

Disentangling the role of environmental and human pressures on biological invasions across Europe

Petr Pyšek^{a,b,1}, Vojtěch Jarošík^{a,b}, Philip E. Hulme^c, Ingolf Kühn^d, Jan Wild^a, Margarita Arianoutsou^e, Sven Bacher^f, Francois Chiron^g, Viktoras Didžiulis^h, Franz Esslⁱ, Piero Genovesi^j, Francesca Gherardi^k, Martin Hejda^a, Salit Kark^l, Philip W. Lambdon^m, Marie-Laure Desprez-Loustauⁿ, Wolfgang Nentwig^o, Jan Pergl^a, Katja Poblížaj^p, Wolfgang Rabitsch^q, Alain Roques^q, David B. Roy^r, Susan Shirley^s, Wojciech Solarz^t, Montserrat Vilà^u, and Marten Winter^{d,f}

^aInstitute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic; ^bDepartment of Ecology, Faculty of Science, Charles University, CZ-128 01 Prague 2, Czech Republic; ^cBio-Protection Research Centre, Lincoln University, 7647 Christchurch, New Zealand; ^dHelmholtz Centre for Environmental Research–UFZ, Department of Community Ecology, D-06120 Halle, Germany; ^eDepartment of Ecology and Systematics, Faculty of Biology, University of Athens, 15784 Athens, Greece; ^fEcology and Evolution Unit, Department of Biology, University of Fribourg, CH-1700 Fribourg, Switzerland; ^gMuséum National d'Histoire Naturelle, Unité Mixte de Recherches 7204, Conservation des Espèces, Restauration et Suivi des Populations, 75005 Paris, France; ^hCoastal Research and Planning Institute, Klaipėda University, LT92294, Klaipėda, Lithuania; ⁱFederal Environment Agency, Department of Biodiversity and Nature Conservation, A-1090 Vienna, Austria; ^jInstitute for Environmental Protection and Research (ISPRA), 4004 Ozzano Emilia BO, Italy; ^kDipartimento di Biologia Evoluzionistica, Università di Firenze, Florence, Italy; ^lBiodiversity Research Group, Department of Evolution, Systematics and Ecology, Institute of Life Sciences, Hebrew University of Jerusalem, Jerusalem 91904, Israel; ^mGlobal Programmes Department, Royal Society for the Protection of Birds, Bedfordshire SG19 2DL, United Kingdom; ⁿInstitut National de la Recherche Agronomique, Unité Mixte de Recherches 1202 Biodiversité, Gènes et Communautés (BIOGECO), Pathologie Forestière, 33140 Villenave d'Ornon, France; ^oInstitute of Ecology and Evolution, University of Bern, CH-3012 Bern, Switzerland; ^pCentre for Cartography of Fauna and Flora, SI-1000 Ljubljana, Slovenia; ^qInstitut National de la Recherche Agronomique, Unité de Recherches 0633, Zoologie Forestière, 45075 Orléans, France; ^rNatural Environment Research Council Centre for Ecology and Hydrology, Wallingford, Oxfordshire OX10 8BB, United Kingdom; ^sDepartment of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331; ^tInstitute of Nature Conservation, Polish Academy of Sciences, PL-31-120, Krakow, Poland; and ^uEstación Biológica de Doñana (EBD-CSIC), E-41092 Sevilla, Spain

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The accelerating rates of international trade, travel, and transport in the latter half of the twentieth century have led to the progressive mixing of biota from across the world and the number of species introduced to new regions continues to increase. The importance of biogeographic, climatic, economic, and demographic factors as drivers of this trend is increasingly being realized but as yet there is no consensus regarding their relative importance. Whereas little may be done to mitigate the effects of geography and climate on invasions, a wider range of options may exist to moderate the impacts of economic and demographic drivers. Here we use the most recent data available from Europe to partition between macroecological, economic, and demographic variables the variation in alien species richness of bryophytes, fungi, vascular plants, terrestrial insects, aquatic invertebrates, fish, amphibians, reptiles, birds, and mammals. Only national wealth and human population density were statistically significant predictors in the majority of models when analyzed jointly with climate, geography, and land cover. The economic and demographic variables reflect the intensity of human activities and integrate the effect of factors that directly determine the outcome of invasion such as propagule pressure, pathways of introduction, eutrophication, and the intensity of anthropogenic disturbance. The strong influence of economic and demographic variables on the levels of invasion by alien species demonstrates that future solutions to the problem of biological invasions at a national scale lie in mitigating the negative environmental consequences of human activities that generate wealth and by promoting more sustainable population growth.

