Socioeconomic legacy yields an invasion debt

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Globalization and economic growth are widely recognized as important drivers of biological invasions. Consequently, there is an increasing need for governments to address the role of international trade in their strategies to prevent species introductions. However, many of the most problematic alien species are not recent arrivals but were introduced several decades ago. Hence, current patterns of alien-species richness may better reflect historical rather than contemporary human activities, a phenomenon which might be called "invasion debt." Here, we show that across 10 taxonomic groups (vascular plants, bryophytes, fungi, birds, mammals, reptiles, amphibians, fish, terrestrial insects, and aquatic invertebrates) in 28 European countries, current numbers of alien species established in the wild are indeed more closely related to indicators of socioeconomic activity from the year 1900 than to those from 2000, although the majority of species introductions occurred during the second half of the 20th century. The strength of the historical signal varies among taxonomic groups, with those possessing good capabilities for dispersal (birds, insects) more strongly associated with recent socioeconomic drivers. Nevertheless, our results suggest a considerable historical legacy for the majority of the taxa analyzed. The consequences of the current high levels of socioeconomic activity on the extent of biological invasions will thus probably not be completely realized until several decades into the future.

exotic plants and animals | species establishment | time lag

Human activities are the most important large-scale determinants of biological invasions (1–4). Human population size and various contemporary indicators of socioeconomic conditions have been shown to correlate positively with regional numbers of alien plants and animals (1, 3–6), most probably because they are surrogates of propagule pressure and human disturbance to natural systems (3, 6–8). However, the impact of human activities on the distribution of species often exhibits a considerable time lag in the cause–effect relationships (9). For example, extinction because of habitat loss and fragmentation may be delayed (10, 11), and hence recent rates of biodiversity loss are better explained by historical than by current socioeconomic drivers (12, 13). The number of species committed to eventual extinction following a forcing event has been termed an "extinction debt" (10, 11). In a similar manner, alien invasions may be characterized by considerable time lags between the date of first introduction of a species to a new territory and its establishment as part of the regional flora or fauna (14, 15). This lag in the cause–effect relationship would mean that, independently of existing biosecurity and trade regulations preventing further introductions, the seeds of future invasion problems have already been sown and can best be described as an "invasion debt."

Pyšek et al. (3) have recently demonstrated that across Europe, human population density and the accumulation of capital are tightly correlated with current numbers of a wide range of alien plant and animal species. However, human population densities and economic performance of individual countries have not developed strictly in parallel during the past century, with some countries seeing more and others less rapid development (16) (Fig. S1). These differential histories offer an opportunity to explicitly test the invasion debt hypothesis: If lag times between introduction and establishment are short for a majority of species, we should expect current numbers of established alien species across different countries to be more closely related to contemporary rather than historical socioeconomic activities. In contrast, if an invasion debt plays an important role, current alien-species richness should rather reflect levels of past socioeconomic activity.

Here, we test these predictions using data on the numbers of currently established alien species from 28 European countries for 10 taxonomic groups: vascular plants, bryophytes, fungi, birds, mammals, reptiles, amphibians, fish, terrestrial insects, and aquatic invertebrates (see Table S1 for details and data sources). As current and historical socioeconomic indicators are correlated over time, despite differences in the development of individual countries (Fig. S1), we did not aim at exclusively selecting a contemporary or historical explanation, but to compare the relative importance of each using a model selection approach based on information theoretical concepts (17, 18). We used linear mixed-effects models with a spatial correlation structure and spatial autoregressive models to relate current patterns of alien-species richness to three indicators of socioeconomic activity evaluated at two different points in time, namely for the years 2000 and 1900 (Table S2). For each time point, the values of the socioeconomic predictor variables were combined into three mutually independent indicators of the intensity of human activities by means of a principal component analysis (PCA) (Table S3). Subsequently we compared the relative support for models using recent and past socioeconomic indicators based on the Akaike Information Criterion (AIC) as well as by Akaike weights derived from the AIC (16).

We have chosen the start and end dates of the 20th century because they encompass a period in Europe representing marked

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growth in the human population, dramatic increases in urbanization, globalization of economic relationships, and technological advances that have revolutionized the origins, volumes, and velocity of trade (2, 6). In parallel to this socioeconomic development, a significant proportion of alien species have also been introduced to the European countries during the 20th century (19, 20) (Fig. 1). The selected predictors were human population density, per capita gross domestic product (GDP) and, as a measure of trade intensity (i.e., openness of an economy), the share of exports in GDP. We used the share of exports in GDP because historical import data are of poor quality. However, imports and exports are known to be closely linked (16, 21, 22), hence the influence on the analyses is expected to be marginal.

