

LETTER

The intermediate distance hypothesis of biological invasions

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Abstract

Biological invasions are a worldwide phenomenon, but the global flows between native and alien regions have rarely been investigated in a cross-taxonomic study. We therefore lack a thorough understanding of the global patterns of alien species spread. Using native and alien ranges of 1380 alien species, we show that the number of alien species follows a hump-shaped function of geographic distance. We observe distinct variations in the relationship between alien species exchanges and distance among taxonomic groups, which relate to the taxa-specific dispersal modes and their pathways of introduction. We formulate a simple statistical model, combining trade volume and biogeographic dissimilarity, which reproduces the observed pattern in good agreement with reported data and even captures variations among taxonomic groups. This study demonstrates the universality of the intermediate distance hypothesis of alien species spread across taxonomic groups, which will help to improve the predictability of new alien species arrivals.

Keywords

Biogeography, exchange, flows, macroecology, non-native species, origin, patterns of global spread, trade.

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INTRODUCTION

The number of alien species and the impacts they cause increased constantly during the last decades (Pyšek *et al.* 2003; Hulme *et al.* 2008; Lambdon *et al.* 2008; Butchart *et al.* 2010; Vilà *et al.* 2011) and this trend is predicted to continue (Essl *et al.* 2011; Bradley *et al.* 2012; Seebens *et al.* 2015). These developments are a consequence of globalisation with its ever increasing demand for trade and transport, as many alien species introductions can be attributed to the import of commodities (Levine & D'Antonio 2003; Meyerson & Mooney 2007; Hulme 2009; Pyšek *et al.* 2010; Bellard *et al.* 2016). Global trading activities are a major driver of biological invasions leading to a re-organisation of the global distribution of species (Capinha *et al.* 2015). Several attempts have been made to explain the observed patterns of species exchanges, such as relating measures of international trade and economic prosperity of a country to the number of introduced alien species (Pyšek *et al.* 2010; Essl *et al.* 2011; Bradley *et al.* 2012; Bellard *et al.* 2016). However, most studies focus on the number of alien species in the recipient regions, while the global spreading dynamics of alien species including their geographic origins were hardly investigated (Drake & Lodge 2004; Kalusová *et al.* 2013; Seebens *et al.* 2013). Consequently, the global flows of alien species and their relationship with the flows of commodities are poorly understood.

In a recent study of the global spread of marine alien species caused by shipping (Seebens *et al.* 2013), distribution data and model predictions agreed that many marine alien species arrived from donor regions at intermediate geographic distances, while comparatively fewer were introduced over short or long distances. That is, the probability of a new invasion follows a hump-shaped curve as a function of geographic distance between donor and recipient regions with the highest probabilities at around 10 000 km, which was formulated as

the intermediate distance hypothesis (Seebens *et al.* 2013). This was explained by a distance-dependent trade-off between the opposing trends of colonisation pressure and the likelihood of surviving the introduction: Over short distances, species have a high chance to survive transport, but the proportion of potentially alien species transported is low, because in many cases, the native ranges of the species extend into the target region and thus are native there. At large distances, the proportion of potentially alien species transported should be high, but the probability to survive transportation is low. However, it is not known if this relationship of alien species and geographic distance is restricted to ship-mediated introductions or whether this is a pattern universal to biological invasions across taxonomic groups, environments and pathways.

Here, we investigate the global spread of alien species and its relationship with global trading dynamics to test the intermediate distance hypothesis across taxa. We use distribution data of 1380 alien species covering a wide range of taxa and environments to analyse the relationship between the number of alien species and geographic distance between their native and alien regions (countries and islands). We then compare the obtained distance-dependent species numbers to the amount of commodities exchanged along the same distance. To account for potential biases due to the size and distribution of regions, we investigate the pattern using a null model based on a random selection of regions. In a second step, we develop a simple statistical model accounting for propagule/colonisation pressure, expressed as exchanged trade volume, and biogeographic dissimilarity, estimated from the geographical distance between native and alien regions, to predict the number of alien species as a function of geographic distance. We found distinct patterns of the global spread of alien species specific to taxonomic groups, which can be explained to a large amount by global trading dynamics and biogeographic

dissimilarity. The observed patterns are in line with the intermediate distance hypothesis, which seems to be a characteristic of biological invasions universal to various taxonomic groups and environments.

