No saturation in the accumulation of alien species worldwide

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No saturation in the accumulation of alien species worldwide

Hanno Seebens et al.†

Although research on human-mediated exchanges of species has substantially intensified during the last centuries, we know surprisingly little about temporal dynamics of alien species accumulations across regions and taxa. Using a novel database of 45,813 first records of 16,926 established alien species, we show that the annual rate of first records worldwide has increased during the last 200 years, with 37% of all first records reported most recently (1970–2014). Inter-continental and inter-taxonomic variation can be largely attributed to the diaspora of European settlers in the nineteenth century and to the acceleration in trade in the twentieth century. For all taxonomic groups, the increase in numbers of alien species does not show any sign of saturation and most taxa even show increases in the rate of first records over time. This highlights that past efforts to mitigate invasions have not been effective enough to keep up with increasing globalization.
The rate at which humans translocate species beyond their native ranges has substantially increased during the last centuries\textsuperscript{1–3}. The unprecedented intensity of human-mediated species exchange leads to the homogenization of floras and faunas\textsuperscript{4}, redefines the classical boundaries of biogeography\textsuperscript{5} and has far-reaching implications for native biota, ecosystem functioning, human health and economy\textsuperscript{6–9}. However, although the general rise in the number of alien species is undisputed, we know little about the temporal dynamics of alien species accumulation and how this might vary among taxonomic groups and geographic regions.

A wide range of motivations underlie the introduction of alien species and the relative importance of these vary considerably in space and time, and among taxonomic groups\textsuperscript{9}. For example, many alien species of taxa such as mammals, plants or birds were released by European explorers and settlers all over the world during 1500–1800 (ref. 9). In the nineteenth century, numerous plants have been brought to Europe for ornamental purposes\textsuperscript{10}, whereas currently bird species are intensively traded in South East Asia, where the accidental or deliberate release of individuals supports the establishment of alien populations\textsuperscript{3}. In addition, most alien species of taxa, such as insects, algae and crustaceans, have been introduced recently through trade and the transport of goods and people\textsuperscript{11}. Differences in the pathways and distribution of alien species introductions suggest that the chronology of invasion probably varies among taxonomic groups and regions, yet a comprehensive analysis of global invasion dynamics of the last centuries is still lacking. Furthermore, we have as yet only limited understanding of whether current rates of alien species accumulation may show signs of saturation or whether we can expect biological invasions to continue at the same rate seen in the past.

To address these gaps in our knowledge, we compiled a global data set of regional first records of alien species that are now established (following the criteria in ref. 12) in multiple geographic regions worldwide (countries and sub-national regions such as islands). This data set of 45,813 first records of 16,926 established alien species from a wide range of taxonomic groups is invaluable for assessing taxonomic and geographic variation in alien species accumulations, and for testing for evidence of slowdown in the accumulation rates. It covers 282 non-overlapping regions from all continents, with particularly intense sampling in Europe, North America and Oceania, and from well-studied taxa such as vascular plants, mammals, insects, birds and fishes (Fig. 1 and Supplementary Fig. 1). This data set allows us to analyse variations in the rate of alien species introductions across space and time in a consistent way over large geographic scales. In particular, we test the following predictions: (1) rates of introductions for species often intentionally introduced such as mammals, birds and vascular plants should decline in recent years as a result of increased awareness of their impacts and tighter biosecurity regulations; (2) rates of introductions for taxonomic groups primarily introduced accidentally such as invertebrates or algae should show steep increases in recent times, as these species are more difficult to regulate and are closely associated with increasing trade; and (3) significant geographic differences in the rates of alien species introductions should be apparent, reflecting variations in socio-economic histories and the strength of biosecurity regulations. We find that the number of established alien species and for most taxonomic groups even the rate of introduction increased until recently with no sign of saturation. We can therefore expect many more invasions to happen in the near future.