Indicators of cumulative economic prosperity, such as wealth, are generally more appropriate to explain the distribution of stocks of alien species than variables that measure the flow of capital and goods within a relatively short time span, such as GDP and trade volumes (3). However, reliable historical data on wealth are scarce, whereas past GDP and trade volumes have been reconstructed for quite a number of countries (16, 21). Moreover, in this analysis, we wanted to compare the imprints of introduction efforts around 1900 and 2000, respectively, on the current patterns of alien-species richness to detect a possible delay in the build-up of these stocks. As measures of contemporary capital and trade flow arguably are related to introduction efforts within the respective time spans (4), we consider GDP and trade intensity reasonable indicators for this purpose.

Results

Across all 10 taxonomic groups, the models with socioeconomic indicators from 1900 provided a clearly better explanation of current alien species-richness patterns in Europe than those using indicators from 2000 (Table 1). Predictor variables were significantly associated to the response in both models, and goodness of model fit did not differ dramatically, most probably because of correlations among predictor variables across time (Fig. S1). However, the absolute difference in AIC values between the two models was > 40 and suggests that the weaker model has essentially no comparative support (23). As a consequence, the historical and contemporary socioeconomic models had Akaike weights close to 100 and 0%, respectively.

Nevertheless, analyzing the 10 taxonomic groups individually reveals that the importance of historical and contemporary socioeconomic conditions in explaining current established species numbers was different (Fig. 2). Whereas historical indicators provided superior models for vascular plants, bryophytes, fungi, mammals, amphibians, fish, and aquatic invertebrates, the distribution of alien birds, reptiles, and terrestrial insects was more closely correlated to the levels of human activities in 2000. Differences in AIC values were particularly pronounced for vascular plants, bryophytes, and terrestrial insects (ΔAIC > 10), but were >2 in all cases (Table S4), and the superior models had Akaike weights >80% throughout. For the better of the two models, correlations among model predictions and observed values were >0.5 (except for aquatic invertebrates, $r = 0.42$), and mostly >0.7, indicating that the models fit the data reasonably well (Table S4). There was no indication of a potential biasing effect of spatial autocorrelation in any of the models (Table S5).

Discussion

Recent studies have demonstrated that on broad spatial scales, the impact of human activities overwhelms the influence of climate and geography on species invasions (3, 4, 24). The results of the current analysis extend our understanding of the temporal dimension of this relationship. We show that, across all 10 taxonomic groups analyzed, indicators of historical introduction efforts around the year 1900 explain current stocks of alien species in Europe significantly better than the same indicators evaluated for the recent past. Given the enormous increase of introduction events during the second half of the 20th century (19, 20) (Fig. 1), this result is strongly suggestive of a considerable delay between the introduction of a species and its sub-

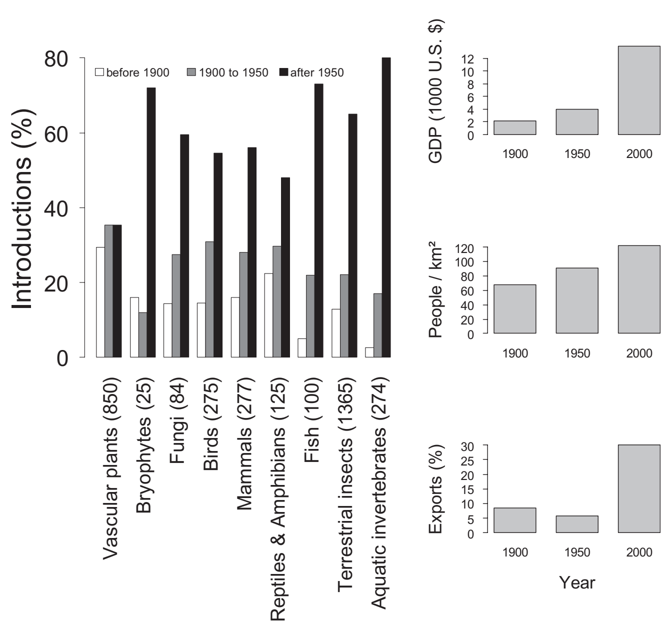

Fig. 1. Trends in species introductions and socioeconomic indicators in Europe over the 20th century. (*Left*) Percentages of alien-species introduction events for different taxa recorded in the European countries covered by the DAISIE project (www.europe-aliens.org) (19) before 1900, between 1900 and 1950, and after 1950. Numbers in parentheses represent the overall number of species per taxon with known introduction dates. Species for which dates on their first record are missing were not considered. (*Right*) Average trends in three socioeconomic indicators: per capita GDP (in standardized 1990 International Geary-Khamis Dollars), population density, and the share of exports in GDP at three different time points (1900, 1950, 2000) for the 28 European countries used in this study.

