

Exploring associations between international trade and environmental factors with establishment patterns of exotic Scolytinae

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Abstract Although invasion of exotic ambrosia beetles (fungus feeders) and bark beetles (phloem feeders) (Coleoptera: Curculionidae: Scolytinae) is considered a major threat to forest health worldwide, no studies have quantitatively investigated the anthropogenic and environmental factors shaping the biogeographical patterns of invasion by these insects across large spatial scales. The primary aim of this study was to assess the relative importance of international trade and several environmental variables of the recipient region on species richness of established exotic Scolytinae. As a reference, we also evaluated the relationships between the same environmental variables and species richness of native Scolytinae. Using an *information-theoretic framework* for model selection and hierarchical partitioning, we

evaluated the relative importance of the potential drivers of species richness of native and exotic Scolytinae in 20 European countries and the 48 contiguous continental US states. Analyses were conducted separately for ambrosia and bark beetle species. Value of imports was a strong predictor of the number of exotic Scolytinae species in both regions. In addition, in the USA, warmer and wetter climate was positively linked to increased numbers of both native and exotic ambrosia beetles. Forest heterogeneity and climatic heterogeneity and secondarily forest area were key drivers in explaining patterns of species richness for native bark beetles but not for exotic species in both regions. Our findings suggest that if current infestation levels continue on imported plants and wood packaging material, increasing international trade will likely lead to more establishments of exotic Scolytinae with concomitant negative effects on forest health in both Europe and the USA. Compared to Europe the risk of invasion appears higher in the USA, especially for ambrosia beetles in the southeastern USA where the climate appears highly suitable for exotic establishment.

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Introduction

Invasive exotic forest insects are considered a major threat to forest health (Gandhi and Herms 2010). In

particular, ambrosia beetles and bark beetles (Coleoptera: Curculionidae: Scolytinae) are amongst the most important forest pests causing significant economic damage to trees worldwide. In the past few decades, establishment of exotic species has steadily increased in both Europe (Roques et al. 2009; Kirkendall and Faccoli 2010; Sauvard et al. 2010) and North America (Haack 2001, 2006; Rabaglia et al. 2006, 2008), posing severe threats to native forest ecosystems (Holmes et al. 2009; Aukema et al. 2010; Haack and Rabaglia 2011).

Exotic insect invasions can be described in terms of a series of ecological barriers or filters, from arrival to establishment to spread, which may prevent an organism from proceeding to the next stage (Liebhold and Tobin 2008). The first stage corresponds to the human-mediated arrival of a pool of exotic species that constitute the potential colonizers of a defined recipient region. The arrival of ambrosia and bark beetles is expected to be enhanced by increases in global trade (e.g. Haack 2006; Haack et al. 2010; Koch et al. 2010). For instance, these organisms can be easily transported in live plants, plant products, wood packaging material, and cargo containers where they are often sheltered from detection (Work et al. 2005; Brockerhoff et al. 2006a, b; Haack 2006; McCullough et al. 2006; Brockerhoff 2009; Colunga-Garcia et al. 2009).

The next stage of the biological invasion process is establishment of a subset of the species that arrived at any given point of entry. Once an exotic insect species arrives in a new ecosystem, establishment will depend on various abiotic and biotic factors (Holmes et al. 2009; Roura-Pascual et al. 2011). At this stage, several factors are expected to determine the number of Scolytinae species that can establish in a region: habitat area (Stevens 1986), resource and environmental heterogeneity (Huston 1979), climate (Coulson 1979), and biotic interactions with native communities (Lu et al. 2007), while availability of novel niches created by humans is not expected to be important. A positive species–area relationship is one of the most consistent biogeographical patterns (Rosenzweig 1995). Two suggested mechanisms underpinning this positive relationship are the area per se and the habitat diversity hypotheses. The area per se hypothesis derives from the island biogeography theory and assumes that the number of species in a region represents an area-mediated equilibrium

between extinction and colonization rates, with higher extinction rates in smaller versus larger areas (MacArthur and Wilson 1967). The habitat diversity hypothesis predicts that larger areas are more likely to contain greater environmental heterogeneity and therefore, more species as predicted by niche theory (Huston 1979). A large body of biogeographical research also supports the view that, in regions of roughly equal habitat area, temperature is the prime determinant of species richness in temperate areas as the amount of available energy sets limits to the species richness of the system (Currie 1991). All of the processes described above are expected to be important for both native and established exotic species. Whereas these environmental factors dominate the larger scale domains, biotic interactions are expected to be important at local and smaller spatial scales (Milbau et al. 2009). However, potential effects of native species on the invasiveness of exotic Scolytinae are complex and difficult to predict as both competition and facilitation can be expected as important forces in the community ecology of Scolytinae that often breed in multiple-species associations within the same host plant (Lu et al. 2007).

Although most studies of factors that contribute to successful establishment of exotic species have largely focused on species traits and local habitat characteristics (both biotic and abiotic) that determine vulnerability to invasion, increasing empirical evidence has demonstrated that propagule pressure is crucially important in both of these stages of invasion (Lockwood et al. 2009; Simberloff 2009). The linkage of vulnerability to invasion with propagule pressure may be especially strong for exotic Scolytinae due to their high facility to be transported accidentally in various commodities through international trade and travel (Work et al. 2005; McCullough et al. 2006). Although recent works indicate that ongoing biological invasions might be well predicted with variables related to human activity (Pyšek et al. 2010; Essl et al. 2011; but see Roura-Pascual et al. 2011), no studies have quantitatively assessed the relative importance of both natural and anthropogenic processes on the patterns of invasion by exotic forest insects across large spatial scales (but see Langor et al. 2009). However, the need for improved understanding of the interactions between species invasions and other global change processes has been

recently highlighted as a research priority for reducing the threat of invasive forests pests (Gandhi and Herms 2010).

