








Around the world in 500 years: Inter-regional spread of alien species over recent centuries

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Abstract

Aim: The number of alien species has been increasing for centuries world-wide, but temporal changes in the dynamics of their inter-regional spread remain unclear. Here, we analyse changes in the rate and extent of inter-regional spread of alien species over time and how these dynamics vary among major taxonomic groups.

Location: Global.

Time period: 1500–2010.

Major taxa studied: Vascular plants, mammals, birds, fishes, arthropods and other invertebrates.

Methods: Our analysis is based on the Alien Species First Record Database, which comprises >60,000 entries describing the year when an alien species was first recorded in a region (mostly countries and large islands) where it later established as an alien species. Based on the number and distribution of first records, we calculated metrics of spread between regions, which we termed “inter-regional spread”, and

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conducted statistical analyses to assess variations over time and across taxonomic groups.

Results: Almost all (>90%) species introduced before 1700 are found in more than one region today. Inter-regional spread often took centuries and is ongoing for many species. The intensity of inter-regional spread increased over time, with particularly steep increases after 1800. Rates of spread peaked for plants in the late 19th century, for birds and invertebrates in the late 20th century, and remained largely constant for mammals and fishes. Inter-regional spread for individual species showed hump-shaped temporal patterns, with the highest rates of spread at intermediate alien range sizes. Approximately 50% of widespread species showed signs of declines in spread rates.

Main conclusions: Our results show that, although rates of spread have declined for many widespread species, for entire taxonomic groups they have tended to increase continuously over time. The large numbers of alien species that are currently observed in only a single region are anticipated to be found in many other regions in the future.

KEYWORDS

accumulation, biological invasions, first records, global, historical, invasion curves, invasion time, long term, spatio-temporal

1 | INTRODUCTION

The numbers of alien species are rising continuously across all continents and in most taxonomic groups (Seebens et al., 2017). These increases in regional alien species richness are driven by increasing human activities that facilitate biological invasions, such as trade, travel, intentional introductions and habitat modifications (Ellis et al., 2013; Levine & D'Antonio, 2003; Pyšek et al., 2020). The relative importance and the rate of these drivers in shaping the long-term dynamics of alien species are likely to have changed over recent centuries (Essl et al., 2011). Thus, we might expect that the rate at which the global distributions of individual alien species have expanded across the globe has also changed during this period.

Despite recent insights into the long-term dynamics of alien species richness world-wide, we lack a good understanding of spatio-temporal trajectories in changes of the distribution of alien species world-wide. The intensification of global trade and transport over recent decades might have increased the number of alien individuals released (i.e., increased propagule pressure) (Hulme, 2009), resulting in increasing rates at which new alien populations establish (Lockwood et al., 2005). Moreover, the intensification of land use can favour the establishment of alien species (Pauchard & Alaback, 2004), which might also result in more frequent new occurrences of populations of alien species. As a result, we might expect not only an increase in overall numbers of alien species (Seebens et al., 2017), but also an increase in the rate of the spread

of individual alien species. Conversely, the expansion of alien geographical ranges must eventually reach a point of saturation owing to environmental constraints, which should slow the spread of individual species (Seebens et al., 2016; Shigesada & Kawasaki, 1997; Wilson et al., 2007). Hence, although the overall dynamics of the spread of alien species across the globe can be expected to have accelerated in recent times owing to increased human pressures, the rate of spread might have decelerated for some alien species as they reach the limits to the number of regions in which they can establish. However, it remains unclear how these processes have developed over time at a global scale, how they interact and how temporal trends in proliferation differ among species and across taxonomic groups.

Spatio-temporal dynamics have largely been investigated either at regional scales or globally for single alien species (Roura-Pascual et al., 2010; Wilson et al., 2007). A well-known relationship between the spatial and temporal dimensions of biological invasions shows that species introduced earlier are more widespread today (Gassó et al., 2010), but it remains unclear whether this regional relationship holds true at the global scale and how it has developed historically. Furthermore, invasion dynamics have been reconstructed for only a few species, again mostly at regional scales, owing to the lack of comprehensive data at larger scales (Pyšek & Hulme, 2005). As a consequence, comparatively little is known about inter-regional dynamics of alien species spread and how they have changed over time.

To analyse the temporal development of inter-regional spread across a spectrum of established alien species, we use the Alien

Species First Record Database, which is the most comprehensive cross-taxonomic source of data on the first detections of alien species in regions world-wide (Seebens et al., 2017). The first record database has been used previously to analyse long-term trends in alien species accumulation across taxonomic groups and continents (Seebens et al., 2017). For most taxonomic groups and regions, the number, and often also the rate of increase, of alien species has risen continuously, particularly since 1800, with further accelerations after 1950. A subsequent study of temporal dynamics of newly recorded alien species showed a surprisingly high proportion of the so-called emerging alien species in recent years, which could be related to a continuous increase in the sizes of source pools from which the species originated (Seebens et al., 2018). However, these studies focused on total numbers of alien species, and it remains unclear how the dynamics of inter-regional spread of individual species has changed over time. Recent emerging alien species, in particular, might have greater potential to spread, whereas species first introduced a longer time ago might have reached their environmental limits and therefore slowed their rate of range expansion. Disentangling both processes should help in explaining the observed long-term trends of alien species accumulation.

Here, we used the first record database to analyse how wide-spread and how frequently individual alien species were recorded at different times. The frequency of records, although affected by sampling intensities, should provide indications of how species proliferated at various times and how likely it is that newly introduced species will start to spread in the future. We analysed the temporal development of inter-regional spread for major taxonomic groups (vascular plants, mammals, birds, fishes, arthropods and other invertebrates) over recent centuries. Specifically, we ask the following questions.

1. How quickly did the geographical distribution of alien species change over recent centuries?
2. How are the numbers of regions occupied by alien species today related to the year of first recording globally?
3. How long has the spread of individual species continued, and do we see indications of slowing?
4. How has the rate of spread changed over time, both for individual alien species and for whole taxonomic groups?