METHODS

Data

Native and alien regions of species were compiled from the 'Global Invasive Species Database' (GISD, www.issg.org, accessed on 22 March 2016) and the CABI Invasive Species Compendium (CABI ISC, www.cabi.org/Iscc, accessed on 10 October 2015). Although these sources contain only a subset of all known alien species, they constitute the most comprehensive global databases for alien species across a wide range of taxonomic groups currently available. They provide distribution data of native and alien ranges of species in a consistent way with a nearly full global coverage (Fig. S1), which is rarely achieved in taxon-specific databases. We used all available information and did not restrict our survey to certain taxonomic groups or time periods. However, we note that very old introduction events (< 1500) are usually poorly documented and likely underrepresented in alien species inventories such as CABI ISC and GISD. Both databases cover many taxonomic groups from bacteria to vertebrates and all environments (marine, terrestrial, freshwater), but most species with provided distribution data are vascular plants (57%), insects (11%), fishes (7%) and mammals (4%). Region names were standardised between databases. Regions mainly refer to countries, while major islands such as Hawaii, Galapagos, Azores, Taiwan etc. were distinguished. Finally, we used native and alien ranges for 1380 species in 253 non-overlapping regions worldwide (Fig. S1).

Using these data, we calculated the flows of alien species from native to alien ranges. As we do not know how often a species was translocated along which routes, we assume that the species was at least introduced once from a native region to an alien region. We further assume that the probability of exchange was the same for all native-alien region pairs of that species. For each species, we calculated the geographic distances as the great circle distance between the centroids of all native-alien region pairs. The country's centroids were provided in the R package 'mapproj' (Bivand & Lewin-Koh 2013), while those of islands were obtained from Weigelt *et al.* (2013). The calculated distances were weighted by the number of native-alien country pairs of that species to ensure that all species contributed equally to the analysis. There are alternative ways to calculate distances between native and alien ranges such as taking the distance between the centroids of the full native and the full alien range or the minimum distance between both ranges, which, however, would distinctly underestimate short and large distances respectively. We therefore considered the distances between all native-alien country pairs as it preserves the full variation in distances between all native-alien country pairs. The obtained weighted numbers of alien species were used for further analysis. We excluded distances between alien-alien regions (secondary spread), because secondary spread can be driven by both

human activity and natural dispersal, which is difficult to disentangle. Considering secondary spread may therefore bias the comparison of alien species spread and trading dynamics.

The calculation of distances between countries is influenced by various factors such as the size of the countries or their distribution on Earth, which have to be considered. Particularly large countries may influence the distance calculation, which may lead to an underestimation of short distances. From CABI ISC, we also obtained subnational regions (provinces or states) for USA, Canada, India, China and Australia, which we used to test for a potential influence of large countries on study results. For this test, we could only use a subset of species provided by CABI ISC ($n = 1084$). We are aware that now subnational data are also provided by GISD, but these data were not available to us at the time of data compilation. Using subnational data affects the calculation of any distance (not only short distances) and reduced small-scale variations (noise), but the overall influence is marginal (Fig. S2). We therefore kept the coarser resolution without subnational levels for these countries, to be able to consider both data sets in our analysis. To address the probably confounding effects of the distribution of countries on Earth, we formulated a null model as a baseline for comparison (see below).

Annual bilateral trade data were used as a predictor for the spread of alien species and were obtained from Gleditsch (2002). This data set comprises trade volumes exchanged between 186 countries during 1950–2000 measured in millions of current-year \$US. Previous studies have shown that historic trade data fit the current distribution of alien species better than recent trade data (Essl *et al.* 2011; Seebens *et al.* 2015). To test for potential lag effects, we used annual data for each year separately. As the best fit between model results and observed data were found using trade data from 1996, we used trade data of the respective year. However, using trade data from other years within the 1990s revealed similar fits (Fig. S3).

A null model

Any analysis of geographic distances between countries is restricted by the size of the globe and biased by the distribution of countries. To account for the influences of both on our results, we formulated a null model thereby calculating the distances in the way described above but with a random selection of countries. That is, the null model considers for each species, the same number of native-alien country pairs as provided by the databases, but the countries were selected randomly out of the pool of all countries. This procedure was repeated 500 times to determine the mean and standard deviation of the randomisation process. The results of the null model serve as a baseline for the interpretation of the observed relationship between species weights and distance: Dynamics, which can also be found in the results of the null model, are likely to be driven by chance alone, while those deviating from the null model are likely to be related to invasion dynamics.

The global invasion model

We use a simple statistical model to predict the number of species translocated from native to alien ranges (Seebens *et al.*

2013). In summary, the model predicts the probability of invasion $P_d(Inv)$ along geographic distance d , as a product of the probability of introduction $P_d(Intro)$, expressed by the volume of commodities exchanged between countries, and $P_d(Alien)$, expressed as biogeographic dissimilarity of countries.