Hence, the primary aim of our study was to evaluate the relative importance of international trade and various abiotic and biotic environmental variables in shaping patterns of established exotic species richness for ambrosia and bark beetles in both Europe and the USA. In particular, we evaluated whether propagule pressure was more important than the quality of the recipient regions in explaining species richness of the exotic Scolytinae. In addition, as a means to identify the unique contribution of propagule pressure and environmental factors to exotic species richness, we studied the relationships of the same environmental variables with native species of ambrosia and bark beetles in Europe and the USA.

Methods

Study regions

We had two study regions: Europe and the continental USA. The European region consisted of 20 countries, while US region consisted of the continental 48 contiguous US states. For each of these countries and states, we had detailed and comparable information about the distribution of both native and exotic ambrosia and bark beetles (Scolytinae).

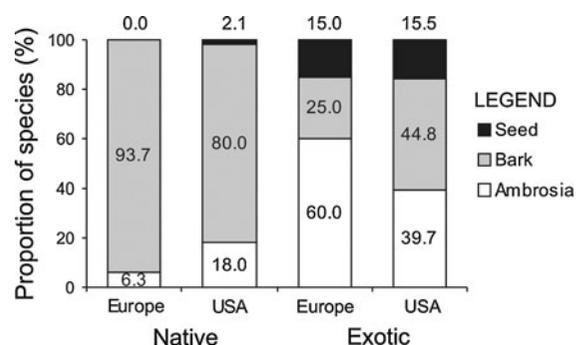


Fig. 1 Frequency distribution of seed-feeding, phloem-feeding (*bark beetles*), and fungus-feeding (*ambrosia beetles*) native and exotic Scolytinae species pool within Europe and the USA. The relative proportion (%) of each feeding guild is also shown. Twig feeders were pooled with bark beetles

Data on Scolytinae distribution

Information on the distribution of native and exotic Scolytinae was gathered in both regions from published and unpublished sources. We included in our analyses only those exotic species that have established self-sustaining populations, regardless of whether they cause ecological or economic impacts.

The list of native Scolytinae species of each European country was obtained from the catalogue of the Palaearctic scolytid species (Knížek 2011). The list of exotic Scolytinae naturalized in Europe was recently compiled by Kirkendall and Faccoli (2010) and Sauvard et al. (2010). The list by country was created using the European database for exotic organisms DAISIE (Delivering Alien Invasive Species Inventories for Europe) (DAISIE 2009), the European Network on Invasive Alien Species (NOBANIS 2010), and the Fauna Europaea (Knížek 2004).

The list of native and exotic Scolytinae naturalized in the USA was initially based on Wood (1977, 1982), Wood and Bright (1992), and Bright and Skidmore (1997, 2002). Updated lists based primarily on scientific literature were published by Haack (2001, 2006), Rabaglia et al. (2006), Cognato et al. (2009), and Haack and Rabaglia (2011). The lists used in the present paper were current through 2010 and integrated with unpublished records of bark beetles in the USDA Forest Service, Early Detection and Rapid Response project (Rabaglia et al. 2008; Rabaglia et al. unpublished data).

Despite the data's coarse spatial resolution, we believe that this is the largest available dataset on the distribution of Scolytinae species in temperate countries and no information at a finer spatial resolution is currently available. We acknowledge that the species counts might be partially incomplete and that the numbers of known native and exotic Scolytinae would likely increase if more thorough surveys were conducted; however, we feel that the relative rankings between countries and states will remain rather stable. We therefore consider the data collated here provide a sound basis for gaining insights into the potential drivers of Scolytinae species richness across the two selected regions.

Scolytinae feeding habits

The Scolytinae exhibit several forms of feeding specialization (Wood 1982), and these different

feeding habits likely affect the probability that individual species will be transported in imported goods and associated wood packaging material. Given the above, and that different feeding habits may also influence establishment success, we split the Scolytinae into three groups:

(i) Phloem-feeding species which feed in the phloem layer, and include species that develop in twigs (hereafter referred to as ‘bark beetles’). The trophic niches of these species are separated by host tree species as well as by host requirements within the same species such as phloem thickness, tree defense chemistry, nutritional quality and water content (Byers 1989).

(ii) Fungus-feeding species, which bore into the wood and feed primarily on symbiotic fungi (‘ambrosia’) that grow along the tunnel walls (hereafter called ‘ambrosia beetles’). These species can develop in both living and dead wood and therefore usually exhibit low host tree specificity.

(iii) Seed-feeding species, which develop in hard seeds and fruit. We excluded this group from the analyses because their numbers were too low to include as a separate analysis.

Explanatory variables

We evaluated the role of several variables indicative of international trade and the local environment for each country/state that were expected to be important drivers of Scolytinae species richness at the spatial scale of our analyses (Table 1). We selected a priori the most likely predictors based on current knowledge of Scolytinae ecology and biogeography as explained below.

International trade

By analyzing exotic Scolytinae interceptions in the USA between 1985 and 2000, Haack (2001) found that 73% of the interceptions were found in association with wood packing material, only 22% in food or plants, and 5% in unspecified material (no similar information is available for Europe). On the basis of these data we used the total value of imports (IMPORT) as proxy for propagule pressure because most products are now transported in crating or on pallets and thereby could serve as a potential pathway

for bark- and wood-boring insects. Total imports are therefore expected to be more related to the introduction of exotic species than simply imports of wood products. Although exotic species richness of other taxonomic groups such as plants or fungi may better reflect historical rather than contemporary human activities, species richness of exotic insects has been demonstrated to be more closely related to current rather than historical socioeconomic variables (Essl et al. 2011). We therefore used the value of recent import data to explain the number of exotic Scolytinae species in both regions.