2 | METHODS

2.1 | Data

Our analyses are based on the Alien Species First Record Database (Seebens et al., 2017). The database contains years of first records of established (naturalized; i.e., forming permanent self-sustaining populations; for definition, see Blackburn et al., 2011) alien populations in regions of the world. The regions largely correspond to countries; however, large islands administered politically by a mainland country but located in biogeographically distinct locations

or with a particularly high number of alien species (e.g., Hawaiian Islands) are considered as different regions. The database has been updated and revised recently. It is now based on 164 individual data sources (22 online databases, 126 scientific articles and reports, and 16 unpublished data sets from individual researchers). The information about occurrences, years and taxon names was standardized and integrated, as explained in detail by Seebens et al. (2017). Altogether, the database contains 63,807 records of 22,320 alien species occurrences in 280 non-overlapping regions with a median size of 33,523 km² (range .43–16,921,565 km²). In comparison to the previous version of the database (Seebens et al., 2018), this represents 5% more records and 13% more taxa. All versions of the Alien Species First Record Database are available online (<https://doi.org/10.5281/zenodo.3690748>).

In this study, we distinguished six major taxonomic groups for which data availability was the most comprehensive, comprising 55,920 first records. These were vascular plants (30,173 first records, representing 54% of the used database), arthropods (15,722, 28%), birds (2,838, 5%), invertebrates other than arthropods (3,052, 5%), fishes (2,709, 5%) and mammals (1,426, 3%). The records are distributed across all continents as defined by the Biodiversity Information Standards organization (Brummitt, 2001), with the greatest proportion (39%) being from Europe, followed by North America (14%), Australasia (16%), South America (8%), Temperate Asia (8%), Africa (6%), Pacific Islands (5%), Tropical Asia (3%) and Antarctica (<1%).

2.2 | Definitions

For analyses, we calculated a number of measures to capture dynamics of changing ranges and frequencies of first records and provide the following definitions of certain key terms used.

- *Inter-regional spread*: We refer to inter-regional spread as the temporal sequence of first records of an established alien species in geographical regions. This definition can include both autonomous dispersal of species without human assistance and human-mediated introductions.
- *Rate of spread*: We define rate of spread as a function of the number of first records per unit time. Thus, it refers to inter-regional spread and should be distinguished from local spreading dynamics of, for example, expanding individual populations. We interpret the frequent recording of an alien species as an indication of a high rate of inter-regional spread. The rate of spread was measured for each individual species separately as the inverse of the time elapsed between consecutive first records of that species.
- *Invaded or alien range*: The invaded or alien range is the number of regions for which the alien species has been recorded with a first record in the database.
- *Global first record*: The global first record denotes when the species was first recorded as an alien anywhere in the world, as documented in the Alien Species First Record Database. This record is a proxy for the onset of the inter-regional spread of a species in its

alien range world-wide. The global first record of a species is used to define the global minimum invasion time of an alien species.

- **Global extent of new occurrences:** The global extent of new occurrences was measured as the variation of coordinates of the centroids of regions where the first records occurred. More specifically, it was calculated as the circular variance of longitudes and latitudes, respectively, of first records for individual species recorded during 10-year intervals since 1500. A large variance indicates more widely distributed first records, whereas a low variance shows a narrow distribution of new first records.
- **Minimum invasion time:** Invasion time describes the time elapsed since the first record of a species in a new region. However, given that there are often substantial time lags involved between the establishment of an alien species and its documentation (Crooks, 2005), the dates of first records used here provide information only on minimum invasion time, because the true (but undocumented) onset of inter-regional spread of a species might have started earlier. The minimum invasion time can be regarded as the global counterpart of the more commonly used “minimum residence time” (Gassó et al., 2010), which, however, is not applicable at the global scale, where all species are resident somewhere.
- **Invasion curve:** Invasion curves describe the increase in the number of invaded regions for individual species over time (Pyšek & Prach, 1993). A steep increase in the invasion curve shows that the species was recorded frequently from new regions in a short period of time, which might indicate rapid inter-regional spread or frequent introductions across regions.

2.3 | Data analyses

We used linear regression analysis and generalized additive models (GAMs) to analyse temporal dynamics of inter-regional spread. Given that we were also interested in the functional forms of observed trends, we fitted different functional relationships, such as linear [$y = a + bt$], quadratic [$y = a - [(x - b)/c]^2$] and saturating [$y = a(1 - e^{-bt})$] forms, to observed long-term trends in y with time x , with a , b and c denoting parameters defining the shape and scale of the functions. We evaluated the goodness-of-fit using Akaike's information criterion (AIC) for individual fits and identified the best-fitting functional relationship by the lowest AIC. According to common standards (Burnham & Anderson, 2004) we considered an improvement in fit as a $\Delta\text{AIC} > 5$. Where appropriate, we calculated standard errors of the mean or interquartile ranges to highlight the variation of the underlying data and performed resampling of subsets of data to obtain measures of variation. More details are provided together with the presented results.

3 | RESULTS

The median number of invaded regions is generally low for all taxonomic groups (Supporting Information Figure S1). On average,

individual species of birds and mammals tend to have more first records compared with other taxonomic groups. For all taxonomic groups, the vast majority of species have a low number of first records, with medians of one or two regions. A few species in all taxonomic groups, however, are widespread. For vascular plants, arthropods and other invertebrates, c. 1% of all species occupy ≥ 20 regions world-wide, and this is true for 6% of birds, 6% of mammals and 3% of fishes. However, a few insect species have very large alien ranges, covering > 100 regions, such as the longhorn crazy ant (*Paratrechina longicornis*; 144 regions), big-headed ant (*Pheidole megacephala*; 115) and ghost ant (*Tapinoma melanocephalum*; 103). Nevertheless, the most widespread alien species is a vertebrate, the feral rock dove (*Columba livia*; 203). Surprisingly, none of the alien vascular plant species has first records in >43 regions [the most widespread being jimsonweed (*Datura stramonium*; 43), Canadian horseweed (*Erigeron canadensis*; 42) and common guava (*Psidium guajava*; 42)], despite a large number of alien species in this group.