In more detail, the number of exchanged species between countries is assumed to be related to the amount of exchanged commodities. Thus, $P_d(Intro)$ is assumed to be proportional to trade volumes exchanged between countries along distance d and was determined by a smoothing spline fitted to the histogram of normalised trade volumes (line in Fig. 2a). The degree of smoothness of the spline was obtained by fitting the model to distribution data obtained from CABI ISC and GISD (see below). Note that $P_d(Intro)$ constitutes the probability that any species will be introduced irrespective of whether the species is alien or not.

$P_d(Alien)$ can be interpreted as the proportion of transported species, which are alien to the recipient region, and is similar to the inverse of the distance decay of the similarity of ecological communities known from biogeography (Nekola & White 1999; Tuomisto *et al.* 2003; Sojininen *et al.* 2007). While the similarity of ecological communities decreases with distance, the dissimilarity should increase and consequently $P_d(Alien)$ increases with distance as well. However, in contrast to the distance decay of ecological communities, which has the steepest slopes at short distances, $P_d(Alien)$ should increase at a reduced rate at short distances due to the lower probability of introducing an alien species in the direct vicinity of the native region. Usually, invasion events occur over larger geographic distances, which are separated by dispersal barriers that are difficult or impossible to overcome for species without human assistance. We therefore assumed a sigmoid increase of $P_d(Alien)$ with distance:

$$P_d(Alien) = \alpha \left(1 + \frac{\beta}{d}\right)^{-\gamma} \quad (1)$$

with γ being a shape parameter, β denoting the geographic scale on which species composition changes at a reduced rate and α indicating the initial invasion probability. The product of the two probabilities reveals the probability of invasion

$$P_d(Inv) = P_d(Intro)P_d(Alien) \quad (2)$$

along distance d . To compare model predictions with species numbers, $P_d(Inv)$ was transformed into the expected number of species $E_d(Inv)$ by

$$E_d(Inv) = -\ln [1 - P_d(Inv)]\tau \quad (3)$$

with τ being the considered time span in years, which was arbitrarily set to 100 years.

As the scale and shape of $P_d(Alien)$ are not known, we estimated α , β , γ and the degree of smoothness of $P_d(Intro)$ by fitting the model to distribution data obtained from GISD and CABI ISC. The deviation between observed S_d and predicted $E_d(Inv)$ species numbers was measured by the root-mean-squared error, $RMSE = \sqrt{(E_d(Inv) - S_d)^2}$. Fitting was done using an optimisation algorithm (Byrd *et al.* 1995), which minimises root-mean-squared error (RMSE). For all analyses, native-alien range distance data were binned into

steps of 500 km. An increase in the bin size resulted in an increase in the match of model predictions and observed data (Fig. S4), which is due to the reduction in the variability of distribution data.

RESULTS

The optimal distance for biological invasions

The weighted number of exchanged alien species is highest at distances of around 10 000 km (Fig. 1a). Weighted species