climate | economy | exotic plants and animals | geography | prediction

The accelerating rates of international trade, travel, and transport in the latter half of the twentieth century have led to the progressive mixing of biota from across the world (1) and the number of species introduced to new regions continues to increase (2, 3). To describe these global movements of plants and animals, invasion ecology relies on historical trends and comparative studies of contemporary alien floras and faunas from different parts of the world (4–6). This approach has been crucially important to describe large-scale patterns in the vulnerability of global regions to biological invasions. For example, it is generally accepted that islands are more invaded than continents (7, but see

ref. 8) and that with increasing latitude the number of naturalized plants, mammals, and birds in temperate regions also declines while their geographical ranges increase (9). However, latitude and insularity interact so that although continental regions in the tropics are less invaded than those in temperate regions there seems to be no difference in invasibility of temperate versus tropical islands (10).

Such geographic patterns assume that the opportunity for biological invasions is similar across regions. However, if introduction effort (also termed propagule pressure) (11) varies across regions then this may not be the case. Unfortunately, detailed data on propagule pressure is often hard to come by and it is often assessed using various surrogates, e.g., the number of visitors to nature reserves (7, 12), human population size or density (12, 13); pathway of introduction to the region (14); the amount of trade and tourism (15–20); extent and density of transport networks (21); or macroeconomic parameters (22, 23). Propagule pressure is therefore closely linked with human activities and, indeed, there is increasing evidence that macroeconomic and macroecological variables need to be integrated in the same model if we are to understand the drivers of biological invasions more precisely (1, 21). To date, such studies are relatively few and most focus on one or a few taxonomic groups (24, 25). A study aimed at revealing general determinants of biological invasions common to a wide range of taxonomic groups that would weigh the relative importance of ecological factors and human factors will be pivotal for policymakers and future management.

A recent compilation of the most up-to-date information on alien species in Europe (2) provides an excellent opportunity to

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¹To whom correspondence should be addressed. E-mail: pysek@ibot.cas.cz.

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perform, at a continental scale, analyses aimed at identifying general predictors of invasion that are applicable to a wide range of taxa in terrestrial and aquatic environments. This data set is unique in covering alien plants, fungi, and animals, which enabled us to analyze both the joint and net effects of macroecological and macroeconomic explanatory variables shaping invasions, while taking into account spatial autocorrelation. Specifically, this paper aims to answer the following two questions: (i) What are the main factors that determine the level of biological invasions, defined as the number of alien species, in European regions? (ii) What is the relative importance of geographical, climatic, land-cover related factors, compared with economic and demographic variables?

However, an obvious problem associated with attempts to explain current levels of invasions by economic data stems from the fact that the economic data are usually recent, whereas the lists of established alien species result from invasion processes that have occurred over several centuries (26). Some papers have used measures of a current flow, such as gross domestic product (GDP) (23, 27, 28), human-development index (HDI) (21), or trade flows (15–17) to explain the cumulative level of invasions drawn over several centuries. However, it is inappropriate to use current economic indicators as the measure of historical processes. Because there is a lack of reliable historical economic data on such a large temporal and spatial scale to which cumulative invasions could be related, an appropriate independent economic variable for such analysis is one based on a stock of capital, which reflects the cumulative effect of historic investments, rather than on capital flow. To overcome these problems we used wealth, an economic variable that characterizes current economic prosperity of European regions, as the cumulative outcome of the economic history of that region, reflecting more accurately an economic development over a longer time span (29). This enabled us to relate the cumulative stocks of alien species to measures of cumulative economic prosperity.

Results

A minimal adequate model (MAM) of the effects on alien species explained 25.1% of variability across all taxa. Most variance was explained for plants (91.0%) and bryophytes (78.9%) and the least for insects (26.8%) and fungi (24.8%). The explained variance for the remaining taxonomic groups was: aquatic invertebrates 51.0%, reptiles 49.1%, birds 39.6%, and mammals 38.9%. No significant variance was explained for amphibians and fish. The results were not at all biased by spatial autocorrelations for the individual taxonomic groups and only a very little biased across all taxa (*SI Text*). Most MAMs were characterized by significant interactions between the individual explanatory variables.