Invasion curves were relatively flat for nearly all species with first records before 1800 (Figure 1). In general, alien species with global first records between 1500 and 1700 did not occupy >10 regions during that time, although undersampling is likely to be an issue for this period. Given our data, only a few conspicuous species, such as the brown rat (*Rattus norvegicus*), domestic pig (*Sus scrofa*), common pheasant (*Phasianus colchicus*) or common guava (*Psidium guajava*), were already found in many regions before 1800. In contrast, steep invasion curves were nearly always observed after 1800 and mostly for species with their global first record after 1800 (blue and turquoise lines in Figure 1). Particularly steep increases in invasion curves were observed for birds and arthropods. Interestingly, none of the arthropods introduced before 1800 spread widely, whereas nearly all arthropods widespread today were first introduced during the 19th century.

Across all taxonomic groups, the number of invaded regions increased continuously with longer minimum invasion times (i.e., the earlier in time a species was initially introduced somewhere in the world, the more first records it has today). The percentage of species with their global first record occurring between 1500 and 1700 and that are still found in only one region is often far below 10% of all species recorded in this time period for different taxa (Supporting Information Figure S2). In contrast, of all species with their global first record between 1950 and 2000, $>50\%$ are still found in only a single region. This pattern is particularly pronounced for vascular plants, for which $\leq 80\%$ of species recorded recently for the first time globally are found in a single region only, but similar patterns are also apparent for vertebrates and invertebrates (Supporting Information Figure S2).

In general, the median alien range size of species increased with minimum invasion time over the last 500 years (Figure 2), which was supported by significant (linear regression models, $p < .001$) relationships between the year and alien range sizes for all taxonomic groups. To test for potential effects of saturation of alien range sizes in time, we compared the fits of a negative exponential (i.e., saturating) and a linear function, but for all taxonomic groups the

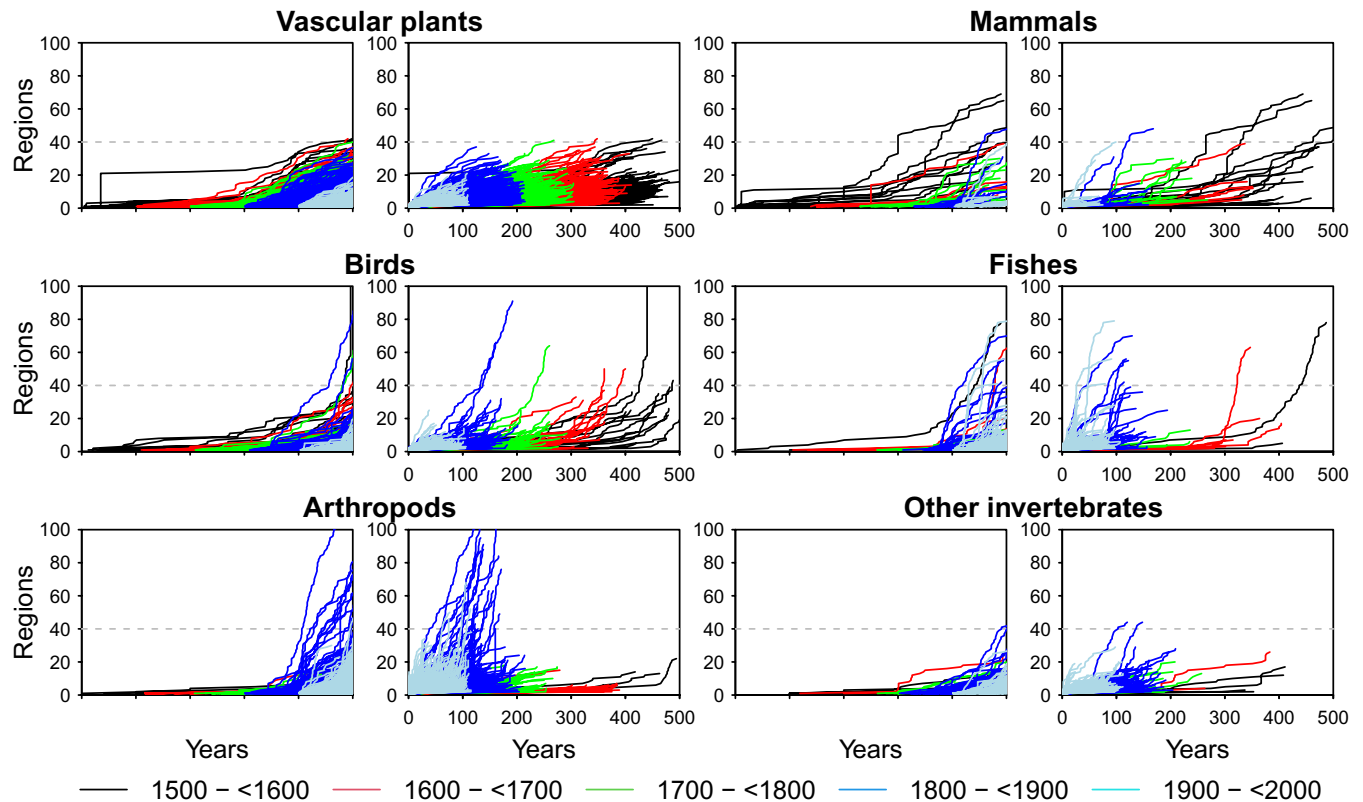


FIGURE 1 Invasion curves for individual alien species of different taxonomic groups. Invasion curves represent the cumulative number of occupied regions for individual species over time. Invasion curves are shown for the original years (left panels) and rescaled to the year of the global first record set as zero for each taxonomic group for better visualization (right panels). Lines are colour coded according to intervals for global first records