Table 1. Alien-species richness across 10 taxa in 28 European countries as explained by historical or current socioeconomic indicators

	1900	2000
PCA 1	0.19 ± 0.02***	0.15 ± 0.02***
PCA 2	0.14 ± 0.03***	0.10 ± 0.04**
PCA 3	−0.06 ± 0.05	−0.24 ± 0.07***
R^2_{MF}	0.36	0.28
AIC	367	408
Akaike weight	>99.99	<0.01

The first three rows provide fixed-effects coefficients, together with their SEs, of predictor variables in each model (the three axes of a PCA on population density, standardized per capita GDP and share of exports in GDP in 1900 and 2000, respectively) as estimated by linear mixed effects models with taxon as a grouping variable, random intercepts, heteroscedasticity in the within-group errors, and an exponential spatial correlation structure within groups. The asterisks symbolize significance levels (**<0.01; ***<0.001), calculated by t tests with 230 degrees of freedom each. R^2_{MF} is McFadden's pseudoR^2, a measure of goodness of model fit, calculated from the ratio of the full and null models' log-likelihoods; the null model was defined as an ordinary least squares model with an intercept only in this case. AIC is the Akaike information criterion. The Akaike weight gives the probability that the given model explains the data best among the set of (two) candidate models.

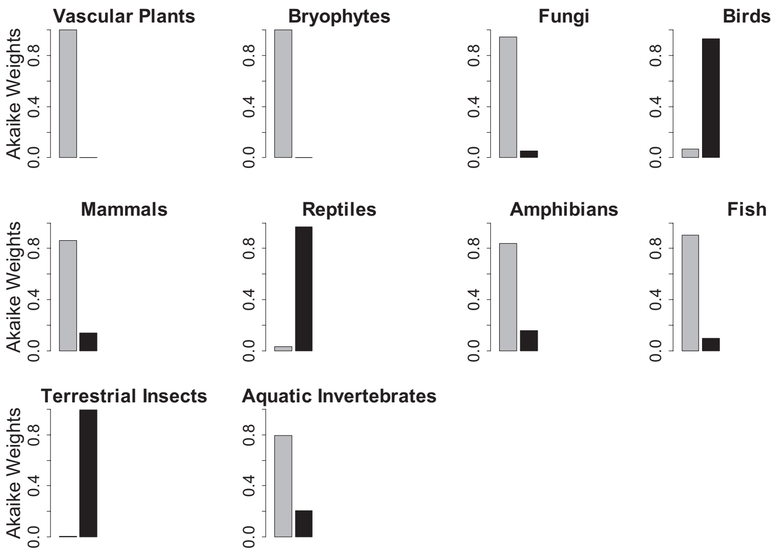

Fig. 2. Alien-species richness of 10 different taxonomic groups in 28 European countries as explained by current and historic socioeconomic models. Bars represent Akaike weights for spatial autoregressive models explaining the current distribution of established alien species across 28 European countries by either current or historical socioeconomic conditions. The predictors in the models are scores on the three axes of a principal component analysis using human population density, standardized per capita GDP, and share of exports in 1900 (gray), and 2000 (black) as input variables.

sequent establishment in the wild (14, 25). Such a delay probably results from the time necessary to exceed critical thresholds of available propagules (8) that will, in turn, depend on factors like the numbers of introduction events and of individuals introduced (7, 8, 24, 26), the type of introduction pathway (9, 27), the match between an alien-species' habitat requirements and the conditions in the new territory (9), the length of generation times (14, 28, 29), or the time necessary for genetic adaptations to the new environments (8). This multitude of potentially interacting factors renders any generalization about the magnitude of such a delay difficult and probably also explains why the relative strengths of historical and contemporary models are not consistent among taxonomic groups. Dispersal capacity likely plays a role in this context, as among the three groups whose current stocks of alien species were better explained by contemporary indicators of socioeconomic activities, two, namely birds and insects, can be considered to be especially mobile. Such mobility facilitates the exploration of habitats and hence likely accelerates naturalization. Moreover, many members of both groups are able to fly and may hence more easily overcome barriers between suitable habitats and the actual places of introduction. The superiority of contemporary models for reptiles, and of historical models for mammals, nevertheless suggest that the accelerating effect of higher mobility is not sufficient to explain the differences among taxonomic groups, and that the complex interplay of factors that determine the lag between introduction and establishment is certainly far from being fully understood. Moreover, interactions with variables not considered in our models may play an additional role. Reptiles, for example, are particularly frequent in Mediterranean countries, probably because their naturalization and spread is constrained by climatic conditions (30). At the same time, these Mediterranean countries have considerably improved their socioeconomic ranking during the 20th century, particularly in comparison with the states of Eastern Europe (Table S2). For this taxonomic group, the superiority of contemporary socioeconomic models might hence be less indicative of reduced lag times but at least partly arise from the increasing congruence of suitable climatic conditions and improved economic status during the recent decades. In addition, for both reptiles and birds, the recent emergence of pet trade and associated frequent deliberate releases (24) may have additionally reduced the times between first introduction and establishment.