Variance partitioning (Fig. 1) for all taxa indicated that joint effects of insularity (as the only significant geographical variable), human factors (including both human population density and wealth), and climate were significant, but of these, only the net effect of human factors ($F = 6.51$; $df = 3,229$; $P < 0.001$; Fig. 1) was significant per se. Variance partitioning for individual taxonomic groups revealed that all variance was explained by significant net effects of human factors in the case of insects (29.5%) and fungi (24.8%). There was a net effect of human factors and climate for birds and aquatic invertebrates, insularity for bryophytes, climate for mammals, and only joint effects for plants and reptiles (Fig. 1).

Regression trees lend further support that wealth and demography had an overwhelming effect on the numbers of alien species. The best tree across all taxa explained 25.6% of variance, of which 18.0% was attributed to human population density, and 7.6% to wealth. High numbers of alien species are supported by a high human population density and great wealth, reaching the highest values in regions with more than 91.1 inhabitants/km² and wealth exceeding about US\$ 250,000 per capita; the smallest numbers of aliens are found in regions with fewer than 8.5 inhab-

itants/km², regardless of wealth (Fig. 2). A high human population density also supported more alien insects, explaining 27.5% of variance. No other explanatory variable appeared in the best regression trees.

Discussion

Our results show that at the regional scale, which in most cases refers to individual countries, the level of invasion, defined as the number of alien species adjusted for the effect of area, can be predicted to a reasonably high degree. Much of the unexplained variance is probably attributable to factors such as local spatial variation of ecological factors influencing establishment success in the site of introduction (30, 31) and differences in the residence time of individual species in studied regions (32) that could not be accounted for at the scale studied because of data availability issues. Working with a wide range of taxonomic groups also requires the use of rather general surrogates of propagule pressure because of the different quality of data available for individual taxa (31). For example, although there is good information on the number of introduction attempts for vertebrates (25, 33), exact information on propagule pressure is not available for other groups such as plants (14) and terrestrial and aquatic invertebrates, which are mostly introduced unintentionally (e.g., 90% of terrestrial invertebrates) (34).

The relative effects of variables shaping the invasions by the individual taxonomic groups (Fig. 1) indicate that the regional patterns are rather complex, but some insights can be obtained by linking them to the pathways of introduction to Europe (35). The overwhelming effect of human factors, i.e., wealth and demography, found for several taxonomic groups translates to human activities responsible for enhancing biological invasions (36). For example, it can be related to the pet trade (resulting in deliberate releases of birds and mammals) (33, 35, 37) or linked with unintentional introductions that are associated with movement of contaminated commodities such as agricultural produce (insects, fungi) and aquaculture stocks (aquatic invertebrates). The invasions by bryophytes are primarily determined by climate due to susceptibility of this group to environmental conditions in the region of introduction (38) and their relatively low importance as either a commodity (ornamentals) or a contaminant of a commodity (timber). The significant although small net effect of climate on mammals suggests that this group is also constrained by unsuitable local climatic conditions, which may be due to frequent opportunistic releases and escapes of pets from captivity, sometimes in regions poorly compatible with their own climatic requirements (39). For example, Mongolian gerbils (*Meriones unguiculatus*) are commonly kept as pets in the United Kingdom and although escapes are common and feral populations have been recorded, these populations do not persist for many years. The complex pattern we found for plants might reflect that the relatively few species introduced deliberately for economic purposes, e.g., forestry and agricultural species, have a higher probability of establishment than species from the considerably larger pool of introduced ornamental species that are less frequently well matched to the local climate (14).

Finally, why the factors included in our study failed to predict the level of invasion by amphibians in Europe is difficult to explain and may also reflect the small sample size; for fish the reason may be historical. The nonsignificant effect of wealth and demography in our models for fish (see also ref. 40) probably reflects that introductions have been a massive phenomenon across Europe for stock enhancement and sport fishing (23, 41). As a result, the pattern of fishery wealth (fishery income as the share of total income) is likely to be different from the overall pattern of national wealth. Indeed, densities of alien fish were also found more difficult to predict than those of plants and birds across counties in the United States (42, but see refs. 23, 43).

