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Naturalized alien floras still carry the legacy of European colonialism

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The redistribution of alien species across the globe accelerated with the start of European colonialism. European powers were responsible for the deliberate and accidental transportation, introduction and establishment of alien species throughout their occupied territories and the metropolitan state. Here, we show that these activities left a lasting imprint on the global distribution of alien plants. Specifically, we investigated how four European empires (British, Spanish, Portuguese and Dutch) structured current alien floras worldwide. We found that compositional similarity is higher than expected among regions that once were occupied by the same empire. Further, we provide strong evidence that floristic similarity between regions occupied by the same empire increases with the time a region was occupied. Network analysis suggests that historically more economically or strategically important regions have more similar alien floras across regions occupied by an empire. Overall, we find that European colonial history is still detectable in alien floras worldwide.

Naturalized alien plant species, that is, species with self-sustaining populations in regions outside their native range after introduction by humans[1], have become an important component of regional floras, leading to floristic homogenization worldwide[2–6]. Alien plant distribution patterns are primarily driven by regional climates[7,8], geographic and environmental characteristics[7,9–11], and past and present socio-economic conditions of the regions[8,12–14].

The global redistribution of alien taxa is inextricably linked to human movement, which accelerated with the onset of European exploration and colonialism in the late fifteenth century[15,16]. The occupation and subsequent establishment of colonial territories by European powers led to the development of global trade and transportation networks that accelerated the introduction, establishment and spread of alien species, such as animals, plants and pathogens[16–18]. While many species were important for economic reasons, their naturalization and spread resulted in the alteration and deterioration of ecosystems in occupied lands[15–20]. The first transcontinental European settlers intentionally introduced plants into new regions mainly to produce food and ensure survival and establishment of settlements, but also for aesthetic and nostalgic reasons[15,16,19]. The exchange of plant species further accelerated in the nineteenth and early twentieth centuries following its institutionalization. Botanical gardens were established by European powers across multiple centuries as a means of testing, growing and transporting species of potential economic value[21–23]. Acclimatization societies fostered plant species exchange to introduce European species into occupied regions and to support the growing fashion for 'exotic' ornamental plants and gardening in Europe[24,25], increasing demand for new species in the horticultural market[26,27]. All these factors drove the global plant exchange, with major trade often constrained within each European empire[21–29] due to market policies designed to favour the respective power. This resulted in up to 2.5 times greater trade volumes for occupied compared to unoccupied regions[30]. Simultaneously, different powers followed different market strategies. The Dutch Empire had open-door policies overall, whereas others combined open-door and preferential trade policies[30]. Such policies should have led to alien plants being predominantly exchanged among regions occupied by the same power, with variation associated with different market strategies and the frequency, intensity and technological development of trade over time.

The empires were largely dissolved after World War II and global trade networks and associated pathways of alien plant exchange have profoundly changed in recent decades, with global trade volume increasing 30-fold since 1950[31]. This reorganization of global trade intensified and accelerated the introduction of alien species worldwide beyond the legacies of colonial empires[32]. However, as alien plants accumulate in regional species pools over a long timeframe[33], the centuries of imperial occupation and organization of trade relations may still leave a lasting imprint on the global patterns of alien floras[5,13,34]. In this study, we expect that current naturalized alien floras continue to carry the signal of past occupation by four of the largest European powers (Britain, the Netherlands, Portugal and Spain). To this end, we reconstructed the spatial and temporal extent of the four European powers by determining the time of colonial occupation for regions worldwide. Using the Global

