of data availability issues. Moreover, species distribution models only provide potentially suitable areas, but they will not necessarily be fully occupied by IAS (Gallien et al. 2010). In addition, we assumed that some socioeconomic activities such as distance to an airport associated with increasing population density, and different land-use classes were not completely independent, an approximation that may slightly influence our results. Yet, our study provides useful information about the current suitable areas for these major IAS (see Bellard et al. 2013 for future scenarios). Besides, we explicitly took uncertainty into account by following the recommendations from Kujala et al. (2013), and therefore we highlighted only the most conservative results.

Implications for adaptive management of these IAS

The last conference of the parties to the convention on biological diversity in Korea in 2014 reaffirmed the need to continue to identify major pathways and develop a system for classifying IAS. Our analyses provide significant insights to identify species that are likely to be problematic (because their potential range distribution is not filled in) and to identify the main pathway. Overall, our results confirmed that these IAS distributions are highly dependent on climatic suitability at a global scale (Wilson et al. 2007). Therefore, in a context of global warming, taking into account future climate change into management strategies regarding IAS is of high relevance (Courchamp et al. 2014, Bellard et al. 2015). Moreover, because the socioeconomic variables, distance to airport and seaport were also highly selected to explain the presence of these IAS (despite a relatively low predictive power compared to climate variables), taking these drivers into account in future research will provide additional insights to identify and prioritize IAS for control. Strengthened policies to prevent new introductions of IAS via airports and seaports should also be considered carefully with implementation of an international blacklist from these species.

Second, we identified potentially "at risk" regions with respect to these global invaders using the cumulated potential establishment of IAS. The highlighted geographic patterns imply that the biological invasion risks differed across regions. We identified Asia as a major source of IAS to several regions (Australia, Europe, North America, and Central America) with 37 IAS that have their native range in Asia. Research should focus on the drivers and characteristics of these IAS native to Asia to explain their success in other regions. Because fast economic development has also been demonstrated to accelerate biological invasions (Lin et al. 2007), other developing countries highlighted in our risk maps should also be closely monitored regarding these IAS. In addition, we argue that classifying alien species based on the magnitude of their current known impacts is not sufficient (e.g., Blackburn et al. 2014). We know that the residence time between the introduction and the impact of species could be a long process. Therefore, many of these IAS did not fill their entire potential suitable habitat and did not show their full range of impacts. Therefore, such classification should also consider the potential risk of species on a mid-term perspective.

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Literature Cited

Alkemade, R., M. Oorschot, L. Miles, C. Nellemann, M. Bakkenes, and B. ten Brink. 2009. GLOBIO3: a framework to investigate options for reducing global terrestrial biodiversity loss. Ecosystems 12:374–390.

Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 46:1223–1232.

Araújo, M. B., and M. Luoto. 2007. The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography 16:743–753.

Araújo, M. B., and M. New. 2007. Ensemble forecasting of species distributions. Trends in Ecology & Evolution 22:42–47.

Aukema, J. E., D. G. McCullough, B. Von Holle, A. M. Liebhold, K. Britton, and S. J. Frankel. 2010. Historical accumulation of nonindigenous forest pests in the continental United States. BioScience 60:886–897.

Bacon, S. J., A. Aebi, P. Calanca, and S. Bacher. 2014. Quarantine arthropod invasions in Europe: the role of climate, hosts and propagule pressure. Diversity and Distributions 20:84–94.

Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution 3:327–338.

Bellard, C., and J. M. Jeschke. 2015. A spatial mismatch between invader impacts and research publications. Conservation Biology 30:230–232.

Bellard, C., W. Thuiller, B. Leroy, P. Genovesi, M. Bakkenes, and F. Courchamp. 2013. Will climate change promote future invasions? Global Change Biology 19:3740–3748.

Bellard, C., J. Russell, B. D. Hoffmann, C. Leclerc, and F. Courchamp. 2015. Adapting island conservation to climate change. Response to Andréfouët et al. Trends in Ecology & Evolution 30:2–3.

BirdLife International and NatureServe. 2011. Bird species distribution maps of the world. BirdLife International, Cambridge, UK and NatureServe, Arlington, Texas, USA.

Blackburn, T. M., et al. 2014. A unified classification of alien species based on the magnitude of their environmental impacts. PLoS Biology 12:e1001850.

Butchart, S. H. M., et al. 2010. Global biodiversity: indicators of recent declines. Science (New York, N.Y.) 328:1164–1168.

Chiron, F., S. Shirley, and S. Kark. 2009. Human-related processes drive the richness of exotic birds in Europe. Proceedings of the Royal Society of London B: Biological Sciences 276:47–53.