Indicators of cumulative economic prosperity such as wealth are often considered better predictors of the distribution of established exotic species than variables measuring flow of capital and goods within shorter time spans (Pyšek et al. 2010). However, we did not include any cumulative measures because exotic Scolytinae do not require further human intervention or novel niches created by humans to establish. The expected main limiting factors for establishment of exotic Scolytinae are suitable climatic conditions, availability of host trees, and biotic interactions with native communities within the same or higher trophic levels.

For Europe, we used the average annual value of goods imported during the period 1999–2009 based on official economic statistics of the European Union (www.ec.europa.eu/eurostat). For the USA, similar data were available for the period 2008–2010 (US Economic Census Bureau, US International Trade in Goods and Services FT900). For both regions, we used data for the final destination of the imports, rather than the first port of arrival because the vast majority of imports arrive in shipping containers that are not opened until they reach their final destination. IMPORT was log-transformed in all analyses to improve linearity and uniformity. Although import data were available only for rather short periods, longer time series were available only for other indicators of flow of capital such as gross domestic product (GDP). For the period for which both variables were available the correlation between imports and GDP was always very high ($r = -0.90$). Preliminary analyses using GDP with longer time series instead of IMPORT yielded very similar results, indicating that relative differences in flow of capital between countries or states have remained almost constant over the last decades.

Table 1 Descriptive statistics of the explanatory variables for both Europe (20 countries) and the USA (48 continental contiguous states) included in this study

Variable name and description	Unit	Mean (SD)		
		Europe ($n = 20$)	USA ($n = 48$)	
IMPORT ^a	Cumulative value of imports (all goods)	10 ⁹ \$ year ⁻¹	181.81 (189.66)	36.80 (59.47)
AREA	Area covered by forest	km ²	68,359 (81,015)	61,607 (74,877)
PRECIP ^b	Mean annual precipitation	mm	799 (786)	909 (352)
TEMP ^c	Minimum temperature of the coldest month	°C	-0.45 (0.47)	-0.06 (0.60)
PRECIP-H	SD of mean annual precipitation	mm	174 (169)	137 (150)
TEMP-H	SD of mean annual temperature ^d	°C	1.99 (1.93)	1.76 (1.62)
FOREST-H	Forest habitat heterogeneity	Shannon H'	1.33 (1.35)	1.41 (0.36)

Refer to methods for details about the data sources

^a Euro-dollar exchange rate: 1€ = 1.30\$

^b Bioclimatic variable BIO12 from WorldClim (<http://www.worldclim.org/bioclim>)

^c Bioclimatic variable BIO6 from WorldClim (<http://www.worldclim.org/bioclim>)

^d Bioclimatic variable BIO1 from WorldClim (<http://www.worldclim.org/bioclim>)

Environmental factors

Given that the vast majority of native and exotic Scolytinae in Europe and the USA utilize trees to complete their life cycle, we used the area covered by forest (AREA) instead of administrative area to account for the species-habitat area relationship (Stevens 1986). As forest area was strongly correlated to administrative area ($r_s = 0.87$ and 0.67 for Europe and the USA, respectively) the simultaneous inclusion of the two variables was not possible. AREA was based on data from CORINE for Europe (www.eea.europa.eu), and the National Forest Inventory and Analysis database for the USA (USDA-FS 2010). We expected that increasing the area covered by forests would likely increase the number of both native and exotic Scolytinae species by increasing habitat availability, irrespective of their feeding habit. AREA was log-transformed in all analyses to improve linearity and uniformity.

Two climatic variables were used based on monthly data: minimum temperature of the coldest months (TEMP) and mean annual precipitation (PRECIP). Both were derived from the WorldClim database and corresponded to the bioclimatic variables BIO6 and BIO12, respectively (Hijmans et al. 2005; 1 km resolution; 1960-1990 period). Both variables were averaged within each country or state. As our two regions cover wide latitudinal gradients, we expected that the number of native Scolytinae

(both ambrosia and bark beetles) would decrease when moving from warmer low-latitude to colder high-latitude areas according to the species-energy hypothesis (Currie 1991). Warmer climates are also expected to generally favor the establishment of exotic species (Walther et al. 2009). Precipitation was included because it is a key climatic variable affecting tree susceptibility and insect physiology (Coulson 1979). For ambrosia beetles, precipitation is also a key factor in the development of their associated fungi (Wood 1982).

Given that broad geographical gradients might be associated with large variations in environmental gradients, particularly as the size of the sampling unit increases, we quantified three measures of environmental heterogeneity. We used the standard deviation of mean annual temperature (bioclimatic variables BIO1 in WorldClim) (TEMP-H) and precipitation (PRECIP-H) within each country and state as a measure of climatic heterogeneity. We expected that the number of both native and exotic Scolytinae should increase with increasing number of climatic niches available. Finally, we quantified forest habitat diversity with the Shannon-Wiener diversity index (FOREST-H) of the forested area covered by different forest categories within each country or state as explained below. We expected this variable to be positively related to the diversity of host tree species, and therefore to the diversity of trophic niches. As ambrosia beetles have lower host specificity than bark

beetle species (Wood 1982), we expected the bark beetles to be more related to forest habitat diversity than ambrosia beetles. For Europe the only information available on forests was the proportion of ICP (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests) plots per forest type within each country. This system classified European forests into 14 broad categories (EEA 2007). Although the latter measure was not optimal to estimate the cover of different forest categories, it was the only variable available for the whole of Europe. For the USA, we retrieved up-to-date information on the area covered by 31 forest categories by state from the USDA Forest Service, Forest Inventory Data Online (FIDO) (USDA-FS 2010). Although the European and US classification systems are not fully comparable the criteria to define the forest categories in both regions were similar. Each category is defined as a physiognomically uniform group of plant associations sharing one or more dominant tree species. The higher number of categories in the USA than in Europe reflects the larger climatic gradient and greater diversity of tree species in the USA.