linear function clearly outperformed the saturating one ($\Delta AIC \gg 10$), which indicates a continuous increase in alien range size with minimum invasion time. The pattern was most pronounced for alien vascular plants. On average, vascular plants continue to establish alien populations in new regions even when global first records are from 500 years ago. For vertebrates, the patterns were less clear. From 1850 until 2000, the median range sizes declined in a similar manner to those of vascular plants, but they did not show clear trends before 1850, which might indicate that alien vertebrate species reach global saturation in range size after c. 150 years on average. However, the largest range sizes were still found for species with early global first records. For invertebrates, the highest median range sizes were observed for species with global first records from the last 200 years; this might, however, be influenced by low sampling intensity in earlier times. The time elapsed between the first and the last first record of individual species in our data was >100 years for 25% of plants, 24% of mammals and 27% of bird species, but <7% for invertebrates. For a considerable number of species of mammals (12%), birds (6%) and plants (4%), new alien populations were recorded even after 300 years of their global first record.

The global extent of new occurrences, as measured by the variation of coordinates of first records for individual species, revealed clear changes over time (Figure 3). For all taxonomic groups before

1800, first records were restricted to certain areas, which is indicated by a low variance in coordinates of region centroids where the species was recorded during that time. During the 19th century, the variance in longitude and latitude increased for all groups, showing that first records of individual species occurred over a much wider geographical extent compared with earlier times. The variance of coordinates declined for vascular plants, fishes and mammals in the 20th century. Conversely, birds showed a steep increase, particularly in longitudinal variation, toward more recent times. The observed patterns might be affected by the large number of first records available for Europe, but repetition of the analysis without records from Europe revealed very similar dynamics (Supporting Information Figure S3), which indicates that the trends are not driven primarily by a geographical sampling bias.

Similar to the extent of new occurrences, the rate of spread was low before 1800 and increased thereafter, but variation across taxonomic groups was apparent (Figure 4). For birds, by far highest spread rates were observed during the last 30 years, whereas for vascular plants, the rate of spread declined toward more recent times, with fewer first records per species, lower spread rates and comparatively slow speed of spread observed in recent decades (Figure 4). Rates of spread of mammals and fishes also tended to decline, although in a less pronounced manner than observed for

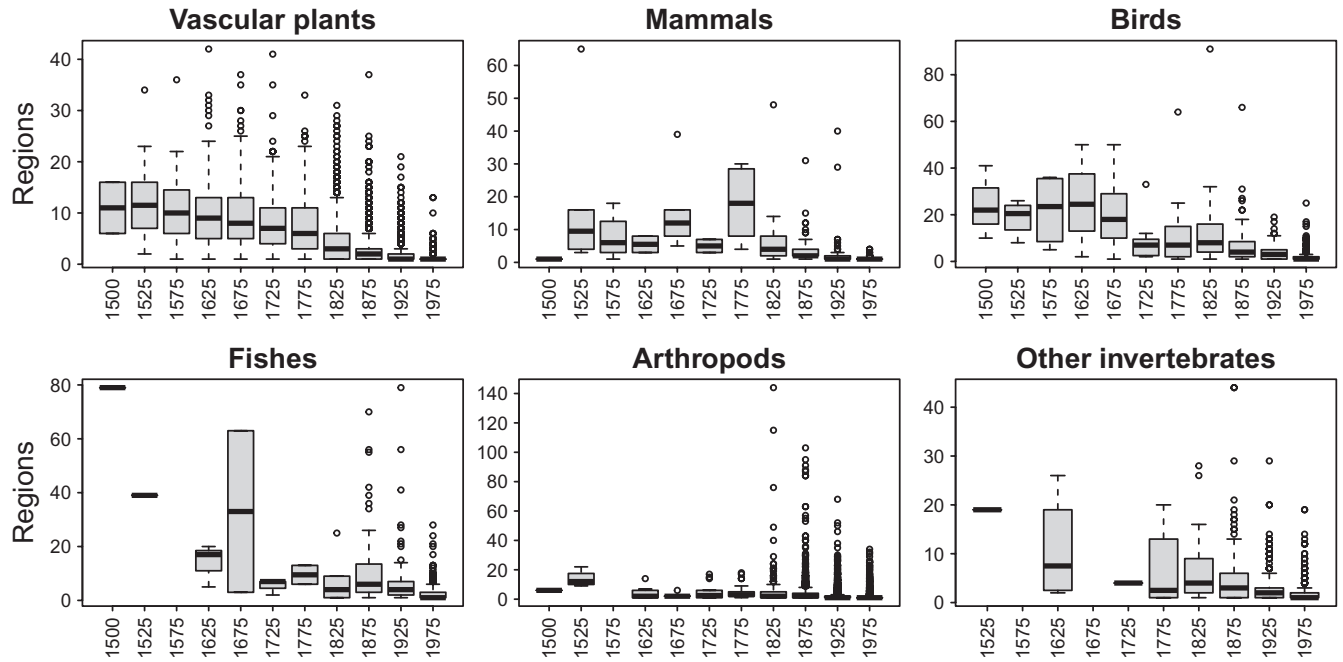


FIGURE 2 Number of regions invaded by a species as a function of the global first record of the species. Numbers of regions were summarized for 50-year intervals from 1500 to 2000 for better visualization. The dynamics were qualitatively very similar using a bin size of 25 years (Supporting Information Figure S7)

plants. The peaks of the highest rate of spread for these taxonomic groups were found at c. 1900. These patterns were found to be very similar using other measures of spread rates, such as the number of first records per 50 years and species and weighted speed of spread (Supporting Information Figure S4).