The level of socioeconomic activities in a country might not only affect the accumulation of alien species via the associated introduction efforts. In addition, the environmental legacies of economic development, such as expansion of road and canal networks (4), loss and fragmentation of natural and seminatural habitats, or agricultural intensification are well-known to foster alien species naturalization and spread (1, 5, 31). As a consequence, a high level of economic development at the turn of the 20th century will also have increased and accelerated the establishment rates of these species, as well as that of subsequently introduced taxa. This finding indicates that various socioeconomic measures may influence alien-species richness in different ways. Annual measures, such as per capita GDP and imports, may correlate with rates of introduction, whereas cumulative measures, such as human population density and wealth may, through their impact on the environment, influence the likelihood of an introduced species becoming established or spreading. It should be borne in mind that the interpretation does not take into account increasing measures to eradicate or prevent the entry of alien species. If such actions tend to be more effective in wealthier economies (2), then this would tend to reduce the correlation between contemporary socioeconomic variables and current alien-species richness. However, up to now such measures have mainly concentrated on especially harmful pests and pathogens (2, 6) and probably had little impact on the bulk of species analyzed here.

In conclusion, our data demonstrate that socioeconomic legacies on alien-species richness are important across a broad array of taxonomic groups and might extend back at least one century. This inertia implies that the consequences of the current socioeconomic activity on the extent of biological invasions will not be completely realized until several decades into the future. This finding should not discourage ongoing European (20, 32, 33) and global initiatives (34) to tackle invasions. In the long term, a more precise identification and a better control of taxon-specific high-risk introduction pathways and a general reduction of propagule pressure will certainly be key to managing the problems arising from biological invasions. However, our results highlight that even if further unintended introductions could be successfully reduced (29, 35) by these ongoing initiatives (20, 32, 34), the midterm impacts of alien species on biodiversity (36, 37) and the economy (38) might even be higher than currently expected. For this reason, in enforcing its commitment to develop a European strategy on invasive alien species (33), the European Union should not only develop more stringent prevention measures, but also include provisions on the control of those alien species that are already present in Europe, including those that are not yet invasive there but known to be invasive elsewhere.

Materials and Methods

Alien Species Data. The DAISIE project (www.europe-aliens.org) (18) has collated detailed information on the distribution of ≈11,000 alien species in 59 countries and subnational regions (e.g., large islands) in Europe for terrestrial and aquatic organisms (see Table S1 for taxa used in this study and data sources). Only established species introduced after 1500 (39) have been included in the analyses.

Socioeconomic Variables. Profound changes in the boundaries of European states during the 20th century have resulted in a lack of comparable historical socioeconomic data for a couple of countries or regions, and hence limited our sample size to 28 (Table S1). The remaining countries are geographically and socioeconomically representative of the broad range of historical European socioeconomic trajectories.

Data on current and historical human population densities have been calculated from the Total Economy Database (http://www.ggdc.net/databases/ted.htm), which contains standardized data on a wide range of socioeconomic indicators that are comparable over time and across countries. Current and historical per capita GDP [in standardized 1990 International (Geary-Khamis) Dollars, a hypothetical currency unit that has the same purchasing power that the U.S. Dollar had in the United States in 1990), was also extracted from the Total Economy Database.

International trade is known to influence propagule pressure and hence to influence levels of invasion (4, 40, 41). Data have been calculated based on Mitchell (16) and Maddison (21) for 1900, supplemented by the International Monetary Fund (http://www.imf.org/external/np/sta/index.htm), Eurostat (http://epp.eurostat.ec.europa.eu/), and the Global Business School (http://economy.alumnieeni.com) for 2000.

Preprocessing of the Data. Before fitting statistical models, both response and predictor variables were preprocessed. With respect to the responses, we first removed any potential effect of country area on alien-species numbers by regressing, for each taxon separately, these numbers against the logarithm of the area of the country. Regressions were performed by means of generalized linear models, with a log-link for Poisson-distributed data (42). The residuals of these models were then used as the dependent variables in all subsequent statistical analyses.