Data analysis

Relationship between native and exotic Scolytinae species richness

Considering that at our large spatial scale there was no clear hypothesis on the direct effects of native species richness on exotic species richness, we did not include native species richness in our multivariate analyses. For ambrosia beetles, we expected weak interactions between natives and exotics due to their low host specificity and broad trophic niches. For bark beetles, no prediction was made on the interaction between native and exotic species, as both competition and facilitation can be expected as important processes in the community ecology of Scolytinae that breed in tree phloem and often in multiple-species associations (Lu et al. 2007). However, we performed a separate univariate analysis where we tested the co-variation between native and exotic species richness separately for ambrosia and bark beetle species in the two regions. According to the ‘rich get richer’ hypothesis (e.g. Stohlgren et al. 2003), we expected that a strong positive co-variation

between native and exotic Scolytinae would indicate strong influence of the same environmental drivers on both species groups, i.e. large-scale environmental factors enhancing native species richness would also increase exotic species richness.

Multi-model inference and hierarchical partitioning

Due to the relatively low number of replicates ($n = 20$ in Europe and $n = 48$ in the USA) and the relatively high number of potential predictors, we used multi-model inference within an information-theoretic framework to evaluate the role of the selected variables in explaining patterns of Scolytinae species richness (Burnham and Anderson 2002). As explained above, all selected variables in Table 1 corresponded to ecological meaningful predictors of exotic Scolytinae species richness patterns. For native Scolytinae, we excluded IMPORT from the analyses because the native species were not expected to be directly related to this variable. Moreover, given that we had no a priori hypotheses supporting interactions between the considered explanatory variables, we did not include any interaction terms in our model selection procedure. We used ordinary least square multiple linear regression to estimate model parameters as model residuals approximated a normal distribution. The number of native or exotic species reported for each country or state was used as the response variable in these models. We ran separate analyses for ambrosia and bark beetles. Similarly, the low number of exotic bark beetles in Europe did not allow for analysis. Given that severe collinearity among explanatory variables can hamper identification of the most causal variables also within an information theoretic framework, we calculated a variance inflation factor (VIF) within our set of predictors relative to all our response variables in both regions. If a predictor has a value of $VIF > 10$, it is considered an indicator of strong collinearity associated with that particular predictor. As none of our predictors had a $VIF > 10$ (maximum VIF was 6.26 for AREA in Europe), we retained all the variables in our multi-model inference procedure.

Our information-theoretic approach compared the fit of all the possible candidate models obtained by the combination of our predictors using second-order Akaike’s information criterion (AICc). The AICc is a measure of relative model fit, proportional to the

likelihood of the model and the number of parameters used to generate it. The best fitting model is the one with the lowest AICc. In a set of n models each model i can be ranked using its difference in AICc score with the best-fitting model ($\Delta\text{AICc}_i = \text{AICc}_i - \text{AICc}_{\text{minimum}}$). The difference in AICc values indicates the relative support for the different models. A model is usually considered plausible if its ΔAICc is below 2 (Burnham and Anderson 2002). For each model i we also calculated an Akaike's weight (w_i), which is the probability that model i would be selected as the best fitting model if the data were collected again under identical circumstances (Burnham and Anderson 2002). Akaike's weight should be interpreted as a measure of model selection uncertainty. The multi-model inference analyses were performed using the 'MuMIn' package (Barton 2010) implemented in R version 2.12 (R Development Core Team 2011).

Although it is possible to use Akaike's model weights to evaluate the relative importance of variables, this approach has been recently criticized in cases of collinearity between the predictors included in model selection (Murray and Conner 2009). We therefore used hierarchical partitioning (HP) (Chevan and Sutherland 1991) to rank the importance of each variable most likely to affect variation in species richness. HP allows the joint consideration of all possible models in a multiple regression attempting to identify the most likely causal factors. This analysis splits the variation explained by each explanatory variable into a joint effect with the other explanatory variables and an independent effect not shared with any other variable. HP was conducted using the 'Hier.Part' package (version 0.5-1, Mac Nally and Walsh 2004) implemented in R version 2.12 (R Development Core Team 2011). We used a normal error distribution and R^2 as a measure of goodness-of-fit.

Results

General results

The total number of Scolytinae species analyzed was 241 for the 20 European countries (221 native and 20 exotic) and 537 for the 48 US states (469 native and 58 exotic). The vast majority of native species were

phloem-feeders in both Europe (93.7%) and the USA (80%), with ambrosia beetles and seed-feeders being less frequent (Fig. 1). Exotic species were more often ambrosia beetles than bark beetles compared with native proportions in both Europe and the USA (Fig. 1). In Europe, native ambrosia beetle species richness was highest in the central European countries (Fig. 2a), while species richness of native bark beetles was largest in the southern countries such as Italy and France (Fig. 2b). The European country with the highest number of exotic ambrosia beetles was Italy followed by the Czech Republic (Fig. 2c). In the USA, native ambrosia beetle species were concentrated in the southern and eastern states (Fig. 2d), while the states with the largest species richness of native bark beetles were located on the west coast (Fig. 2e). Species richness distribution of exotic ambrosia beetles reflected that of native ambrosia beetle species (Fig. 2f), while species richness hotspots of exotic bark beetles were distributed on both the east and the west coast (Fig. 2g).