Although the rate of spread tended to increase over time (Figure 4), it varied for individual species. In general, rates of spread of individual alien species followed a hump-shaped function of the number of regions already occupied by that species (Figure 5); spread rates were highest at intermediate numbers of invaded regions, but lower at small and large numbers of occupied regions. This hump-shaped pattern was most pronounced for vascular plants and mammals and less so for birds, fishes, arthropods and other invertebrates (Figure 5). For the last four groups, the initial increase at small ranges is clearly visible, whereas the decline at large ranges is less clear. The interquartile range, which is indicated by bars in Figure 5, shows considerable variation, but the relationship between the number of alien regions and rate of spread was still clearly significant for all taxonomic groups (GAMs for all groups $p < .001$). To test for the existence of declines at large range sizes (i.e., slowing spread), we fitted linear, negative quadratic and saturating functions to the observed relationships and compared their goodness-of-fit using the AIC (see Methods). The lowest AIC was obtained for the quadratic function for vascular plants and mammals, for the saturating function for birds, fishes and arthropods and for the linear one for other invertebrates. The differences between AIC values were, however, mostly less than five. Nevertheless, this confirmed what is apparent from visual inspection, that spread rates declined at large range sizes for vascular plants and mammals.

A reduced spread rate at large range sizes might indicate that species approached the limits of available regions to which the species could potentially be introduced and establish new populations. This is supported by the fact that the decline in spread rates was not apparent for vascular plants or mammals when using first records before 1900 (Supporting Information Figure S5), when invasions were generally less frequent. Thus, more vascular plants and mammals seemed to have reached the limits of potentially invaded regions during the 20th century. With the definition of widespread alien species as species occupying ≥ 20 regions, around half of these widespread alien species showed declining spread rates towards the end of their time series (i.e., the rate for their last three steps was lower compared with the mean of the preceding three steps), indicating that the inter-regional spreading dynamics of these species tended to slow down (Table 1). The proportion of widespread species with declining rates of spread among all widespread species was c. 50% for all taxonomic groups except for fishes, for which the proportion was 90% (Table 1). Examples of widespread alien species with declining spread rates are given in Table 1.

Species reached their maximum spread rates at different time periods, but within individual taxonomic groups the species showed a tendency toward earlier or later timings (Supporting Information Table S1). The highest rates of spread were recorded very early for mammals [species and date of highest spread rates: domestic pig (*Sus scrofa*) in 1598]. For birds and vascular plants, the highest rates were found during the 19th century [budgerigar (*Melopsittacus undulatus*) in 1850 and common sowthistle (*Sonchus oleraceus*) in 1832], and these were recorded in the 20th century for fishes [rainbow

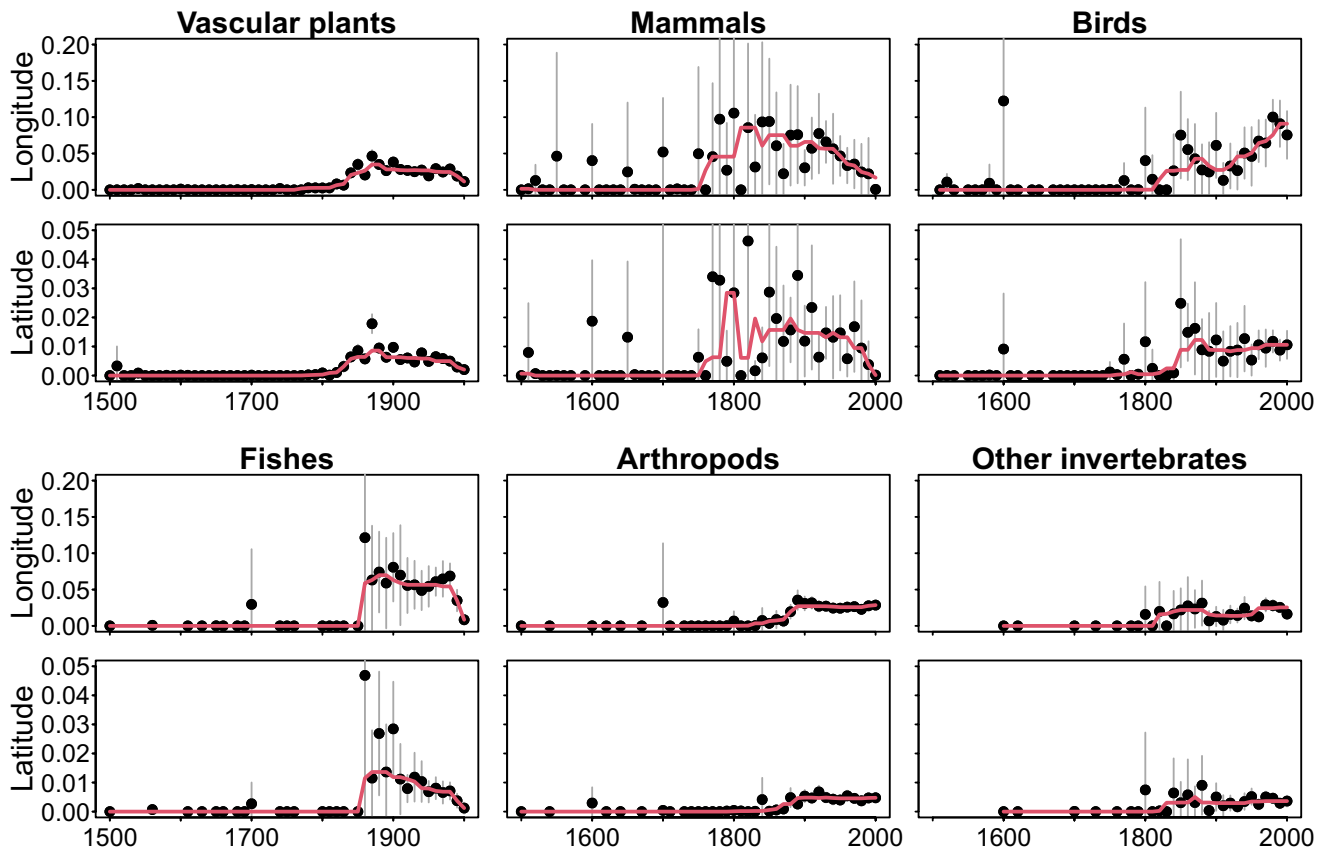


FIGURE 3 Variances in longitudinal and latitudinal distributions of first records across taxonomic groups. Variances in longitudes and latitudes were calculated as circular variances of coordinates for first records of individual species for time intervals of 10 years. For each time period and taxonomic group, coordinates were then averaged across all species of that group. This calculation was repeated 100 times using random subsets of 50% of all coordinates to calculate means (dots) and standard deviations (error bars). Trends are shown as smoothed splines (red lines)

fish (*Poecilia reticulata*) in 1922], arthropods [West Indian drywood termite (*Cryptotermes brevis*) in 1908] and other invertebrates [Australian tubeworm (*Ficopomatus enigmaticus*) in 1940].