The most important conclusion is that human population density and wealth appear to be the major statistically significant predictors in the majority of models when analyzed jointly with

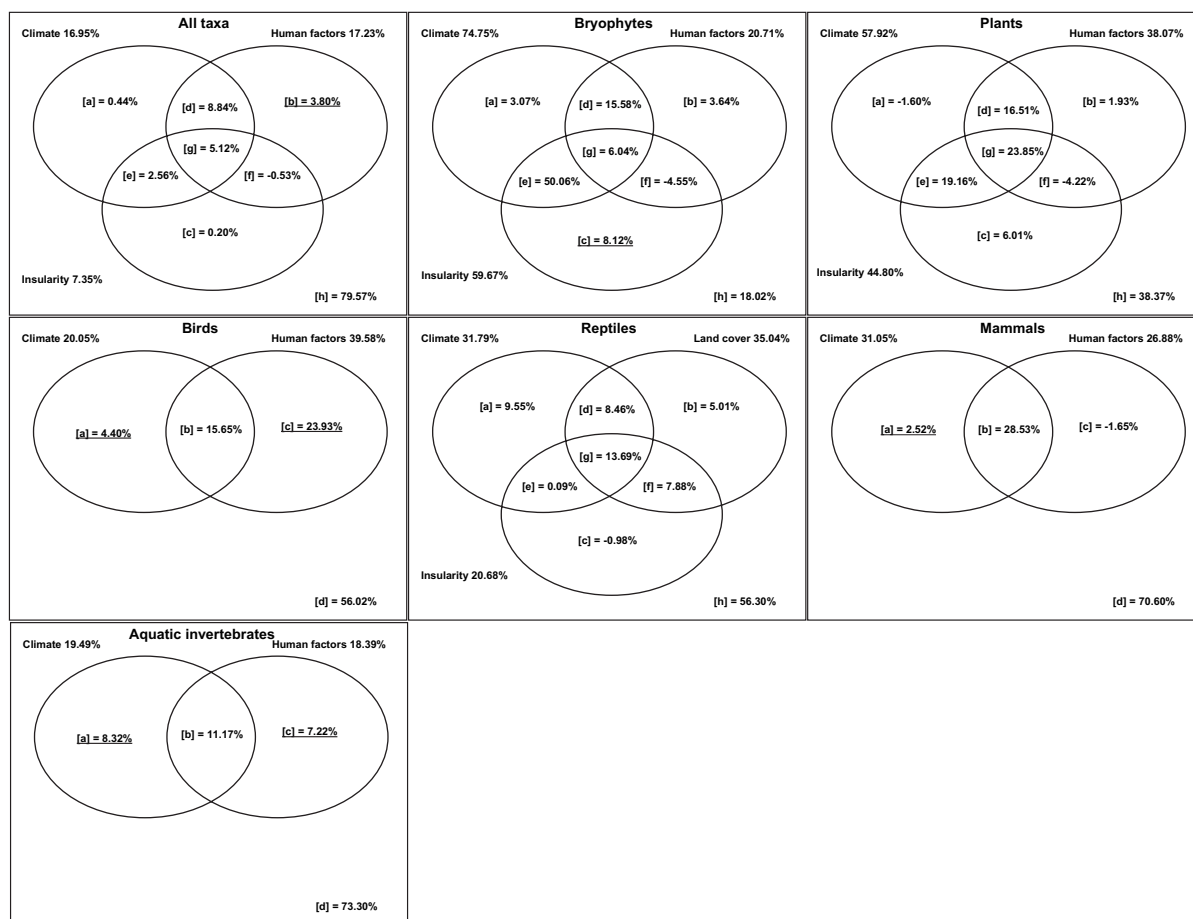


Fig. 1. Partitioning of the variance of standardized alien species numbers in each region adjusted for the effect of area among classes of explanatory variables representing insularity (as the only fitted geographic variable), human factors (including wealth and human population density) and climate. Model for all taxa and for individual taxonomic groups, ranked according to explained variance, are presented. Only the classes of variables for which their joint effects appear significant ($P < 0.05$) are shown (i.e., three classes of variables for all taxa, bryophytes, plants and reptiles, and two classes for birds, mammals and aquatic invertebrates). Intersections of circles in the Venn diagrams represent the variance jointly explained by two or three classes of variables; their negative fractions are given by the correlation structure of the explanatory variables, in which direct and indirect positive and negative effects of the individual variables are combined (ref. 70, p. 533). The rectangles represent 100% of the variance, of which [h] (for taxa having three classes of variables with significant joint effects) or [d] (for taxa having two such classes) is the unexplained part. Only the net effects ([a], [b] and [c] for taxa in which three classes of variables have significant joint effects, and [a] and [c] for taxa with two such classes) can be tested statistically; of these, significant ($P < 0.05$) net effects are underlined. Intersections ([d]–[g] for taxa with three classes and [b] for taxa with two classes) cannot be tested. Note that there is no variation partitioning for insects and fungi because all variance in these taxa was explained by the explanatory variables from only human factors (29.5% for insects and 24.8% for fungi) and that no explanatory variable appeared significant for amphibians and fish.