Relationship between native and exotic Scolytinae species richness

On the one hand, we found a positive relationship between native and exotic ambrosia beetle species richness in both Europe (Fig. 3a) and the USA (Fig. 3b). The relationship was much stronger in the USA than in Europe. On the other hand, we found no association between species richness of native and exotic bark beetles in the USA (Fig. 3c). In Europe, the number of exotic bark beetle species was too low to perform the analysis.

Multi-model inference and hierarchical partitioning

For both regions, model selection indicated that no single best model was supported and that several candidate models were plausible in explaining patterns of Scolytinae species richness for both native and exotic species. There was therefore considerable model selection uncertainty, as reflected by the low Akaike's weights (w_i). However, we found contrasting results concerning the relative importance of the variables included in the sets of plausible models for each species groups, i.e. native versus exotic species and ambrosia versus bark beetles.

Fig. 2 Native and exotic species richness for ambrosia beetles and bark beetles in Europe (20 countries) and the 48 contiguous US states. The number of exotic bark beetle species in Europe was too low and therefore is not shown

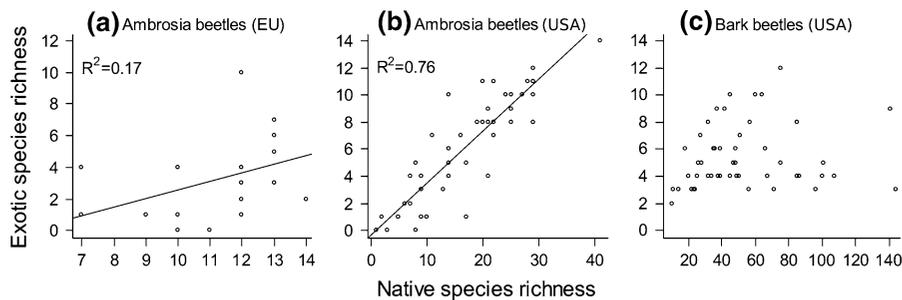
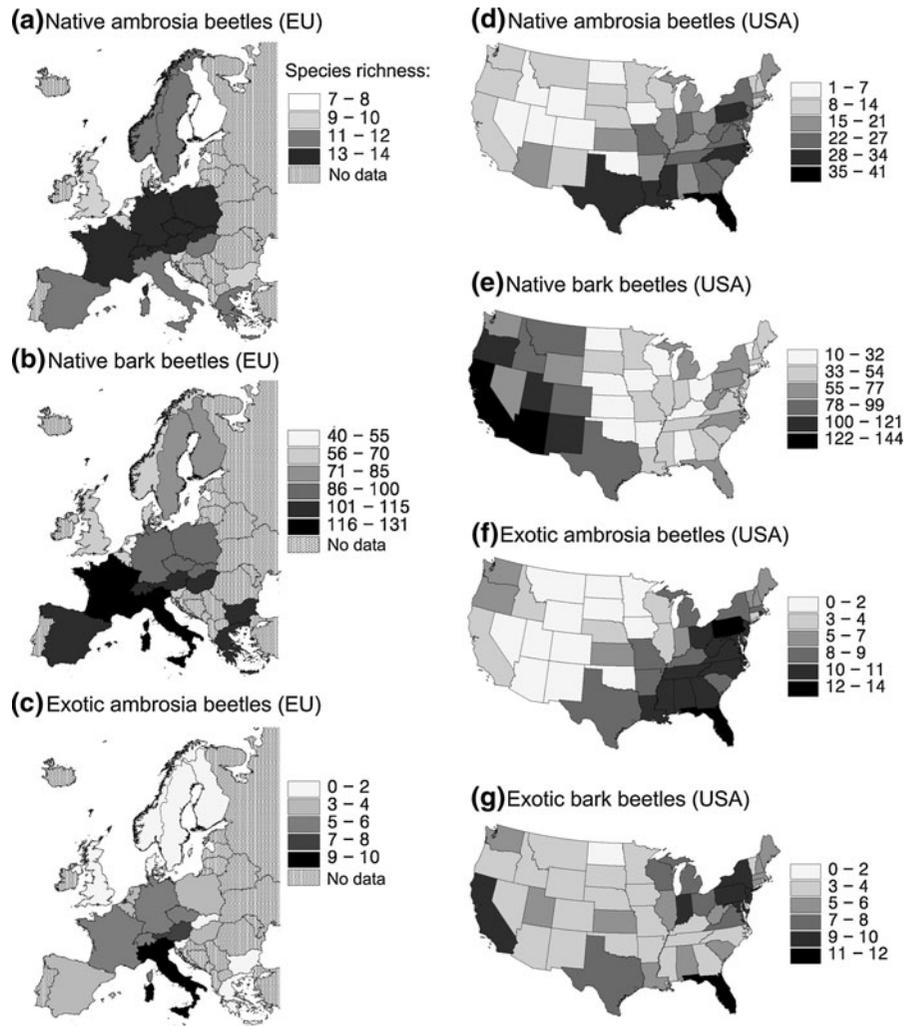


Fig. 3 Relationship between exotic species richness and native species richness for **a** ambrosia beetles in Europe, **b** ambrosia beetles in the USA, and **c** bark beetles in the USA.

Europe

For native European ambrosia beetles there was support for four models including mostly forest

A fitted line indicates a significant linear regression ($P < 0.05$). The number of exotic bark beetle species in Europe was not sufficient to perform the analysis

heterogeneity (Table 2a). The proportion of explained variation by these models was relatively low (22–31%). For native European bark beetles, we found three plausible models (i.e. $\Delta AICc < 2$) which

included mostly forest heterogeneity and temperature heterogeneity variables. These models explained a larger proportion of the total variation in species richness (60–69%) than did the models for native ambrosia beetles (Table 2b). Concerning the exotic ambrosia beetles, we found three plausible models which always supported the hypothesis that exotic species richness was positively associated with the value of imports and secondarily to temperature heterogeneity (Table 2c). The low number of exotic bark beetle species in Europe did not allow for analysis.