4 | DISCUSSION

Here, we have shown that the inter-regional spread of individual alien species has extended historically over long time periods, often >100 years (Figure 1). The process of inter-regional spread is ongoing for the majority of species, including those that were first introduced to new regions as early as several hundred years ago (Figure 2). Furthermore, our data suggest that spreading dynamics intensified after 1800, resulting in higher numbers of first records per species (Figure 4), with a wider distribution (Figure 3), although this result might also reflect the paucity of first record data from earlier centuries. Although it is known that within a region, such as an individual country, range expansion is a long-lasting process that often takes many decades or even longer (e.g., Gassó et al., 2010; Hudgins et al., 2017; Mandák et al., 2004; Roques et al., 2016), here we document that similar and even much longer time spans are also required for inter-regional spread at a global scale.

Most of the species that were observed as alien in recent times were often found in only a single region. However, the vast majority (>90%; Supporting Information Figure S2) of species that were observed as being alien centuries ago now inhabit more than one region. For vascular plants in particular, the proportion of species occurring in a single region declined continuously the further back in time the global first record occurred. Although this has been reported frequently on the much smaller scale of individual countries (Pyšek & Jarošík, 2005; Williamson et al., 2009), here we show that this trend also applies to global distributions and spans the full study period of 500 years (Figure 2). For other taxonomic groups, this trend was not as clear as it was for vascular plants, and vertebrate alien range sizes tended not to increase much 150–200 years after initially being recorded as alien somewhere. This might also be attributable to changes in introduction pathways, such as a reduction in the intentional introduction of game birds and mammals. Overall, the process of spread for many species has continued over centuries, which implies that alien species that were recorded for the first time only recently are likely to establish new alien populations in more regions in the decades to come.

The rate of spread has varied over time, with a clear tendency for increasingly steep invasion curves (Figure 1) and higher rates of

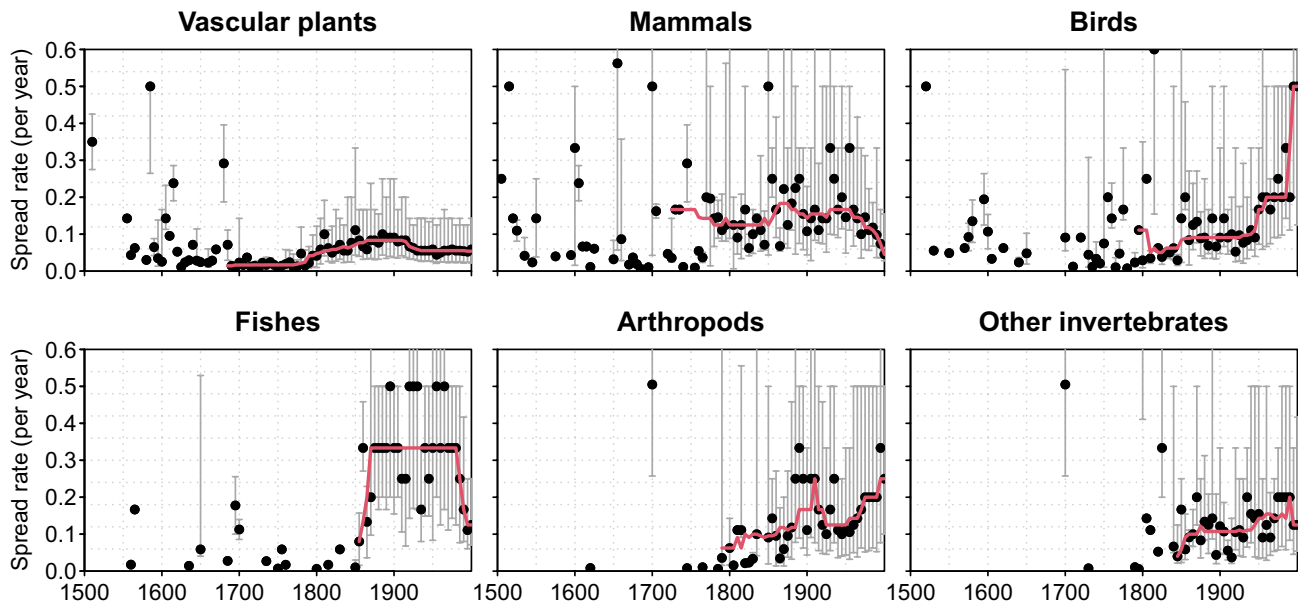


FIGURE 4 Time series of spread rates for different taxonomic groups. Spread rates were calculated for each alien species separately. Dots represent medians of all rates at a given time across all species of the respective group, and bars denote the interquartile range (i.e., 25%–75% interval). Trends were indicated by running medians (red lines) for time series without gaps. Two other measures of spread rate are shown in the Supporting Information (Figure S4)

spread in more recent times (Figure 4). Variation in estimated spread rates was very high before c. 1800, which is probably attributable to lower sampling effort and makes it difficult to compare estimated spread rates in more recent times. Nevertheless, invasion curves showed a clear distinction between being mostly flat before 1800 versus often steep rises thereafter. This pattern is consistent across taxonomic groups. Explanations might include lower sampling intensity before 1800 and uncertainties in taxonomic classification, because this was before the binominal taxonomic classification scheme of Linnaeus became widely applied. However, it is unlikely that the distinct increases after 1800, even for well-researched taxa, such as vascular plants, mammals and birds, were a consequence only of changes in species classification and sampling intensities. Rather, the intensification of alien species introductions during this time is more likely to correspond to patterns of increasing globalization, although varying sampling intensities certainly affected observations. In line with this, the steepest increases in global invasion curves were observed for arthropods during the 20th century, which might be a consequence of the distinct increases in global trade and transport and the associated likelihood of unintentional introductions of these species (Bertelsmeier et al., 2017; Roques et al., 2016).