Chytrý, M., et al. 2012. Projecting trends in plant invasions in Europe under different scenarios of future land-use change. Global Ecology and Biogeography 21:75–87.

Courchamp, F., B. D. Hoffmann, J. C. Russell, C. Leclerc, and C. Bellard. 2014. Climate change, sea-level rise, and conservation: keeping island biodiversity afloat. Trends in Ecology & Evolution 29:127–130.

Dalmazzone, S., and S. Giaccaria. 2014. Economic drivers of biological invasions: a worldwide, bio-geographic analyses. Ecological Economics 105:154–165.

Dormann, C. F., et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30:609–628.

Drake, J. M., and J. M. Bossenbroek. 2004. The potential distribution of zebra mussels in the United States. BioScience 54:931.

Elith, J., S. Ferrier, F. Huettmann, and J. Leathwick. 2005. The evaluation strip: a new and robust method for plotting predicted responses from species distribution models. Ecological Modelling 186:280–289.

Elith, J., S. J. Phillips, T. Hastie, M. Dudı, M. Dudík, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17:43–57.

Essl, F., et al. 2011. Socioeconomic legacy yields an invasion debt. Proceedings of the National Academy of Sciences of the United States of America 108:203–207.

Ficetola, G. F., W. Thuiller, and C. Miaud. 2007. Prediction and validation of the potential global distribution of a problematic alien invasive species – the American bullfrog. Diversity and Distributions 13:476–485.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Gallardo, B., and D. C. Aldridge. 2013. The "dirty dozen": socio-economic factors amplify the invasion

potential of 12 high-risk aquatic invasive species in Great Britain and Ireland. Journal of Applied Ecology 50:757–766.

Gallardo, B., A. Zieritz, and D. C. Aldridge. 2015. The importance of the human footprint in shaping the global distribution of terrestrial, freshwater and marine invaders. PLoS ONE 10:e0125801.

Gallien, L., T. Münkemüller, C. H. Albert, I. Boulangeat, and W. Thuiller. 2010. Predicting potential distributions of invasive species: where to go from here? Diversity and Distributions 16:331–342.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.

Hulme, P. E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology 46:10–18.

Hulme, P. E., P. Pysek, W. Nentwig, and M. Vilà. 2009. Ecology. Will threat of biological invasions unite the European Union? Science (New York, N.Y.) 324:40–41.

IUCN. 2013. Available at: http://www.iucnredlist.org/.

Jeschke, J. M. 2014. General hypotheses in invasion ecology. Diversity and Distributions 20:1229–1234.

Jeschke, J. M., and D. L. Strayer. 2005. Invasion success of vertebrates in Europe and North America. Proceedings of the National Academy of Sciences of the United States of America 102:7198–7202.

Jiménez-Valverde, A., and J. M. Lobo. 2007. Threshold criteria for conversion of probability of species presence to either–or presence–absence. Acta Oecologica 31:361–369.

Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. Nature 417:636–638.

Kharouba, H. M., J. L. McCune, W. Thuiller, and B. Huntley. 2013. Do ecological differences between taxonomic groups influence the relationship between species' distributions and climate? A global meta-analysis using species distribution models. Ecography 36:657–664.

Kucharik, C. J., J. A. Foley, C. Delire, V. A. Fisher, M. T. Coe, J. D. Lenters, C. Young-Molling, N. Ramankutty, J. M. Norman, and S. T. Gower. 2000. Testing the performance of a dynamic global ecosystem model: water balance, carbon balance, and vegetation structure. Global Biogeochemical Cycles 14:795–825.

Kujala, H., M. A. Burgman, and A. Moilanen. 2013. Treatment of uncertainty in conservation under climate change. Conservation Letters 6:73–85.

Leadley, P. W., et al. 2014. Progress towards the Aichi Biodiversity Targets: an assessment of biodiversity trends, policy scenarios and key actions. Technical Series 78. Secretariat of the Convention on Biological Diversity, Montreal, Canada, 500 pages.

Leroy, B., C. Bellard, N. Dubos, A. Colliot, M. Vasseur, C. Courtial, M. Bakkenes, A. Canard, and F. Ysnel. 2014. Forecasted climate and land use changes, and protected areas: the contrasting case of spiders. Diversity and Distributions 20:686–697.

Levine, J. M., and C. M. D'Antonio. 2003. Forecasting biological invasions with increasing international trade. Conservation Biology 17:322–326.

Lin, W., G. Zhou, X. Cheng, and R. Xu. 2007. Fast economic development accelerates biological invasions in China. PLoS ONE 2:e1208.

Lobo, J. M., A. Jiménez-Valverde, and R. Real. 2008. AUC: a misleading measure of the performance of predictive distribution models. Global Ecology and Biogeography 17:145–151.