### Results

#### Global patterns of alien species introductions

The global rate of first records (measured as the number of first records of established alien species per time unit) remained low between 1500 and 1800 (on average 7.7 first records annually, Fig. 2a). Since 1800, first records have increased constantly, only slowing during the two World Wars, to a maximum of 385 in 1996 (reflecting on average more than 1.5 new records per day). Our data set does not cover all alien species recorded in every region of the world and thus inevitably underestimates first record rates. The continuous rise in first record rates during the last 200 years is consistent across taxa (Fig. 2), except for mammals and fishes, whose rates have declined in recent decades (Fig. 2e,i). Remarkably, barring mammals and fish, there is no clear indication of a slowdown in the first records rates of alien species: rather, they are still increasing. This trend was consistent for both mainlands and islands (Supplementary Fig. 2).

Three general patterns emerge in the first record trajectories of alien species. The first pattern consists of weak increases until 1950, followed by strong increases thereafter (Fig. 2) and is best described by an exponentially increasing function of time (Supplementary Fig. 3). This pattern is typical of species mainly introduced accidentally as stowaways on transport vectors or contaminants of commodities (for example, algae, insects, crustaceans, molluscs and other invertebrates; Fig. 2d,j–l,o). Many of these taxa have been introduced intentionally as pets, particularly in recent times\textsuperscript{13}, increasing the likelihood of the establishment of alien populations. First record rates produced by a simple neutral colonization model that assumes that the probability of introduction increased proportional to the value of imported commodities showed rates similar to those observed for most invertebrates and algae, with a steep increase after 1950 (Supplementary Fig. 5j–l). This finding supports the suggested importance of trade as a major driver of alien species introductions at least for invertebrates and algae.

Second, first record rates of mammals and fishes increased until around 1950, then declined subsequently (Fig. 2e,i), and were best fitted by a hump-shaped function of time (Supplementary Fig. 3d,h). A similar pattern can also be found for the time series of other taxonomic groups after taking into account most recent first record rates (>2000, that is, including grey dots in Fig. 2). However, these recent data are likely to be influenced by a reduced sampling intensity due to delays in detection and reporting of new alien species and thus should be interpreted very carefully. A longer sampling time and more recent data are needed to reliably assess these trends. For mammals, the findings are in line with our expectations that the rates of first records of species mostly introduced intentionally should decline in recent years. Despite the observed declines, first record rates are still high with 19 first records for mammals and 104 for fishes during 1996–2000 (Fig. 2). The decline seemed to result from a reduction in the deliberate introduction of mammals as, for example, game animals or for the fur industry, and stricter regulations for animal farming, which resulted in fewer escapes than was historically the case. For instance, Acclimatisation Societies founded after 1860 in the United States, Australia and New Zealand were responsible for introductions of numerous mammals, birds and plants\textsuperscript{9,14,15}. In the twentieth century, their activity in these regions declined due to decreasing public and scientific support\textsuperscript{13}. The decrease in first record rates may also be related to changes in manner and to stricter
regulations of animal farming, which should result in fewer escapes. Some of these explanations may also apply to fishes; in Europe, however, first record rates of fishes have increased continuously (Fig. 4), which may be at least partly attributed to the ongoing immigration of new fish species through the Suez Canal\textsuperscript{16}.

Third, first record rates of vascular plants increased steeply in the nineteenth century and remained at high levels until the present (Fig. 2b), which was best represented by a sigmoidal increase of first record rates with time (Supplementary Fig. 3a). This trend can again be at least partly attributed to the colonization of North America and Oceania by European settlers and corresponding activities of institutions such as Acclimatization Societies in the nineteenth century. In addition, the foundation of many botanic gardens worldwide, a major pathway for plant introductions\textsuperscript{17}, together with the increased international transport of living plants and propagules, and inventions such as the Wardian Case in 1829 (a mobile greenhouse to transport live plants), have promoted the establishment of alien plant species. In contrast to mammals and fishes, and contrary to our expectations, the first record rates of vascular plants remained high in the twentieth century, which is likely to be a consequence of the intensification of global trade\textsuperscript{18} and increasingly widespread cultivation of plants in agriculture, botanic and private gardens\textsuperscript{19}.