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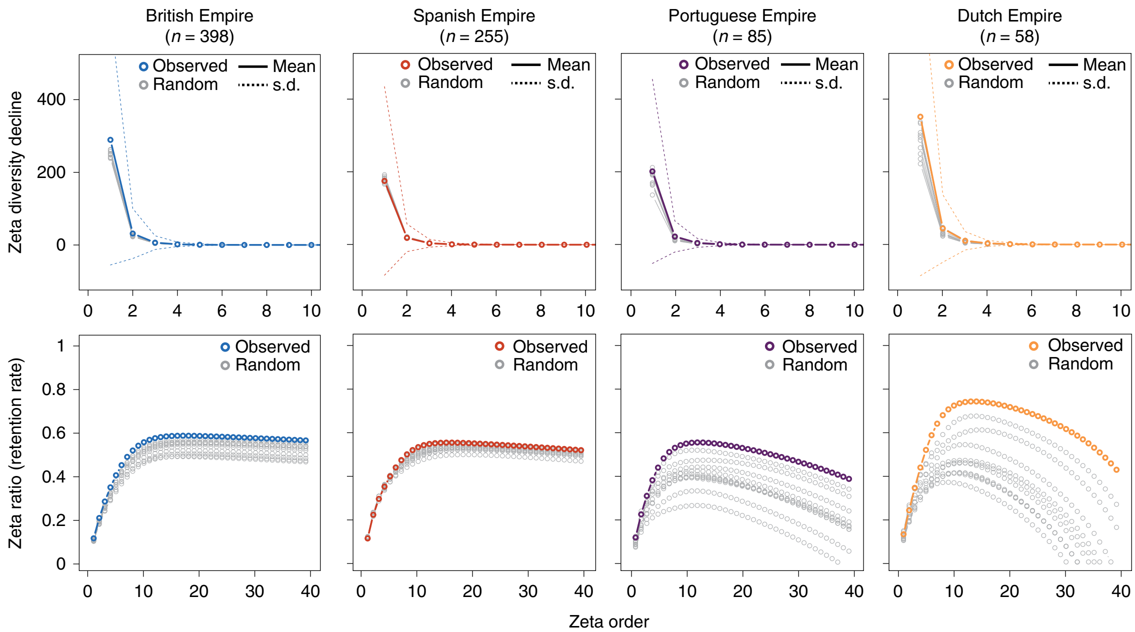

Fig. 1 | Zeta diversity decline and retention rate for each empire. Zeta diversity decline (upper row) for each empire from ζ_1–ζ_{10}. Zeta orders indicate the number of regions for which compositional similarities are computed (ζ_2 indicates mean compositional similarities among all pairwise region combinations). The trend for the observed empire is given in colour, including the 95% confidence interval (broken lines), and the trends for ten random empire draws are given in grey. The zeta ratio or retention rate (lower row) is shown for ζ_1–ζ_{40}. Again, trends for the observed empire are given in colour and for the random draws in grey.

Naturalized Alien Flora (GloNAF) database[3,35] to obtain naturalized alien floras for the formerly occupied regions, we compiled a dataset covering a total of 1,183 regions (779 mainland regions and 404 islands). We then used zeta diversity (a metric for measuring compositional similarity among species assemblages that captures the contribution of rare to widespread species to turnover) and network analysis to quantitatively test hypotheses H1 and H2 and qualitatively investigate H3 (Extended Data Fig. 1):

H1. Regions formerly occupied by the same European power show greater similarity in naturalized floras than do random collections of regions of similar size and extent.

H2. Regions occupied by a power for longer periods of time will, on average, have more similar naturalized floras compared to other regions occupied by the same power.

H3. Regions of important strategic role for the occupying power (for example, trade hubs and administrative centres) share more of their naturalized alien flora with other regions than less strategically important ones.

Results

Alien flora similarity among regions occupied by an empire. Across all four empires, the average number of species shared between regions (zeta (ζ) diversity; Extended Data Fig. 1) rapidly declined with an increasing number of regions considered (that is, across zeta orders) until ζ_5. In five regions, the average compositional similarity was 0.6 species for Great Britain, 0.4 species for Spain, 0.6 species for Portugal and 1.5 species for the Netherlands (Fig. 1 and Table 1). Regions occupied by the British and Dutch had floras with greater similarity than did random collections of regions, whereas regions occupied by the Spanish and Portuguese were not more similar than random region collections (Fig. 1 and Table 1). Retention rate (zeta ratio) of species was calculated as the probability that any given species remains within the naturalized flora of each region sequentially added to the particular European empire. When comparing these retention rates to randomly constructed collections of regions, observed retention rates were always higher than random, for all empires (Fig. 1). This supports our assumption that alien floristic similarity is, overall, higher among regions occupied by the observed empire compared to the random collection of regions of similar extent and spatial configuration due to more widespread species across regions.