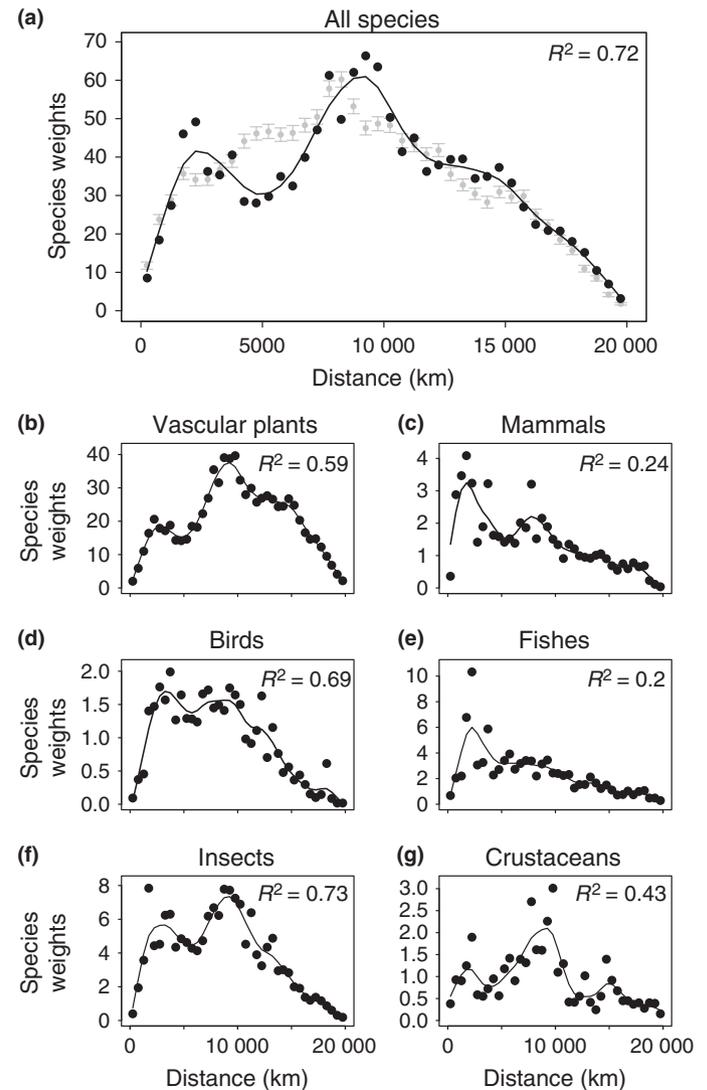


Figure 1 The reported weighted number of alien species as a function of geographical distance between native and alien regions (dots) for all species (a) and for six taxonomic groups (b–g). The trend is indicated by a smoothed spline (lines). In (a) the results of a null model using randomly depicted species ranges (grey dots and error bars indicating mean and standard deviation respectively) shows largest deviations to reported data at around 5000 km. The relationships between the observed species weights and the results of the null model are indicated by the coefficient of determination (upper right corner). As the null model is independent of the taxa-specific characteristics, the results are the same for all taxonomic groups. Data are binned over 500 km.

numbers show two distinct peaks roughly corresponding to intracontinental exchange of species (~ 3000 km) and species flows between the large economies, that is, North America–Europe, North America–East Asia and Europe–East Asia (8000–12 000 km). A plateau at $\sim 15\,000$ km reflects exchanges between North America–Australasia and Europe–Australasia. Similar patterns were found when distinguishing taxonomic groups, though the heights of the peaks varied considerably among taxa (Fig. 1b–e, Fig. S5). For instance, the peak at 3000 km is low for vascular plants, while it is very pronounced for mammals and fishes. For nearly all taxonomic groups, species weights initially increased with distance below 3000 km. This is largely due to the restriction of our analysis to primary introductions, which denote the very first introduction of that species from the native to an alien region. Considering secondary spread within the alien range in addition by including distances between alien regions revealed a stronger decline of species weights with distance (Fig. S6).

The spherical shape and the size of the earth already predetermine a hump-shaped relationship between the number of country–country pairs and their distances. For illustration, consider a random selection of sites on the globe. The histogram of all great circle distances between these sites has a maximum at a quarter of the earth's circumference, which is approximately 10 000 km. Indeed, the null model assuming random distributions of countries reproduces this relationship, though skewed to shorter distances, and explains 72% of the observed variability in distances between native and alien ranges (grey dots in Fig. 1a). The null model, however, deviates from the observed pattern of alien species exchanges at larger and shorter distances. Furthermore, the null model fails to reproduce the variability in peak heights among taxonomic groups (Fig. 1b–e), and performs particularly worse when the observed pattern differs from the dominant peak at 10 000 km (e.g. fishes or mammals).

Trade and biogeography

In general, the amount of exchanged commodities decays with distance with a minor peak at intermediate distances (Fig. 2a). The overall decay of bilateral trade with distance is one of the best established empirical results in international economics (Disdier & Head 2008), resulting from the effort of minimising transport costs. From these figures, it is obvious that trade volume alone constitutes a poor predictor for the spread of alien species as it can only explain a minor fraction of the variability in weighted species numbers (compare Figs. 1a and 2a, $R^2 \leq 0.11$, Table 1).

Goods are frequently exchanged between neighbouring countries, which is not the case for species translocated from their native range to a new region, where they are likely to become established as alien species. Often, the native range of a species is separated by hundreds to thousands of kilometres from its alien range (Fig. 1). Neighbouring countries share a large species pool as many species ranges extend over several adjacent countries and these species usually do not qualify as potential invaders for countries close-by. Nevertheless, it seems safe to assume that the number of species transported per commodity is either similar for all distances or higher at short distances due to increased survival probability of