The calculation of spread rates is certainly affected by varying sampling and recording intensities through time. As has been shown in other studies (Costello & Solow, 2003), an increase in first records does not necessarily mean that rates of spread accelerated when, for instance, sampling intensities increased in parallel. Disentangling the influence of sampling intensities requires knowledge and data about the underlying drivers to construct appropriate models (Costello et al., 2007) or to include data about species introduction efforts. Unfortunately, both options are not possible owing to the lack of

data on drivers and propagule pressures. However, it seems valid to assume that sampling intensity and research efforts have increased over time, hence we would assume an increase in records simply because of that. This might be the case for birds, but we observe constant or even declining rates of spread in other well-investigated taxonomic groups, such as mammals and vascular plants (Figure 4), which are difficult to explain with increased sampling intensities. We, therefore, acknowledge that records are certainly influenced by varying sampling intensities, but we believe that the observed dynamics were not driven predominantly by that.

Interestingly, rates of spread varied among most of the well-sampled groups (Figure 4). Rates for alien birds increased distinctly over time, which indicates rapid and widespread range expansions by many species, particularly during the last 50 years. In contrast, inter-regional spread has tended to slow for mammals since 1900, probably owing to more stringent regulations on species movements across international borders and a rising appreciation that introduction of such species can be highly detrimental (e.g., New Zealand; McDowall, 1994). For alien vascular plants, spread rates peaked in the late 19th century. During that time, many plants were exchanged world-wide as a consequence of a distinct increase in horticultural activities (van Kleunen et al., 2018). However, many records for plants originate from herbarium records, which were sampled intensively during that time, and it is not clear how this might have affected the overall trends. Although overall spreading dynamics seemed to have accelerated, rapid spreading events were already observed in early times for certain species (Supporting Information Table S1). For mammals, for example, the highest spread rates were recorded before 1800. This might, however, be affected by sampling effort, because individual surveys might result in a high frequency

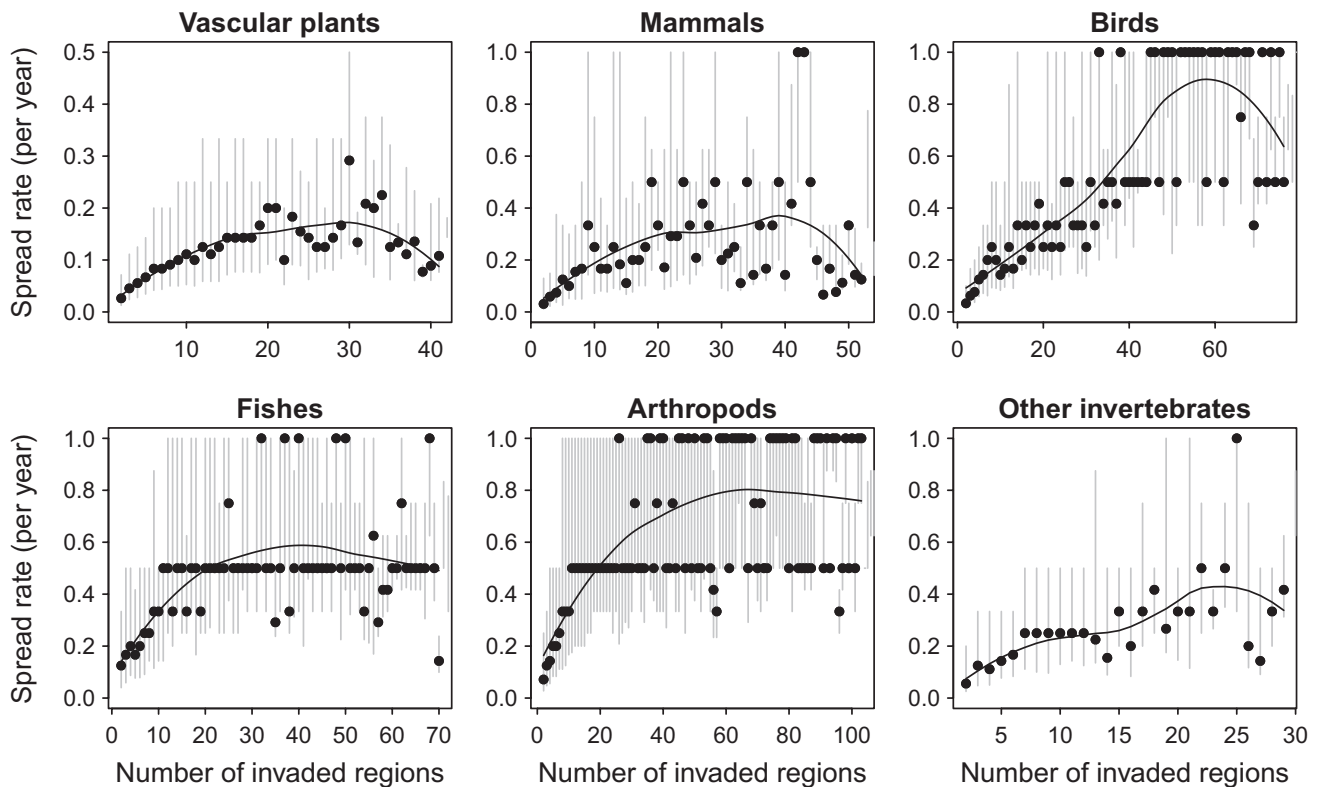


FIGURE 5 Median rates of spread as a function of the number of invaded regions for different taxonomic groups. Spread rates were calculated initially for each individual species separately. Dots represent median values of rates over all species from the respective taxonomic group at a given number of already-invaded regions. Variation around the median is indicated by interquartile ranges (25%–75% intervals, grey bars). Trends are indicated by LOESS-smoothed lines. Medians were calculated only if at least three values of spread rates were available, in order to avoid influences of individual widespread species