Temporal patterns in the rates of first records on a continent (thereby excluding subsequent within-continental spread) vary distinctly across continents and taxonomic groups (Fig. 4 and Supplementary Fig. 6). Within taxonomic groups, there may be different pathways driving invasions of species that differ in their ecology and temporal patterns in these pathways are likely to vary among world regions. Indeed, we did not find a consistent pattern in the temporal trends within a taxonomic group across continents (Supplementary Fig. 7). Some of the observed inter-continental variation seems to be a consequence of European colonization, such as the steep increase of first record rates of alien vascular plants in the nineteenth century in North America and Oceania (Fig. 4). However, most of the inter-continental variation is difficult to explain, due to the lack of knowledge and data of the underlying processes, and the high inter-annual variation of the first record rates. Remarkably, most of these temporal variations in first record rates are nearly impossible to detect using cumulative numbers of alien species (Supplementary Fig. 8), a common way of presenting alien species accumulations.

The first record of an alien species may be the result of a human-mediated introduction of that species into a region, or a consequence of previous introductions into neighbouring areas and subsequent natural spread into adjacent regions. To remove the influence of introductions due to the species natural range expansion in the alien range, we considered only the first records of alien species on a continent, which revealed qualitatively similar, although less clear, trends compared with the full data set (Supplementary Fig. 9). First records are often influenced by a time lag between the actual introduction of a species and its detection\textsuperscript{19}. The delay is likely to have decreased with time due to more intense sampling (for example, national species inventories) in recent decades, resulting in earlier detections of alien species after their introduction into new regions. However, the chronology of first record rates within the same taxonomic group should not change qualitatively (see Supplementary Notes for a detailed assessment of data quality and a discussion of the potential influence of varying sampling intensity on study results).

**Figure 1 | Number of first records of established alien species per region (mainlands and islands) for major taxonomic groups.** (a–f) Colour and size of circles indicate the number of first records of established alien species. Circles denote first records on small islands and archipelagos otherwise not visible. The world maps were created using the ‘maptools’ package\textsuperscript{40} of the open source software R\textsuperscript{36}.
Predicting alien species accumulations. Trade is consistently reported as a crucial predictor for the number of alien species in a country\(^6,18,20\). Although these studies used total alien species numbers, we here test the congruence of the temporal development of import values and alien species accumulations. The relationship between alien species numbers and the values of imported commodities was found to be nonlinear, best described by a function saturating at large import values\(^{20,21}\). This was confirmed for some taxonomic groups (for example, algae, insects and molluscs), but not for others (vascular plants, mammals, fishes and crustaceans; Fig. 3).

In theory, the accumulation of species should slow down at some time, for example, due to the depletion of incoming species pools or regional saturation. Knowledge about the future development of alien species accumulation would be important for management strategies to counteract new alien species introductions and impacts. The results of our model indicate that the prediction of future trajectories of alien species accumulation highly depends on the size of the pool of potential invaders (Fig. 5) and how the probability of introduction changes with time (Supplementary Fig. 5). Introducing other mechanisms relevant for the establishment of alien populations, such as an Allee effect, delayed the process of invasion, but revealed qualitatively similar results (dashed lines in Fig. 5c). The pool of potential invaders consists of those species, which are capable of being introduced into the focal region and establish an alien population. This species pool results from the complex interplay of species’ native distributions, their abundances in the native range, environmental matches and colonization and propagule pressure, which further depends on the pathways connecting native and focal region and their rates of transport (for example, import volumes)\(^{5,22–24}\). All of these factors are likely to have changed during the last centuries. Although it may be possible to dissect the interactions of these factors in case studies of...
individual guilds of species in specific regions, such an analysis is nearly impossible to perform on a global scale. Yet, without a thorough knowledge about the underlying mechanisms driving past invasion dynamics, it will be very difficult to determine trajectories of future alien species accumulations other than extrapolating fitted trends, which are, however, associated with high uncertainty (but see ref. 18 when time lags are involved).