Concerning predictors, we eliminated correlations among the three variables (population density, standardized per capita GDP, and share of exports in GDP in 1900 or 2000, respectively) by subjecting them to the PCA and then used the scores of the 28 countries on the three axes of these PCAs (one per time point) as predictors in the models. The PCAs were done by means of a single value decomposition of the centered and scaled data matrices as implemented in the *R*-function *prcomp* (43). The three variables per time point were thus transformed to a 3D indicator of socioeconomic activities, with the three axes being independent of each other. However, the three PCA-axes were still correlated across time (the first PCA axis of the variables from 1900 is correlated to the first PCA axis of the variables from 2000, and so on) (Fig. S1): that is, the overall pattern of socioeconomic activity levels across these 28 countries was conservative to a certain degree.

The loadings of GDP, population density, and export shares on the three axes of the PCAs for 1900 and 2000 are given in Table S3. To provide a more direct indication of their relative impacts on alien-species numbers, we also applied the subsequently described regression techniques and fitted, separately for each time point, models with all seven possible combinations of GDP, population density, and export shares as predictor sets (without prior transformation by PCA). The relative importance of the three predictor variables was then expressed as the sum of the Akaike weights (23) of all of the models that contained the respective variable (Table S6).

Mixed Models. To compare current and historical socioeconomic indicators with respect to their explanatory value for current alien-species richness across all 10 taxonomic groups, we fitted linear mixed effects models with the residuals of the taxon-specific Poisson regressions as a response and the PCA axes of the indicators from 1900, respectively, and from 2000, as predictors. We used taxon identity as a grouping variable but estimated random effects for the intercept only. A more complicated model structure with random effects for each predictor variable did not converge with the available algorithms for fitting linear mixed effects models. The models allowed for unequal variances in species numbers across taxa. Possible spatial autocorrelation of the numbers of species within each taxon was accounted for by an exponential within-group correlation structure. The models were fit by maximizing the model parameters' likelihood using the *lme* function in the R-package *nlme* (44).

Spatial Autoregressive Models. To analyze the importance of historical and current socioeconomic indicators for each taxon individually, the residuals of the taxon-specific Poisson regressions were correlated to the PCA axes of the indicators from 1900 and 2000, respectively, by means of spatial autoregressive error models (SAR_{err}). These models assume that the autoregressive process occurs in the error term of a regression model only and were shown to have an overall good performance in analyzing spatially structured data in comparative studies (45, 46). The spatial error term is predefined from a neighborhood matrix. Using the geographical coordinates of their respective capitals to define the spatial positions of the countries, we tried matrices with different neighborhood distances (500, 1,000, 1,500, and 2,000 km, respectively) and finally used 1,000 km as the distance where most countries had at least one neighbor and the autocorrelation in the models' residuals was effectively reduced in all combinations of taxa and predictor sets (Table S5). All models were fitted using the function *errorsarlm* in the R-package *spdep* (47).

Model Comparison by Akaike Weights. For each SAR_{err} of each taxon, we then calculated the corrected AIC_c, which includes a second-order bias correction appropriate for small sample sizes (23). The AIC_cs of the two candidate models (with the indicators for 1900 and 2000) (Table S5) per taxon were subsequently compared by means of Akaike weights (23). Goodness-of-fit of the individual SAR_{err}s was evaluated by calculating Pearson's correlation coefficients between the response variables and the fitted values of the models (Table S4).

Akaike weights of the two linear mixed-effects models used for correlating species numbers of all 10 taxonomic groups to historical and current socioeconomic indicators were calculated in the same way as for the SAR_{err}s, except for taking account of the larger sample size by computing the uncorrected AIC (23). Goodness-of-fit of the mixed-effects models was assessed by means of McFadden's pseudo R^2 (48). R^2_{MF} is calculated from the ratio of the full and null models' log-likelihoods. We defined the appropriate null model as an ordinary least-squares model with an intercept only. Note that models with an $R^2_{MF} > 0.2$ are meant to fit the data well (48, page 307).

We note that we repeated all analyses using an alternative way to account for species-area relationships. Specifically, we directly included the logarithm of area as an additional predictor into the regression models instead of removing its effects on species numbers beforehand and, concomitantly, replaced human population density by human population size as an input to the PCAs. This alternative approach revealed qualitatively identical results, although differences in AICs between 1900 and 2000 were somewhat less pronounced. The lower discriminative ability of this approach is a consequence of an increased correlation among the two predictor sets (of the 1900 and 2000 models), which results from including a constant term (country area) to both of them.

All statistical analyses were done in R 2.9.2 (43).

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