Generally, results of the HP analyses reflected those ascertained by model selection, but revealed slightly different results concerning the relative importance of some variables. The variable ranking indicated that forest heterogeneity was always the best predictor with the highest independent effect on the number of native species for both ambrosia beetles and bark beetles (Fig. 4a, b). For exotic ambrosia beetle species the value of imports was the only predictor with a large independent effect (Fig. 4c).

USA

For native ambrosia beetles in the USA, we found two plausible models that included mainly temperature, precipitation, precipitation variability, and forest area explaining 64 and 67% of the total variation in species richness, respectively (Table 3a). For native bark beetles, we found six plausible models mostly including minimum temperature and standard deviation of mean temperature, forest heterogeneity, and forest area explaining more than 80% of the total variation in species richness (Table 3b). For exotic ambrosia beetles, we found three plausible models mainly including positive effects of minimum temperature, value of imports and precipitation explaining 71–73% of the total variation (Table 3c). For exotic bark beetles, we found four plausible models, which included mostly the value of imports explaining alone c. 40% of the total variation in species richness (Table 3d).

The results of the HP analyses indicated that native ambrosia beetles were mostly associated with climatic variables (minimum temperature and

Table 2 Plausible candidate models (within 2 ΔAIC of top model) explaining Scolytinae species richness in Europe, separately for (a) native ambrosia beetles, (b) native bark beetles, and (c) exotic ambrosia beetles

Intercept ^a	FOREST-H	AREA	TEMP	PRECIP	PRECIP-H	TEMP-H	IMPORT ^b	k	R ²	Adj. R ²	AICc	ΔAICc	w _i
<i>(a) Native ambrosia beetles (EU)</i>													
11.25	0.968	–	–	–	–	–	n.a.	3	0.22	0.18	86.87	0.00	0.18
11.25	1.027	–	–	–	0.607	–	n.a.	4	0.31	0.23	87.66	0.79	0.12
11.25	0.921	0.468	–	–	–	–	n.a.	4	0.27	0.19	88.66	1.79	0.07
11.25	0.898	–	–	–	–	0.437	n.a.	4	0.27	0.18	88.86	1.99	0.06
<i>(b) Native bark beetles (EU)</i>													
89.7	14.90	–	–	–7.949	–	11.83	n.a.	5	0.69	0.63	174.12	0.00	0.25
89.7	15.93	8.66	–	–	–	–	n.a.	4	0.61	0.56	175.10	0.98	0.15
89.7	15.45	–	–	–	–	8.439	n.a.	4	0.60	0.55	175.51	1.40	0.12
<i>(c) Exotic ambrosia beetles (EU)</i>													
3.250	–	–	–	–	–1.125	1.537	1.720	5	0.51	0.41	94.00	0.00	0.16
3.250	–	–	–	–	–	0.853	1.474	4	0.39	0.32	94.57	0.57	0.12
3.250	–	–	–	–	–	–	1.384	3	0.28	0.25	94.64	0.64	0.11

The number of exotic bark beetles in Europe was not sufficient to perform the analysis. Models are ranked according to their second-order Akaike’s information criterion (AICc). Parameter estimates, number of parameters (k), adjusted R² and model weight (w_i) are reported. All explanatory variables were standardized (mean = 0, SD = 1). Variables names are presented in Table 1

^a For each response variable, the plausible candidate models have the same intercept value because the explanatory variables were standardized (mean = 0, SD = 1)

^b n.a. Not applicable. The variable IMPORT was not included in the analyses for native species

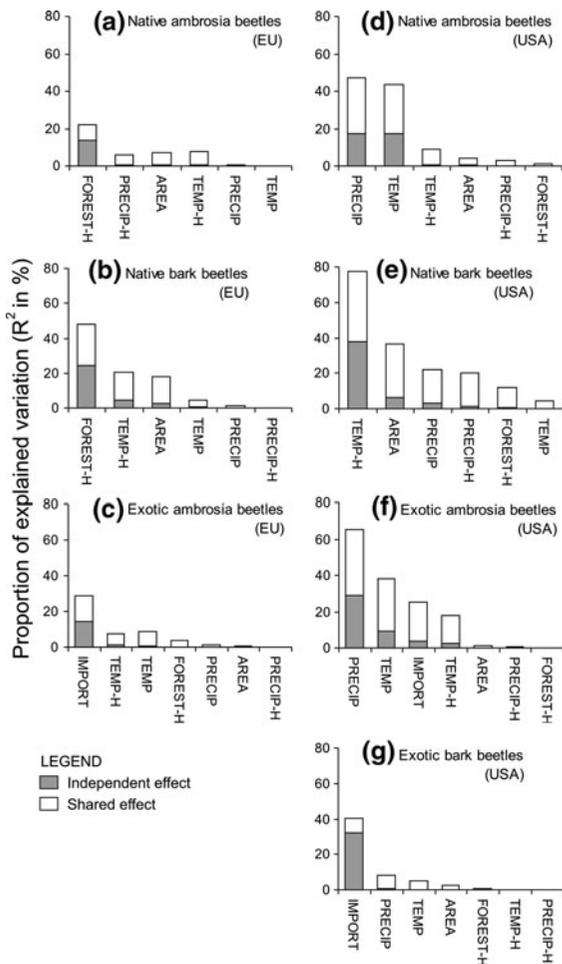


Fig. 4 The independent and shared contributions estimated from hierarchical partitioning of each explanatory variable for the number of native and exotic Scolytinae in both Europe (EU) **a–c** and the USA **d–g**, presented separately for ambrosia and bark beetles. Variable ranking is conducted according to the size of the independent effect, i.e. variable importance declines from *left to right*. Variable names as given in Table 2. AREA and IMPORT were log-transformed. The number of exotic bark beetles in Europe was not sufficient to perform the analysis

precipitation) (Fig. 4d), while native bark beetles were more associated with temperature heterogeneity and forest area (Fig. 4e). Amongst the exotic species, we found that annual precipitation was the most important variable for exotic ambrosia beetles, followed by temperature and the value of imports (Fig. 4f), while for exotic bark beetles the only variable with a large independent effect was the value of imports (Fig. 4g).