Lockwood, J. L., P. Cassey, and T. M. Blackburn. 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. Diversity and Distributions 15:904–910.

Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the world's worst invasive alien species a selection from the global invasive species database. Invasive Species Specialist Group, Auckland, New Zealand.

Lowry, E., E. J. Rollinson, A. J. Laybourn, T. E. Scott, M. E. Aiello-Lammens, S. M. Gray, J. Mickley, and J. Gurevitch. 2012. Biological invasions: a field synopsis, systematic review, and database of the literature. Ecology and Evolution 3:182–96.

Luque, G. M., C. Bellard, C. Bertelsmeier, E. Bonnaud, P. Genovesi, D. Simberloff, and F. Courchamp. 2013. Monster fern makes IUCN invader list. Nature 498:37.

Marmion, M., M. Parviainen, M. Luoto, R. K. Heikkinen, and W. Thuiller. 2009. Evaluation of consensus methods in predictive species distribution modelling. Diversity and Distributions 15:59–69.

Mattingly, W. B., and J. L. Orrock. 2013. Historic land use influences contemporary establishment of invasive plant species. Oecologia 172:1147–1157.

McNyset, K. M. 2005. Use of ecological niche modelling to predict distributions of freshwater fish species in Kansas. Ecology of Freshwater Fish 14:243–255.

Molnar, J. L., R. L. Gamboa, C. Revenga, and M. D. Spalding. 2008. Assessing the global threat of invasive species to marine biodiversity. Frontiers in Ecology and the Environment 6:485–492.

Pysek, P., et al. 2010. Disentangling the role of environmental and human pressures on biological invasions across Europe. Proceedings of the National Academy of Sciences of the United States of America 107:12157–12162.

Root, T. L., J. T. Price, K. R. Hall, and S. H. Schneider. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60.

Roura-Pascual, N., et al. 2011. Relative roles of climatic suitability and anthropogenic influence in determining the pattern of spread in a global invader. Proceedings of the National Academy of Sciences of the United States of America 108:220–225.

Seebens, H., M. T. Gastner, and B. Blasius. 2013. The risk of marine bioinvasion caused by global shipping. Ecology Letters 16:782–790.

Simberloff, D., et al. 2012. Impacts of biological invasions: what's what and the way forward. Trends in Ecology & Evolution 28:58–66.

Spear, D., L. C. Foxcroft, H. Bezuidenhout, and M. McGeoch. 2013. Human population density explains alien species richness in protected areas. Biological Conservation 159:137–147.

Stohlgren, T. J., D. T. Barnett, and J. T. Kartesz. 2003. The rich get richer: patterns of plant invasions in the United States. Frontiers in Ecology and the Environment 1:11.

Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. Science 240:1285–1293.

Tatem, A. J. 2009. The worldwide airline network and the dispersal of exotic species: 2007-2010. Ecography 32:94–102.

Tatem, A. J., and S. I. Hay. 2007. Climatic similarity and biological exchange in the worldwide airline transportation network. Proceedings of the Royal Society of London B: Biological Sciences 274:1489–1496.

Thuiller, W., M. B. Araújo, and S. Lavorel. 2004. Do we need land-cover data to model species distributions in Europe? Journal of Biogeography 31:353–361.

Thuiller, W., D. M. Richardson, P. Pysek, G. F. Midgley, G. O. Hughes, and M. Rouget. 2005. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Global Change Biology 11:2234–2250.

Thuiller, W., B. Lafourcade, R. Engler, and M. B. Araújo. 2009. BIOMOD – a platform for ensemble forecasting of species distributions. Ecography 32:369–373.

Tingley, R., M. Vallinoto, F. Sequeira, and M. R. Kearney. 2014. Realized niche shift during a global biological invasion. Proceedings of the National Academy of Sciences 28:10233–10238.

Vilà, M., et al. 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers in Ecology and the Environment 8:135–144.

Waage, J. K., J. W. Woodhall, S. J. Bishop, J. J. Smith, D. R. Jones, and N. J. Spence. 2008. Patterns of plant pest introductions in Europe and Africa. Agricultural Systems 99:1–5.

Wilson, J. R. U., D. M. Richardson, M. Rouget, M. A. Amis, L. Henderson, and W. Thuiller. 2007. Residence time and potential range: crucial considerations in modelling plant invasions. Diversity and Distributions 13:11–22.

Wisz, M. S., et al. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biological Reviews of the Cambridge Philosophical Society 88:15–30.

Xu, H., K. Chen, Z. Ouyang, X. Pan, and S. Zhu. 2012. Threats of invasive species for China caused by expanding international trade. Environmental Science & Technology 46:7063–7064.