**Discussion**

We show for the first time at a global scale that the increase in numbers of alien species does not show any sign of saturation. For most taxa, even the rate of first records increased over time with highest rates of first records being observed in recent times. Likewise, the implementation of national legislation and international agreements aiming to reduce alien species threats to biodiversity, economy and human well-being has also distinctly increased during the last 100 years 25 and, without these, the number and impact of alien species would have probably been much worse. For example, the rates of alien insects decreased for certain feeding guilds in the United States likely to be as a consequence of the implementation of the Plant Quarantine Act in 1912 (ref. 26). However, the continuous increases in the rates of alien species first records show that these regulations have not been effective enough to keep up with increasing rates of global trade and slow down alien species accumulation, especially those arriving mainly accidentally, such as invertebrates and pathogens. An exception is the Biosecurity Act in New Zealand adopted in 1993, which represents the most comprehensive and stringent national law for the prevention of alien species introductions currently in force. Consequently, first record rates of vascular plant species in New Zealand clearly dropped in the 1990s (Supplementary Fig. 10). This probably reflects the strength of using a white-list of permitted species, which requires any unlisted species to be fully risk assessed before entry into the country is allowed. Most other comprehensive national regulations now in force, and constantly evolving (for example, in Japan, Australia, South Africa, the United States and the European Union), are based on blacklists of unwanted species. The effectiveness of these procedures needs further research and improvements are desirable 22,27, the more as many recently introduced alien species were not known as problematic in their country of origin, or even unknown to Science. Assessments of specific biosecurity regulations require more detailed analyses than are possible in this study, due to its broad geographic and taxonomic scope.
The lack of saturation in the global accumulation of alien species has important implications for understanding biodiversity patterns. Certainly, extinctions (irrespective of the influence of alien species) have increased in recent times, but at lower rates than first records of alien species. Consequently, the net numbers of species in most regions have increased over time. This may indicate that regional species pools are unsaturated and may only be reached in the long-term. New levels of regional species richness are expected to be higher than those witnessed in the past, but these increases would come at the cost of a variety of impacts on native species, which will then consist of fewer native and more established alien species—may only be reached as current tools to prevent biological invasions are not effective enough to slow down the ever-increasing alien species numbers. The pathways by which alien species are introduced into new areas are also changing rapidly, in particular through increased global trade, tourism, agriculture, horticulture, and the construction and formation (for example, through climate change) of new transportation corridors, such as the opening of the Arctic Ocean shipping routes. Future threats due to alien species may be greatest in emerging economies due to these factors. Although deleterious impacts caused by alien species have been recognized widely in legislation, there is an urgent need to implement more effective prevention policies at all scales, enforcing more stringent national and regional legislations, and developing more powerful international agreements. As highlighted by the mid-term analysis of the Strategic Plan for Biodiversity 2020 (refs 2,35), current efforts are still largely inadequate to reduce the accumulation of alien species.

Methods

Data compilation. Data on first year of record of established alien species were gathered from various sources including online databases, scientific peer-reviewed publications, reports, books and personal collections (Supplementary Table 1). We standardized scientific names of species with global checklists or adopted taxonomic functions provided in the R package ‘Taxonstand’ and for avifauna we adopted the taxonomy of the Global Avian Invasions Atlas, which provides most first records of birds in the database (>90%). In case of multiple entries of the same species in the same region, only the first record was kept. Although removing these duplicated entries, preferences were given to high-quality sources.
Weibull distribution was fitted to test for a potential decline in recent years. The year of first record was provided in the vast majority of cases as a single year (87% of all records). If time periods were provided such as 1940–1950 or 1940s, a year within the respective range was randomly selected to avoid arbitrary peaks at, for example, the mean value of the ranges. Data with time periods longer than 20 years such as 'first half of nineteenth century' were not considered for the analysis. If only the last year of a range was given such as ‘<1890’, the respective year was taken as the first record. Finally, the database contained 55,099 first records of 19,031 introduced alien species. The status of invasion (natural or established) was assessed based on information provided in the original source. To exclude ephemeral alien species, casuals were removed from the analysis. We restricted the analysis to first records after 1500 due to data availability, which resulted in a total of 45,813 first records for 16,926 established species.