Discussion

Our cross-continental study supports the view that both climate and imports are strong predictors of species richness of exotic Scolytinae, despite some differences between regions and feeding guilds. In Europe the only predictor of the number of established ambrosia beetles was the value of imports while in the USA, the feeding guild of an exotic species appeared to modify the probability of its establishment. Here, along with the strong influence of imports, a warmer and wetter climate appeared linked to an increase in the number of established exotic ambrosia beetles, while climate was not important for bark beetles. By contrast, measures of environmental heterogeneity played no important role in explaining species richness of exotic Scolytinae in either region, while they were key drivers in explaining patterns of native species richness. In both regions, exotic Scolytinae were more often ambrosia beetles than bark beetles compared with the relative proportions in the native species pool. There are several life history traits of exotic ambrosia beetles that can favor their arrival and establishment in a new environment: (1) low host specificity and thus the ability to breed in both living and dead wood of many tree species, (2) sib-mating, i.e. brother-sister mating prior to emergence from the host tree, and (3) symbiotic trophic specialization with fungi that obviates the need to overcome many host defenses and reduces competition with native species (Kirkendall 1983). Along with these life-history traits the increasing share of imports from Asian countries, which have a rich ambrosia beetle fauna, may also help explain why the ambrosia beetles represent such a large proportion of the exotic Scolytinae fauna in both Europe and the USA (Rabaglia et al. 2008; Kirkendall and Faccoli 2010).

We found a positive co-variation between native and exotic ambrosia beetles species richness in both regions while no such correlation was found for bark beetles (no data were available for Europe). The positive co-variation for ambrosia beetles was probably related to the fact that both native and exotic species responded strongly to the same climatic factors, while at the scale of our analysis potential interspecific interactions within this feeding guild could not be elucidated (Wood 1982). The lack of correlation amongst bark beetles indicates that native

Table 3 Plausible candidate models (within 2 Δ AIC of top model) explaining Scolytinae species richness in the USA, separately for native (a) ambrosia beetles and (b) bark beetles, and for exotic (c) ambrosia beetles and (d) bark beetles

Intercept ^a	FOREST- H	AREA	TEMP	PRECIP	PRECIP- H	TEMP- H	IMPORT ^b	<i>k</i>	<i>R</i> ²	Adj. <i>R</i> ²	AICc	Δ AICc	<i>w</i> _i
<i>(a) Native ambrosia beetles (USA)</i>													
17.08	–	1.68	3.88	3.81	–2.39	–	n.a.	6	0.67	0.64	305.77	0.00	0.33
17.08	–	–	4.36	3.60	–1.90	–	n.a.	5	0.64	0.62	307.18	1.41	0.17
<i>(b) Native bark beetles (USA)</i>													
52.73	–	4.17	4.96	–	–	25.29	n.a.	5	0.82	0.81	394.55	0.00	0.13
52.73	3.44	–	6.13	–	–	26.52	n.a.	5	0.82	0.81	394.62	0.07	0.13
52.73	3.04	3.69	5.14	–	–	24.68	n.a.	6	0.83	0.82	394.82	0.27	0.11
52.73	–	–	6.07	–	–	27.49	n.a.	4	0.81	0.80	395.03	0.47	0.10
52.73	3.34	5.03	7.3	–4.75	–	20.77	n.a.	7	0.84	0.82	395.85	1.29	0.07
52.73	–	5.34	6.77	–4.05	–	22.03	n.a.	6	0.83	0.81	395.99	1.43	0.06
<i>(c) Exotic ambrosia beetles (USA)</i>													
6.27	–	–	0.88	2.51	–	–	0.56	5	0.73	0.71	215.59	0.00	0.14
6.27	–	–	1.10	2.62	–	–	–	4	0.71	0.70	215.71	0.11	0.13
6.27	–	–	0.97	2.40	–0.33	–	0.63	6	0.73	0.71	217.16	1.56	0.06
<i>(d) Exotic bark beetles (USA)</i>													
5.38	–	–	–	–	–	–	1.51	3	0.40	0.39	200.06	0.00	0.15
5.38	–	–	–	–	–0.32	–	1.57	4	0.42	0.39	201.02	0.95	0.09
5.38	–	–	–0.24	–	–	–	1.62	4	0.41	0.38	201.83	1.77	0.06
5.38	–	–0.18	–	–	–	–0.18	1.52	4	0.41	0.38	201.99	1.93	0.06

Models are ranked according to their second-order Akaike's information criterion (AICc). Parameter estimates, number of parameters (*k*), adjusted *R*² and model weight (*w*_i) are reported. All explanatory variables were standardized (mean = 0, *SD* = 1). Variables names are presented in Table 1

^a For each response variable, the plausible candidate models have the same intercept value because the explanatory variables were standardized (mean = 0, *SD* = 1)

^b *n.a.* not applicable. The variable IMPORT was not included in the analyses for native species

and exotic species richness is related to different environmental factors (see below). Direct biotic interactions between native and exotic bark beetles can be complex and therefore difficult to predict. For instance interspecific competition may be more common amongst native and exotic bark beetle species, given that they feed in the relatively thin layer of phloem as compared with ambrosia beetles that tunnel into the wood (Byers 1989). However, recent studies also found that facilitation may occur, as bark beetles often breed in multiple-species associations and native species can favor the attack of exotics (Lu et al. 2007).