environmental factors such as climate, geography, and land cover. Therefore it is not surprising that previous studies using only economic factors successfully predicted the numbers of alien plant species in the United States and Canada (15, 22). Our results, however robust, need to be interpreted with caution because the economic variables are not direct causal determinants of the invasion process but reflect the intensity of human activities and integrate the effect of factors that directly determine the outcome of invasion such as propagule pressure (11), pathways of introduction (35), intensity of disturbance (28, 44), and eutrophication (45, 46). However, the precise mechanisms are difficult to disentangle using current data (47), because historical data on where and when an individual species first naturalized are still rather scarce and often uncertain. Therefore, relating the current, cumulative levels of established alien species with an economic measure of cumulative historic investments such as the capital stock, and with current population density in the regions studied seems to be a more credible approach (29).

That wealth and population density are most important does not mean that geography, climate, and land cover have no role in

the outcome of invasions. A few studies have considered both environmental and economic factors at the same time (12, 16), albeit without statistical analysis aimed at determining net effects of individual variables and their relative importance. Our paper shows that effects of the former are overwhelmed by that of human variables. This implies that the effects of noneconomic variables may be overestimated in analyses of factors shaping macroecological patterns of invasions over large spatial scales (48). This raises questions regarding the validity of studies that, in the absence of economic data, concluded that geographic factors are the main determinants of variation in the numbers of alien species at regional and continental scale (9, 10, 49). Therefore, future studies should not ignore the effects of human-related factors when testing the effect of underlying factors and predicting the distribution of alien species (17, 22, 50).

The strong influence of economic factors on the level of invasion by alien species demonstrates that future solutions to the problem of biological invasions will be a considerable challenge (22, 51). How can this knowledge be used to address these problems? The growth in the volume and diversity of trade has