Drivers of regional alien plant species turnover. Multi-site generalized dissimilarity models (MS-GDM) revealed how different geographic, environmental and socio-economic drivers shape naturalized alien floras across regions occupied by the same empire. The set of variables (Supplementary Table 1) explained turnover of species between any two naturalized floras reasonably well for all empires ($0.32 < R^2 < 0.54$ at ζ_2) but the explained variance (R^2) decreased with increasing numbers of regions compared ($0.07 < R^2 < 0.20$ at ζ_5; Supplementary Fig. 10 and Supplementary Table 2). This decrease across zeta orders indicates decreasing explanatory power of the selected geographic, environmental and socio-economic drivers for the turnover of widespread alien species. Below we discuss the importance of the drivers on turnover for rare (ζ_2) and widespread (ζ_5) alien plants for the European empires, with a focus on occupation time.

Alien species turnover in the different European empires was driven mainly by climate (mean annual temperature and aridity index) and geographic distance, indicated by the amplitude of the *I*-splines (Fig. 2 and Table 2). Alien species turnover due to climate was high, especially for the British and Spanish empires and less strong for the Portuguese and Dutch empires, suggesting that differences at high temperatures are more important than at low temperatures (Fig. 2), as commonly observed in the literature[5]. Geographic distance showed high turnover at short distances and almost no importance for turnover between distant regions (Fig. 2), reproducing established distance decay dynamics with high species similarity for close regions that decreases for more distant regions[36].

Occupation time (time a region was occupied by an empire) had a moderate effect (amplitude for ζ_2 0.05–0.64 and for ζ_5 0.42–0.96) compared to the climate variables (amplitude for ζ_2 0.25–2.22 and

Table 1 | Model results for the mean estimated compositional similarity (zeta diversity) across zeta orders 1–5 for the four observed European empires and the random empires

Zeta orders	Observed empire	Random empires
British Empire		
ζ_1	289.2	250.1 (±8.52)
ζ_2	31.6	24.7 (±1.44)
ζ_3	6.4	4.5 (±0.40)
ζ_4	1.8	1.1 (±0.14)
ζ_5	0.6	0.3 (±0.06)
Spanish Empire		
ζ_1	174.5	178.4 (±8.37)
ζ_2	18.9	20.0 (±1.13)
ζ_3	4.1	4.4 (±0.35)
ζ_4	1.2	1.3 (±0.13)
ζ_5	0.4	0.4 (±0.06)
Portuguese Empire		
ζ_1	200.7	178.6 (±21.98)
ζ_2	22.5	15.8 (±3.83)
ζ_3	4.9	2.9 (±1.16)
ζ_4	1.5	0.7 (±0.41)
ζ_5	0.6	0.2 (±0.16)
Dutch Empire		
ζ_1	350.6	282.7 (±39.1)
ζ_2	44.4	32.9 (±8.3)
ζ_3	10.5	7.1 (±2.8)
ζ_4	3.5	2.1 (±1.1)
ζ_5	1.5	0.7 (±0.5)

For the random empires, mean values and standard deviations are given across ten random empires, respectively.

for ζ_5 0.30–3.98) on rare and widespread alien plant turnover across regions once occupied by the European empires (indicated by the amplitude of the *I*-splines; Fig. 2 and Table 2). The only exception was for rare alien species turnover in the Portuguese Empire, for which occupation time had no effect. For rare alien species turnover, occupation time was the most important socio-economic driver for the Spanish Empire and the second most important driver after gross domestic product per capita (GDPpc) for the British Empire. For the Dutch Empire, occupation time was the third most important socio-economic driver, almost equally important as GDPpc (amplitudes 0.27 and 0.30, respectively). A similar ranking was detected for widespread alien species turnover consistently in all empires (Table 2).