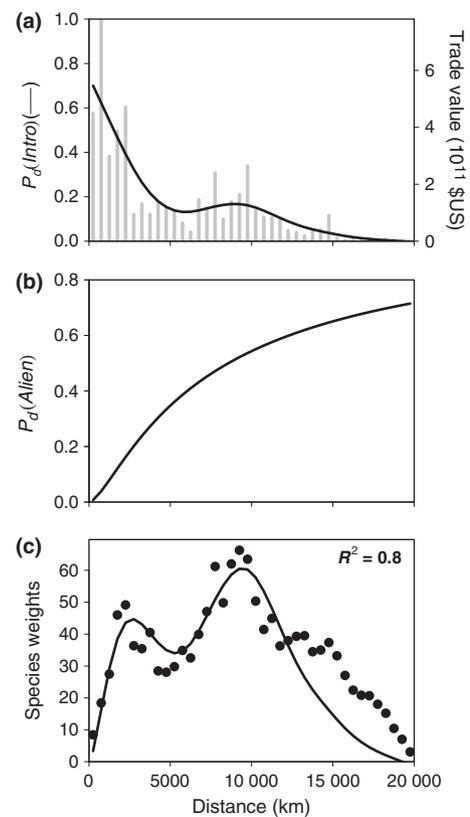


Figure 2 Model components $P_d(Intro)$ (a) and $P_d(Alien)$ (b) and comparison of reported alien species weights (dots in c) and predicted alien species ones, $E_d(Inv)$ (line in c), as a function of geographic distance d . (a) $P_d(Intro)$ is assumed to be direct proportional to exchanged trade values and expressed by a smoothed spline (line) fitted to normalised trade data (grey bars). (b) $P_d(Alien)$ is a sigmoidal function obtained by fitting the model to reported alien species weights. (c) The comparison of the reported and predicted weighted number of alien species reveals a high congruence indicated by the R^2 in the upper right corner.

propagules and individuals. Consequently, we should expect that indeed many species should arrive from neighbouring countries. To resolve this puzzle, we hypothesise that most of the species transported over short distances are native in the recipient country as well, while species transported over long distances are mostly alien to the recipient region. We therefore have to distinguish between the transportation of native and alien species to understand the relationship between trade and alien species exchanges.

A simple model of invasion dynamics

Despite its simplicity, the invasion model can describe species weights in good agreement with observed data ($R^2 = 0.80$, line in Fig. 2c, Table 1). Remarkably, the first two peaks at short and intermediate distances, which are apparent in the distribution data, are well reproduced by the model. Applying the same approach to single taxonomic groups reveals fits ranging from $R^2 = 0.63$ (fishes) to $R^2 = 0.88$ (birds, Fig. 3). The model is even able to capture the variation in the first peak among taxonomic groups. Only the plateau at around 15 000 km is lacking in some taxonomic groups (e.g. vascular plants). The

Table 1 Summary of model fits using either trade or biogeographical dissimilarity alone or both in conjunction as described in the main text

Model	DF	RMSE	R^2	AIC
Trade, $P_d(Intro)$	38	24	0.11	332
Biogeography, $P_d(Alien)$	38	15	0.04	336
Trade + Biogeography, $P_d(Intro)P_d(Alien)$	38	10	0.80	273

DF, degrees of freedom; RMSE, root-mean-squared error; R^2 , coefficient of determination; AIC, Akaike's Information Criterion.

The best fit is indicated by a low RMSE and AIC and a high R^2 , which was obtained for the model incorporating both trade and biogeography.

reason for this distinct increase in predictive power is that trade volume and biogeography are decreasing or increasing, respectively, roughly continuously with distance. Each of these predictors alone is therefore not able to capture the hump-shaped pattern of species weights. But their product gives a hump-shaped function and thus can explain a large amount of the observed variability in species weights.

DISCUSSION

Trade plays a pivotal role for the global spread of alien species, resulting in a distinct positive relationship between the import volume of a country and the number of alien species (Levine & D'Antonio 2003; Westphal *et al.* 2008; Hulme 2009; Pyšek *et al.* 2010). This study clearly shows that trade volume is also a good predictor for the spread of alien species but only in conjunction with the consideration of biogeographic dissimilarity. While at large distances (> 5000 km) the weighted number of alien species distinctly follows the amount of imported commodities, at short distances the relationship between trade volume and weighted species numbers turns into a negative one as trade volume decreases with distance while the weighted number of alien species increases. We show that this discrepancy can be solved by the consideration of biogeographic dissimilarity. Biogeographic dissimilarity is particularly low at short distances and consequently suppresses invasion probabilities at these distances. While trade volume or biogeography alone can only explain a very low amount of the variability in observed data ($R^2 \leq 0.11$, Table 1), their combination distinctly increased the predictive power of the model to 63–88% explained variability depending on the taxonomic group.

