LETTER

Reply to Keller and Springborn: No doubt about invasion debt

We recently showed (1) that, for a wide range of taxa, the current numbers of established alien species in 28 European countries were generally more closely related to socioeconomic indicators from the year 1900 than 2000. Thus, the establishment of alien species seemed to lag considerably behind one of the main drivers of alien species introductions (2). We concluded that current high socioeconomic activity could result in considerable additional accumulation of alien species in the future, a phenomenon that we have called invasion debt.

Keller and Springborn (3) suggest that cumulative numbers of established alien species would be better explained by variables that are a function of the cumulative human activity rather than by socioeconomic data from any given year. Moreover, they argue that socioeconomic conditions show temporal autocorrelation, and as a result, the power of the 2000 data to explain variation in socioeconomic activities over a longer time frame is truncated, because we do not know how economic indicators will develop in the future.

We have previously applied cumulative socioeconomic variables to show the relative importance of socioeconomic factors over geographic and climate variables in current patterns of alien species richness in Europe (2). Unfortunately, cumulative measures are not available for 1900, but in any case, variation across countries in measures such as wealth is highly correlated with gross domestic product (GDP) for individual years. The pitfalls of temporal autocorrelation are addressed in our paper (figure S1 in ref. 1). More generally, we noted that current stocks of alien species were necessarily driven by past species introductions (1). Independently of statistical concerns, data about future socioeconomic development are, hence, hardly relevant for explaining current numbers of established alien species. Rather, proxies for explaining these stocks should be representative of socioeconomic activities of the years before 2005 (the approximate date of alien species data analyzed in ref. 1). Keller and Springborn (3) show that the 2000 data fulfill this requirement because of close temporal autocorrelation of socioeconomic indicators across the second half of the 20th century.

In support of our evidence of invasion debt, we repeated our previous analyses including data from the year 1950 (figure 1 in ref. 1). If truncation drives a spurious superiority of historical correlations, then the 1950 data, which are hardly affected by such truncation, should turn out to be superior to the 1900 data in explaining current alien species richness. In fact, the 1950 data provide a strictly intermediate explanatory power, still clearly inferior to the 1900 data (Table 1). We, hence, conclude that the close correlation between current numbers of established alien species and socioeconomic indicators from 100 y ago is a reality, not an artifact, and that it actually indicates the legacy of past introductions realized by a delayed process of species establishment. Because species introductions have increased during the second half of the 20th century (4), there actually seems to be no doubt about invasion debt.

Table 1. Alien species richness across 10 taxa in 28 European countries as explained by socioeconomic indicators in 1900, 1950, and 2000

	1900	1950	2000
R^2_{MF}	0.36	0.32	0.28
AIC	367	387	408
Akaike weight	>99.99	<0.01	<0.01

Results of linear mixed effects models with human population density, standardized per capita GDP, and share of exports in GDP in the respective years as independent variables, taxon as a grouping variable, random intercepts, heteroscedasticity in the within-group errors, and an exponential spatial correlation structure within groups. R^2_{MF} is McFadden's pseudo-R^2, a measure of goodness of model fit. AIC is the Akaike information criterion. The Akaike weight represents the probability that the given model explains the data best among the set of candidate models.

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