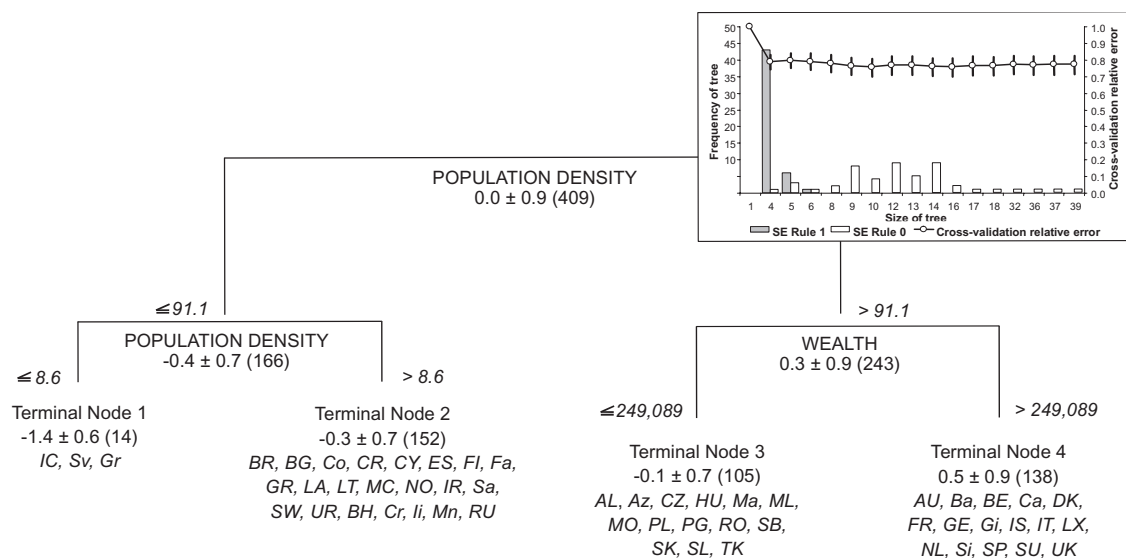


Fig. 2. Regression tree analysis of standardized alien species numbers in each region adjusted for the effect of area for all taxa. Each node of the tree is described by the splitting variable and its split value (population density in inhabitants/km², wealth in US\$ per capita, mean and SD of standardized alien species numbers adjusted for area, and the number of samples at that node). Vertical depth of each node is proportional to its improvement value that corresponds to explained variance at each node. The total variance explained is $R^2 = 0.256$. (Inset) Cross-validation processes for selection of the best regression trees. Line shows a single representative 10-fold cross-validation of the most frequent (modal) best trees with SE estimates of each tree size. Bar charts are the numbers of the optimal trees of each size (frequency of tree) selected from a series of 50 cross-validations based on the minimum cost tree, which minimizes the cross-validated error (white, SE rule 0), and 50 cross-validations based on the one-SE rule (gray, SE rule 1), which minimizes the cross-validated error within one SE of the minimum. The most frequent (modal) trees have four terminal nodes. See Table S1 for region codes.

increased the frequency of new introductions and hence the probability that an introduced species will spread and have an impact (1, 50, 52). Identifying the responsibilities of the key actors involved in trade and targeting legislation appropriately may go some way toward managing invasions (35). Where commodities themselves pose a risk either as deliberate releases or escapes e.g., pets, ornamental plants, new crops, etc., a possible solution would be to ensure the market price also reflects the likelihood and subsequent cost should the species prove to be invasive (51). Yet, the main impediment to adopting this principle is that the World Trade Organization and the international agreement regulating international trade (GATT) have no effective mechanisms by which to internalize the invasion externalities of international trade (51). This is especially true for unintentional introductions such as contaminants and stowaways (35) for which higher tariffs might be required to cover the cost of monitoring and inspecting high-risk pathways (53). However, tariffs may be misused as protectionist tools and disadvantage many developing countries for which the problems of contaminants and stowaways may be more difficult to manage (54). Although an indirect function of trade, the increasing development of transport infrastructures provides corridors for the spread of alien species and increasingly the environmental impact assessment of such projects should address their potential role in biological invasions and mitigate these invasions where possible (1, 35).

Nations do not have a good track record in forsaking future economic prosperity for environmental benefits. As a future challenge, there is a critical need for a multidisciplinary effort to identify the specific economic pressures that are the most proximate causes of the alien species problem (e.g., factors leading to high propagule pressure) and that could serve as indicators that can be mitigated by policy makers to prevent invasions (35). Only if the true determinants are identified, will it be possible to predict and manage alien species invasions adequately without adverse effects on other economic sectors. A much higher precision for predicting invasions will undoubtedly help current attempts in Europe to design management strategies for alien species (3, 55, 56).

Methods

Data Collection. The present paper is based on numbers of naturalized (established) alien species that form self-reproducing populations in the wild without direct intervention of humans and that were introduced to Europe after 1500 A.D. (hereafter termed “alien”; see ref. 57). Data on numbers of alien species were collated for 55 countries, administrative regions, or major islands (hereafter termed “regions”; Table S1) and 10 taxonomic groups, including vascular plants ($n = 20$, number of regions for which the data were available), bryophytes ($n = 32$), fungi ($n = 51$), mammals ($n = 45$), birds ($n = 53$), amphibians ($n = 26$), reptiles ($n = 38$), terrestrial insects ($n = 53$), fish ($n = 38$), and aquatic invertebrates ($n = 34$) (see Table S1 for data sources). Two groups, fish and aquatic invertebrates, occur in inland waters, the remaining eight primarily in the terrestrial environment. Although the coverage of particular taxonomic groups differed among regions (Table S1), the data, collated by the DAISIE project (2), provided a sound basis for analyzing the level of invasion across Europe (sensu refs. 5, 7).

Thirteen explanatory variables were attributed to each region and divided into four classes related to environmental (I–III) and human (IV) factors. (I) Geography: (i) insularity (island versus continent; yes/no); (ii) latitude and (iii) longitude (taken as region mid points); (iv) total area of the region; (v) total surface area of inland waters. (II) Climate, based on data from 1970 to 2000 at 10 arc-min pixel resolution (58) or on data of similar resolution taken from www.worldclim.org (59) for regions outside continental Europe: (vi) mean annual precipitation; (vii) mean annual temperature; (viii) continentality expressed as the difference in mean July and January temperature. (III) Land cover: (ix) number of habitats, expressed as the number of CORINE land-cover classes (60, version 8/2005 obtained from the European Environment Agency); (x) habitat heterogeneity measured as Gini coefficient of equitability of habitat distribution (61), based on the area of individual CORINE land-cover classes in the region. (IV) Human factors, include both economic and demographic variables: (xi) human population density per km² (62); (xii) road density (km/km²; taken from ref. 63) and (xiii) national wealth estimates, based on produced, natural, and intangible capital (62).