Region names were standardized to obtain a unique set of 282 non-overlapping regions (countries and sub-national regions such as islands). In addition, we included a data set of alien insect first records only available for the United States and Canada combined. In case of duplicated entries from different sources, we preferred the information provided for the individual country (United States or Canada) and removed the entry from the combined data set. In most cases, the names of the countries were adopted. Only islands politically belonging to a mainland country were analyzed independently. For example, the Hawaiian Islands and Puerto Rico were distinguished from the United States. Data of bilateral trade between countries were taken from the ‘Correlates of War’ project. This data set provides bilateral trade data in current US$ between 1870 and 2009. To test for potential influences of the lack of deflation of trade data, we corrected the value of imported commodities by dividing by the Consumer Price Index (CPI) of the same year. As the CPI is only available during a limited time period, we tested two pairs of CPI data sets of varying resolution: (1) CPI of 183 countries during the entire time span of 1870–2000; and (2) CPI of the US spanning a longer period (1913–2000) provided by the US Bureau of Labor Statistics (available at www.inflationdata.com). The latter was taken for all countries. The year of foundation of botanic gardens were obtained from the online database of the Botanic Gardens Conservation International (www.bgci.org). This database contains 1,633 entries of the year of foundation of botanic gardens in 150 countries worldwide. All maps were created using the delineation of countries provided in the freely available ‘maptools’ package of the open source software R. Coordinates of islands were extracted from the same package and supplemented with data from Weigelt et al.41

**Statistical analysis.** The statistical analysis was restricted to first records until the year 2000, to avoid a potential bias due to lags in the recording of new species. To test for different shapes of the temporal trends of first record rates, we fitted five functions to the time series of first record rates: linear \[ y = a + bx \], exponential \[ y = a*(1-e^{-bx}) \] and sigmoidal \[ y = a*(e^{bx}*(1 + e^{bx})) \] increase of first record rates \( y \) with time \( x \), with \( a, b \) and \( c \) denoting constants. In addition, a Weibull distribution was fitted to test for a potential decline in recent years. The functions were fitted individually to the time series of first record rates using the Nelder–Mead optimization algorithm implemented in the ‘optim’ function in the statistical software R. The algorithm tries to reduce the deviation between observed and predicted data by minimizing Akaike’s Information Criterion. After fitting each function individually, the one which describes the time series’ of first record rates best was selected by comparing Akaike’s Information Criterion.

To investigate the relationship between the values of imported commodities and first record rates, a correlation analysis between the temporal developments of the annual values of imported commodities in current US$ of a country and the temporal dynamics of first record rates was performed. The relationship between import values and alien species introductions is assumed to be nonlinear, saturating at large import values. Thus, a Michaelis–Menten curve was fitted, which is described as \( R = \frac{R_{\text{max}}M(K + M)}{M + R_{\text{max}}} = \frac{\text{annual value of imported commodities}, \text{}}{K} \) and \( R_{\text{max}} \) and \( K \) being constants. This model produces a convex (saturating) curve; it was previously applied to model cumulative species numbers as a function of cumulative trade, but here we fitted the model to non-cumulative values. Trade data were available only during 1870–2000 and for countries; thus, correlation analysis was only performed for those time periods and countries with available data of import values and first record rates. The analysis was repeated using deflated and non-deflated import values for the respective time periods to test for the potential influence of using non-deflated values. As the differences were marginal (Supplementary Table 2), we used the non-deflated import values because of the longer time period available.

**Model description.** A simple colonization model was developed to investigate the influence of a temporally variable introduction rate on the accumulation of alien species. The model is based on ideas from Neutral Theory, assuming that all propagules of the community have the same chance of being translocated and establish a new population.

Consider an arbitrary mainland community with \( M \) species and \( I \) propagules drawn from a log-normal distribution (for example, Supplementary Fig. 5a). At
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