The largest discrepancy between observed data and model predictions can be found at long distances around 15 000 km (Fig. 2c), which is the distance between Europe-Australasia and North America-Australasia. Many vascular plant species have been introduced to Australia and New Zealand already in the 19th century, which cannot be fully captured using recent trade data. Partly, the reason for the underestimation of the minor peak at 15 000 km is due to the degree of smoothing to fit the trade volumes. Indeed, using a less smoothed spline, with the degree of smoothness manually reduced, reproduces this minor peak as well, though still at a lower level than observed (Fig. S7). The model seems to consistently underestimate long-distance invasion events particularly for vascular plants (Fig. 3), which indicates that vascular plants have been introduced at higher rates over such extended distances than suggested by trade exchanges only.

Our data analysis revealed that native and alien ranges are often separated by thousands of kilometres with highest alien species weights found at around 10 000 km (Fig. 1a). This pattern can be explained in two ways: A peak at this distance can be generated by chance alone as it is approximately a quarter of the earth's circumference and a random selection of distances between randomly distributed sites on the globe would also give a peak at 10 000 km. The peak of alien species may therefore be considered as purely driven by the geometry of the earth. On the other hand, the peak may also be explained by trade volume showing a local maximum at around 10 000 km (Fig. 2), which is the average distance between most of the large economies. The relative importance of trade volume compared to random processes becomes apparent at shorter distances of around 5000 km. At this distance, both trade volume and weighted alien species numbers have a local minimum, which is not reproduced by the null model. But most importantly, the null model contradicts the known fact that species introductions are not geographically random but depend on, for example, native ranges, pathways and environmental conditions. Taking secondary spread into account increased species weights particularly at short distances (Fig. S6), which supports previous findings that the first step of invasion is often a long-distance step, followed by subsequent shorter ones within the alien range (Seebens *et al.* 2016a).

The patterns presented in this study are the result of a combination of different data sets and using other data sources may yield deviating results. In particular, one may argue that the usage of the species ranges from the GISD limits the explanatory power of this analysis because GISD focuses on invasive species posing impacts to the native environment, which only reflects a subset of all alien species. However, our conclusions are confirmed by the observation that a similar pattern was found in a different study of marine invasion dynamics using other sources of distribution data (Seebens *et al.* 2013). The histogram of both distribution data and model predictions even show the three peaks as shown in Fig. 1. Although the amount of distribution data included in the analysis in Seebens *et al.* (2013) was much lower, the congruence of the intermediate distance patterns found in both studies indicates that similar results can be expected when using different data sources.

The pattern of spread of alien species is likely to have changed during the last centuries. Long-distance dispersal invasion events should be more prominent in recent decades due to high intensity of international trade and traffic, while in past centuries the proportion of short-distance invasion events should be higher compared to today. Particularly, very old invasion events (< 1500) were mostly restricted to a continent and thus can be expected to vary only within a more restricted range of distances (di Castri 1989). The influence of this temporal variation on study results is, however, difficult to test as these very old invasion events were poorly documented and often these alien species were not included in alien species inventories, because species were considered to be native, the invasion status was unclear (cryptogenic) or the focus of the inventories was on neobiota (i.e. species introduced after 1500). We can therefore not exclude a potential bias of the data sets towards more recent long-distance invasion events. However, the