Statistical Analysis. Response variables were the numbers of alien species in each region. These numbers were square root + 0.5 transformed (64) to normalize the data (65) and then standardized to zero mean and a variance of one, separately for each taxonomic group. This made it possible to compare the level of invasion across taxa as it varied across two orders of magnitude (Table S1). To account for species–area relationships, the transformed and standardized numbers were regressed on log region area and a MAM was

established. This MAM described significant ($P < 0.05$) group-specific slopes on area. Pearson's standardized residuals (66) from this MAM were used as the response variable (i.e., describing standardized alien species numbers adjusted for the effect of area) fitted separately for each taxonomic group and across all groups.

Of the geographic variables only insularity was directly used as an explanatory variable; the other geographic variables were used to standardize the response variable or to test for effects of spatial autocorrelation. As we were interested in generic trends of invasions across all taxa corrected for area (see above), the total region area was also used for groups found in aquatic environments because there was a very close correlation between the total area of the region and that of its inland water surface area (Pearson's product-moment correlation = 0.87; Spearman's rank correlation = 0.89). The midpoint of latitude and longitude for each region was used to test for spatial autocorrelation (*SI Text*).

All other variables were included as explanatory variables. In linear models, human population density was log transformed before analyses to normalize the data, and all covariates standardized to zero mean and unit variance to achieve their comparable influence. Using the standardized values, collinearity was checked by calculating tolerance values among all of the explanatory variables (67).

To establish MAMs, backward simplifications of full models were performed (68). Because it was impossible to fit the full models directly due to a high number of explanatory variables, the analyses were first run within the factors/classes of variables related to geography, climate, land cover, and human factors (67). To achieve the common MAMs, the model simplifications were then repeated on all significant explanatory variables and their interactions, which were established by these previous analyses. All chosen variables characterizing geography, climate, land cover, and human factors were checked for all possible mutual one- and two-way interactions. All MAMs were also checked for normality and heteroscedasticity of the residuals (69). Their explained variance was expressed by R^2_{adj} (%), taking into account sample sizes and number of predictors (e.g., 67).

For each taxonomic group, variance partitioning (70) was used to split the variance in alien species richness into the net effects of each class of variables and their joint effects. Before the partitioning, stepwise selection procedures based on Akaike Information Criterion were applied, separately on each class of explanatory variables (70) to choose the appropriate variables from each class. This stepwise selection differed from previous simplifications of full models, because the simplification did not include inter-

actions among the explanatory variables. The variance partitioning then proceeded on classes of variables, selected by the stepwise procedure. Net variations due to the individual selected classes, and variations related to their joint effects, were obtained by subtraction, which were made on the basis of adjusted coefficients of explained variance R^2_{adj} (following ref. 70). Statistical significance of individual parts of the variance was calculated by parametric tests (70).

Regression trees (30, 71, 72) were used to provide understandable and generally interpretable results of interactions between explanatory variables of MAMs. The trees were constructed by repeatedly splitting the response variables using binary recursive partitioning in CART v. 6.0 (71, 73). To find the best tree, a sequence of nested trees of decreasing size, each being the best of all trees of its size, was grown, and their resubstitution relative errors, corresponding to residual sums of squares, were estimated. Tenfold cross-validation was used to obtain estimates of cross-validated relative errors of these trees. These estimates were then plotted against tree size, and the best tree chosen both on the basis of the minimum cost tree rule, which minimizes the cross-validated error (the default setting in CART v 6.0; ref. 73), and on the one-SE rule, which minimizes cross-validated error within one SE of the minimum (71). Following ref. 72, a series of 50 cross-validations was run, on the basis of each rule, and the modal (most likely) single tree chosen for description. To prevent missing explanatory variables having an advantage as splitters, the explanatory variables were penalized in proportion to the degree to which they were missing and treated by back-up rules that closely mimicked the action of the primary splitters (71, 73). Total variance explained by the best single tree was calculated as $R^2 = 1 - \text{resubstitution relative error}$. The quality of each split was expressed by improvement, corresponding to proportion of the total sum of squares explained by the tree at each node.

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