TABLE 1 Overview of widespread alien species with declining rates of spread in recent years

Taxonomic group	Widespread species [n (%)]	Widespread species with slowed inter-regional spread [n (%)]	Examples of widespread species with slowed inter-regional spread
Arthropods	55 (3)	26 (47)	<i>Paratrechina longicornis</i> , <i>Pheidole megacephala</i> , <i>Monomorium destructor</i> , <i>Cardiocondyla emeryi</i> , <i>Anoplolepis gracilipes</i>
Birds	31 (11)	12 (39)	<i>Passer domesticus</i> , <i>Phasianus colchicus</i> , <i>Acridotheres tristis</i> , <i>Cygnus olor</i> , <i>Anas platyrhynchos</i>
Fishes	21 (6)	19 (90)	<i>Cyprinus carpio</i> , <i>Oncorhynchus mykiss</i> , <i>Oreochromis niloticus</i> , <i>Gambusia holbrooki</i> , <i>Ctenopharyngodon idella</i> , <i>Hypophthalmichthys molitrix</i>
Mammals	20 (14)	13 (65)	<i>Oryctolagus cuniculus</i> , <i>Rattus rattus</i> , <i>Ondatra zibethicus</i> , <i>Mus musculus</i> , <i>Felis catus</i>
Other invertebrates	7 (1)	4 (57)	<i>Magallana gigas</i> , <i>Melanoides tuberculata</i> , <i>Dreissena polymorpha</i>
Vascular plants	86 (2)	54 (63)	<i>Datura stramonium</i> , <i>Psidium guajava</i> , <i>Galinsoga parviflora</i> , <i>Galinsoga quadriradiata</i> , <i>Eichhornia crassipes</i>

Note.: Widespread species were defined as alien species occupying ≥ 20 alien regions. Percentages indicate the proportional amount of widespread species and widespread species with slowed spread, respectively, for the respective taxonomic group.

of records during the time the survey was conducted, which would cause an increase in our metrics of spread. Moreover, rapid spreading events might have also taken place among other groups, which went unnoticed.

For individual species, spread rates clearly peaked at intermediate range sizes (Figure 5). The hump-shaped pattern could be

explained by a combination of interacting alien populations, which facilitate the establishment of new alien populations (Seebens et al., 2019), and constraints on available habitat restricting occurrence. At small range sizes, the total alien population is comparatively small, and populations of the different regions might be interconnected only weakly. Each new alien population might

act as an additional source for establishment of new populations, which caused a rise in spread rates. At intermediate range sizes, the larger number of regions occupied by an alien species makes it likely that individuals will arrive from various regions simultaneously, increasing the likelihood of additional establishment events (Drury et al., 2007; Seebens et al., 2019). At the same time, there are still enough unoccupied and suitable regions that the species can colonize new regions. At large range sizes, most of the suitable regions are already occupied, and the spread rate has to slow. The same pattern was found in a study of marine invasions, which showed that the highest probabilities of spread into new areas were predicted to happen at intermediate range sizes (Seebens et al., 2016). For taxonomic groups other than vascular plants and mammals, the phase of slowing spread has seemingly not yet been reached. An alternative explanation is that rates of spread increase with the maximum potential range size of a species. This means that species with the potential to occupy large ranges are also fast spreaders, whereas species dispersing slowly can occupy only a small number of regions. However, this is less likely because it implies that there are no slow-spreading alien species that occupy large ranges, which is contrary to our findings.

Clearly, given that first records of alien species are an amalgamation of true inter-regional spread and recording intensity, and that only a fraction of alien species first records are included in the Alien Species First Record Database (Seebens et al., 2020), the metrics applied here can only represent proxies for the true rate of spread. However, we believe that the results we show here are robust. Sensitivity analyses indicate that even under the assumption of very large changes in sampling rates, such as misclassification of first records of a maximum of 100 years, similar time series result, albeit at reduced rates and for lower species numbers (Seebens et al., 2018). In addition, the observed variation in spread among well-investigated groups, such as vascular plants, mammals and birds, is difficult to explain with changes in sampling rate alone (Figure 4). It would require nonlinear variation in sampling rates specific to individual taxonomic groups (i.e., a peak for plants in the 19th century, a peak for birds in the 20th century and a constant rate for mammals), which is unlikely to be the case. Although there is certainly a spatial bias towards Europe inherent in the data, repeating the analyses using first records only from Europe revealed very similar patterns (Supporting Information Figure S6). This also shows that the high variation of region sizes in our database did not affect our conclusions. Thus, although several biasing factors are likely to have affected the observed dynamics, the overall results are robust to these gaps and uncertainties.

In conclusion, the vast majority of species have expanded their ranges after their global first record, although this process can take centuries. Some species of vascular plants and mammals show signs of declining spread rates as they reach large range sizes, indicating that at least some widespread species in these groups are saturating their potential global ranges defined by environmental constraints. We expect many new records of alien populations to occur in the

future for the many alien species currently found in only a single region, because most of them were recorded only recently. As a consequence, even if the introduction of new alien species is stopped completely, an increase in their numbers per region will be observed for many decades to come owing to the spread of species already established.

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AUTHOR CONTRIBUTIONS

H.S. conducted the analyses. H.S. and F.E. wrote the first draft of the manuscript. All authors contributed to design of the analyses, interpretation of results and writing the manuscript.

DATA AVAILABILITY STATEMENT

All analyses are based on the First Record Database, which is freely available at: <https://doi.org/10.5281/zenodo.3690748>

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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