The value of imports was the strongest predictor of the number of exotic ambrosia beetles in Europe and of exotic bark beetle species in the USA, while for exotic ambrosia beetles in the USA the value of imports was less important. These results indicate

that the number of established ambrosia and bark beetle species might be primarily determined by the identity of the trading partners and by the volume of imports rather than by local environment of the recipient region. Previous studies of the pathways by which Scolytinae species are commonly introduced to new countries have shown that they are strongly associated with wood packaging material such as pallets, dunnage, and crating (Brockerhoff et al. 2006a; Haack 2001, 2006; Rabaglia et al. 2008), which helps explain why the value of imports was a good predictor of the number of exotic species in both Europe and the USA. Our measure of imports is expected to be positively related to various aspects of propagule pressure such as the number of exotic species arriving, the population abundance, and the frequency of introduction events. From a community perspective the number of exotic species established

in a region should be positively related to the number of species arriving. That is, when the number of arriving species is large the probability increases that at least one species will match the appropriate conditions for establishment (Lockwood et al. 2009). Similarly at the population level increasing the number of individuals arriving is expected to enhance establishment probability primarily by weakening effects of demographic stochasticity, whereas high frequency of introduction events should diminish impacts of environmental stochasticity in the recipient region (Simberloff 2009). This interpretation conforms to the findings of Brockerhoff et al. (2006a) and Haack (2006) who revealed positive associations between interception frequency at ports of entry and establishment rate of exotic Scolytinae.

Concerning climate, we found contrasting results between ambrosia beetles and bark beetles and between the two regions. In the USA, we found a positive association between both minimum temperature and annual precipitation with ambrosia beetle species richness (both for natives and exotics), while we found no such effect in Europe. The contrasting response between the two regions is probably related to difference in their macroclimate. While in the USA warm and rainy subtropical climates are present in the southern states, in southern Europe the warm Mediterranean climates are characterized by much drier conditions. The nutritional dependency that ambrosia beetles have for their symbiotic fungi may limit the geographic distribution of many species of ambrosia beetles to wetter and warmer regions, which provide favorable conditions for the growth of their fungi (Furniss and Carolin 1977). Analyses of interception frequency of exotic Scolytinae (Brockerhoff et al. 2006a) suggest that the great majority of introduced ambrosia beetle species do not become established. Many species likely fail to establish because of unsuitable climate at the point of arrival. Considering that the large majority of the recently introduced ambrosia beetle species arrived from southeastern Asia (Kirkendall and Faccoli 2010; Rabaglia et al. 2008), one might expect a larger number of establishments if the climate becomes warmer and wetter (Williams and Liebhold 2002; Walther et al. 2009).

Concerning forest and climate heterogeneity, we found a contrasting response between ambrosia and bark beetles, i.e. native species richness of bark

beetles was primarily related to measures of environmental heterogeneity such as forest habitat diversity and climatic heterogeneity while these variables were not important predictors for ambrosia beetles (both native and exotic). Forest habitat diversity is clearly related to the diversity of host trees available for colonization by Scolytinae species. As described above, bark beetles are much more host specific, usually to at least the family or genus level, than are ambrosia beetles (Wood 1982), explaining why the effect of environmental heterogeneity was stronger for bark beetles.

Our cross-continental comparison indicates that growing international trade could contribute to escalating rates of invasion by Scolytinae worldwide, while in the USA the effects of climate appears to be more important for ambrosia beetles as compared with bark beetles. Considering the strong positive relationship between imports and the number of established exotics, and that international trade is steadily increasing, the probability that more exotic species will continue to arrive and have serious impacts on forest ecosystems appears likely (Work et al. 2005; Brockerhoff et al. 2006a; McCullough et al. 2006; Rabaglia et al. 2008; Piel et al. 2008; Aukema et al. 2010; Koch et al. 2010). While the environmental variables studied were not important predictors in Europe, colder and dryer climatic conditions appeared to constrain the distribution of exotic ambrosia beetles in the USA. The southeastern US states with their warm and wet climates will probably continue to be subjected to high rates of establishment for exotic ambrosia beetles even with current levels of imports, while US states with colder and dryer climates will probably not often be invaded successfully by ambrosia beetles even if imports increase in the future. Increasing numbers of these exotic forest pests is particularly worrisome considering that the economic impact by exotic Scolytinae is already significant in both natural and plantation forests as well as in urban ecosystems (Haack and Rabaglia 2011).

International quarantines and phytosanitary policies such as the International Standards for Phytosanitary Measures are very important tools to reduce the arrival rates of exotic species through international trade (Brockerhoff et al. 2006b; Haack and Petrice 2009; Haack et al. 2010; Haack et al. 2011). Although international standards for wood packaging

material used in international trade have been adopted since 2002 (Haack et al. 2010, 2011), individual countries can further reduce the likelihood of establishment and spread of exotic organisms through pest and pathway risk assessments, improved inspection techniques, and early detection survey programs (Brockerhoff et al. 2006b; Coulston et al. 2008; Rabaglia et al. 2008; Brockerhoff 2009; Colunga-Garcia et al. 2010; Koch et al. 2010). Given the likelihood of increasing international trade it is important that additional research and regulation be considered to reduce the risk of pest invasion through the wood packaging material pathway, which could threaten forest health in Europe and the USA, as well as other countries worldwide.

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