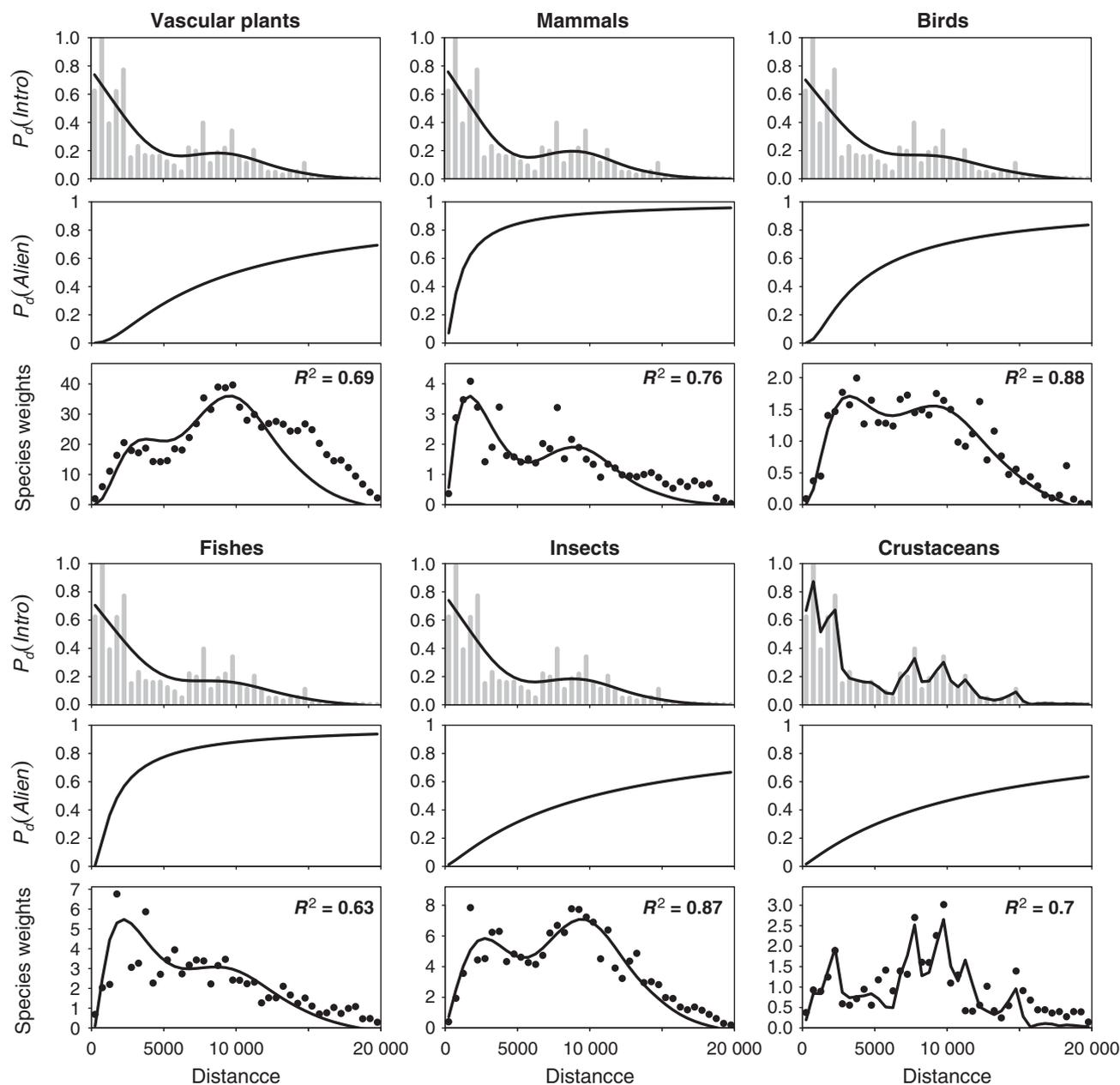


Figure 3 Taxon-specific model results. The model was fitted separately to alien species of various taxonomic groups resulting in different shapes of $P_d(\text{Intro})$ (upper panels) and $P_d(\text{Alien})$ (middle panels) and in lower species weights due to a lower number of species (lower panels). The comparisons of reported (dots) and predicted (lines) alien species weights are shown in the lower panels with the resulting R^2 values.

number of invasion events drastically increased during the last centuries with 76% of all reported first records of established alien species during 1900–2014 (Seebens *et al.*, 2016b). We therefore believe that very old short-distance invasion events play only a minor role in the global data sets and do not affect our results significantly.

We found distinct deviations of the distributions of weighted alien species numbers among taxonomic groups. Particularly, the relative heights of the short distance peak (ca. 3000 km) and the intermediate distance peak (ca. 10 000 km) varied among taxonomic groups. While the short distance peak was most pronounced for non-flying vertebrate groups (mammals, amphibians and reptiles), the intermediate

distance one was most distinct for invertebrates (insects, crustaceans and molluscs), algae and vascular plants (Fig. 1b–f, Fig. S5). Many mammals, amphibians and reptiles spread with human assistance among islands in the Caribbean, South-East Asia or Oceania (Helmus *et al.* 2014). Many of these islands are known for their high proportion of endemic vertebrates, indicating a dispersal limitation despite the comparatively short distance between islands (Kier *et al.* 2009; Helmus *et al.* 2014). The introduction of these species to nearby islands has therefore led to many short-distance invasion events resulting in high species weights at short distances. For those taxonomic groups, which are at least partly dispersed by wind or water currents, such as vascular plants,

insects, crustaceans or molluscs, this dispersal barrier likely played a less important role, resulting in a much lower peak at short distances relative to the one at intermediate distances. Taxa-specific dispersal modes may similarly affect the spread in other regions of the world.

The large amount of variation explained by our model suggests that the most important mechanisms driving alien species spread have been correctly implemented. However, the functional forms of $P_d(\textit{Alien})$ and $P_d(\textit{Intro})$ are still unknown and the ultimate drivers are not fully understood. In Seebens *et al.* (2013), $P_d(\textit{Intro})$ was considered to be driven by a distance-dependent survival rate of species inoculated in ballast water tanks of ships, while here $P_d(\textit{Intro})$ is related to the amount of exchanged commodities. The latter seemed to be a more general explanation, which is applicable to all taxonomic groups. Nevertheless, for some species assemblages like those transported in ballast water, the mortality during transportation may still play an important role (Gollasch *et al.* 2000). Furthermore, the exact functional relationship of $P_d(\textit{Alien})$ and distance is unclear. Fitting the model to distribution data reveals that for all taxonomic groups combined, vascular plants and birds, $P_d(\textit{Alien})$ is best captured by a sigmoid function (Figs 2 and 3). For other taxonomic groups, $P_d(\textit{Alien})$ may be also described by an exponential function such as $P_d(\textit{Alien}) = 1 - e^{-\beta d}$, which would be in line with the inverse of the distance decay fitted in other studies (Nekola & White 1999; Tuomisto *et al.* 2003; Soininen *et al.* 2007). This has to be studied in more detail in the future.

As a logical next step, one may incorporate environmental matches between donor and recipient countries to improve the predictive power of the model (Thuiller *et al.* 2005; Pyšek *et al.* 2010; Gallardo *et al.* 2015; Bellard *et al.* 2016). In contrast to expectations, incorporating environmental conditions such as annual temperature, precipitation and altitude according to Seebens *et al.* (2013) only leads to a minor improvement of the fit. The reason is that environmental distances between countries are correlated with trade flows because most commodities have been exchanged between countries of similar climatic conditions like the large economies in North America, Europe and East Asia, which are all located in subtropical to temperate climates. Indeed, 50% of the world trade volume is exchanged between countries with low differences in latitude (Δ_{ij} latitude $< 11^\circ$), temperature (Δ_{ij} temperature $< 5^\circ\text{C}$), precipitation (Δ_{ij} precipitation < 300 mm) and altitude (Δ_{ij} altitude < 300 m) (Fig. S8). Consequently, variability in alien species numbers due to environmental conditions may already be explained by bilateral trade data though without any direct causative relationship of both variables. However, it seems safe to assume that environmental conditions are still crucial predictors for invasion dynamics although it may be difficult to disentangle the influence of both drivers statistically on coarse geographic scales as applied here. The spurious correlation between trade and environmental conditions shows that trade – though a good predictor for alien species spread – does not have to be the ultimate driver for the spread of species. Indeed, trade may at least partly reflect other important drivers such as ship movements, human migration, tourism or colonial ties, which does not have to be related to recent trade.

In this study, we used trade data from 1996 as a predictor, while other studies have shown that historic trade data were a better predictor for the recent distribution and spread of alien species compared to most recent trade data due to involved time lags (Essl *et al.* 2011; Seebens *et al.* 2015). Although trade data from 1996 may also be regarded as historic ones, their high predictive power does not necessarily have to be due to time lags as 1996 may simply be the year of highest spread intensity on average. Note that a lack of a time lag does not contradict the results of the other studies. The coarse geographic resolution applied in this study may not be appropriate for a detailed analysis of time lags. This is supported by the fact that even environmental matches are masked by trade.

The invasion of an alien species in a new region is often considered to be very complex depending on species-specific traits, introduction efforts, local biotic interactions and numerous other aspects, which renders the prediction of single invasion events difficult. While this is true for single species, this study shows that on average invasion dynamics follow simple rules, which can be predicted using simple models. A large amount of the observed variability in invasion dynamics can be explained using only two predictors: propagule/colonisation pressure and biogeographic dissimilarities. These findings show that invasion models can be much simplified without a great loss of predictive power at least at coarse resolutions. Supporting results of many other studies, we show that global invasion dynamics are tightly coupled to trading activities; however, the amount of traded commodities can only serve as a reliable predictor for invasions while considering the biogeographic dissimilarity between donor and recipient countries. We here provide a simple and intrinsic explanation as to why many alien species originated from regions at intermediate distances at a global scale, which suggests that the intermediate-distance hypothesis is a universal characteristic of biological invasions.

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AUTHORSHIP STATEMENT

HS and BB designed the study, HS performed the analysis and wrote the manuscript with major inputs from BB and FE.

DATA ACCESSIBILITY STATEMENT

Raw data used for this study are freely available online (s. Methods). These data were taken to calculate geographic distances between native and alien species ranges and species

weights. A table containing species names, ranges, distances and species weights is available in the Senckenberg Data Repository (www.dx.doi.org/10.12761/SGN.2016.01.024).

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