How occupation time affected turnover (the shape of the mean *I*-spline) differed across empires. For the British Empire, turnover increased and slightly accelerated across the entire value range, indicating small turnover between regions occupied for similar time periods (regardless of how long and during which time these regions were occupied) and high turnover for regions occupied for different time periods (Fig. 2). For the Spanish Empire, differences in occupation time had no effect on turnover in rare and widespread species for regions occupied for short and intermediate time periods and effects were apparent for regions with long occupation times (>290 years; about 0.6× maximum occupation time; Fig. 2). We found a similar trend for the Dutch and Spanish Empires for rare species, although the effect on turnover started to appear earlier (>140 years; about 0.4× maximum occupation time; Fig. 2). For widespread alien species, differences in occupation time had the same effect on turnover regardless of the value of occupation time (Fig. 2). Finally, in the Portuguese Empire, the effect of the difference in occupation time on the turnover of widespread species increased across the whole value range but the *I*-spline showed a deceleration for long occupation times. This indicates that for regions with long occupation times, widespread alien species are probably spread across the empire and thus differences in occupation time do not have a substantial effect on turnover anymore (Fig. 2).

Identifying central regions via network analysis. On the basis of the compositional similarity of the alien floras, modularity analyses identified three or four regional clusters (for the British and Spanish Empires and the Portuguese and Dutch Empires, respectively) and five regions per cluster that were most similar (that is, with highest centrality per cluster) to other regions in the network (Fig. 3 and Table 2).

For the British Empire three clusters emerged, with the first including the tropics and subtropics (185 regions), the second in northern and southern extratropical regions (159) and the third mainly located on the Indian subcontinent (56) (Fig. 3). Most similar regions per cluster were located in Northern Australia, China and India (centrality 0.96–0.91; cluster 1), eastern Australia and South Africa (centrality 1.00–0.93; cluster 2) and India (centrality 0.94–0.90; cluster 3) (Fig. 3).

In the Spanish Empire, the first cluster (117 regions) was located mainly in Central America (including the Caribbean), the West African coast and the west Pacific (Fig. 3). The second cluster was mainly situated in southern South America and Northern America (106) and the third cluster included mainly Mexican regions, Macaronesian and Mediterranean islands (33). Most central regions were in Mexico (centrality 0.85–0.71; cluster 1), Mexico and Colombia (centrality 0.95–0.84; cluster 2) and Mexico and Chile (centrality 1.00–0.96; cluster 3) (Fig. 3).

For the Portuguese Empire, four clusters were identified. The first was located in southeast Africa, Indonesia and West Africa (24 regions), the second mainly on the Indian subcontinent and West Africa (22), the third in South America (21) and the fourth included mainly island regions in the Atlantic Ocean (19) (Fig. 3). Most central regions were in Mozambique (centrality 0.43–0.31; cluster 1), India and East Timor (centrality 0.64–0.61; cluster 2), Brazil (centrality 0.99–0.96; cluster 3) and the Azores, St. Helena and China (centrality 0.49–0.41; cluster 4) (Fig. 3).

The four Dutch Empire clusters were in South America and the Caribbean (25 regions), South Africa and Northern America (16), the Malay Archipelago (11) and the Indian subcontinent and Mauritius (7) (Fig. 3). Most similar regions were in Brazil and the Caribbean (centrality 1.00–0.90; cluster 1), South Africa (centrality 0.95–0.86; cluster 2), Malaysia, Sulawesi, Sumatra and Java (centrality 0.59–0.37; cluster 3) and in India (centrality 0.84–0.75; cluster 4) (Fig. 3).

Discussion

We found strong evidence that the legacy of European empires is still detectable in today's naturalized plant distributions. The compositional similarity of alien floras among regions once occupied by the same European power was higher than among regions of randomly constructed empires of similar geographic distribution and regional extent (Fig. 1). Within an historical empire, occupation time had a substantial impact on alien species turnover among regions (Fig. 2 and Table 2). Furthermore, network analysis suggested that regional hubs of floristic similarity within historical empires may coincide with regions of greater economic or strategic importance within the respective empire (for example, important trade hubs and administration centres; Fig. 3).

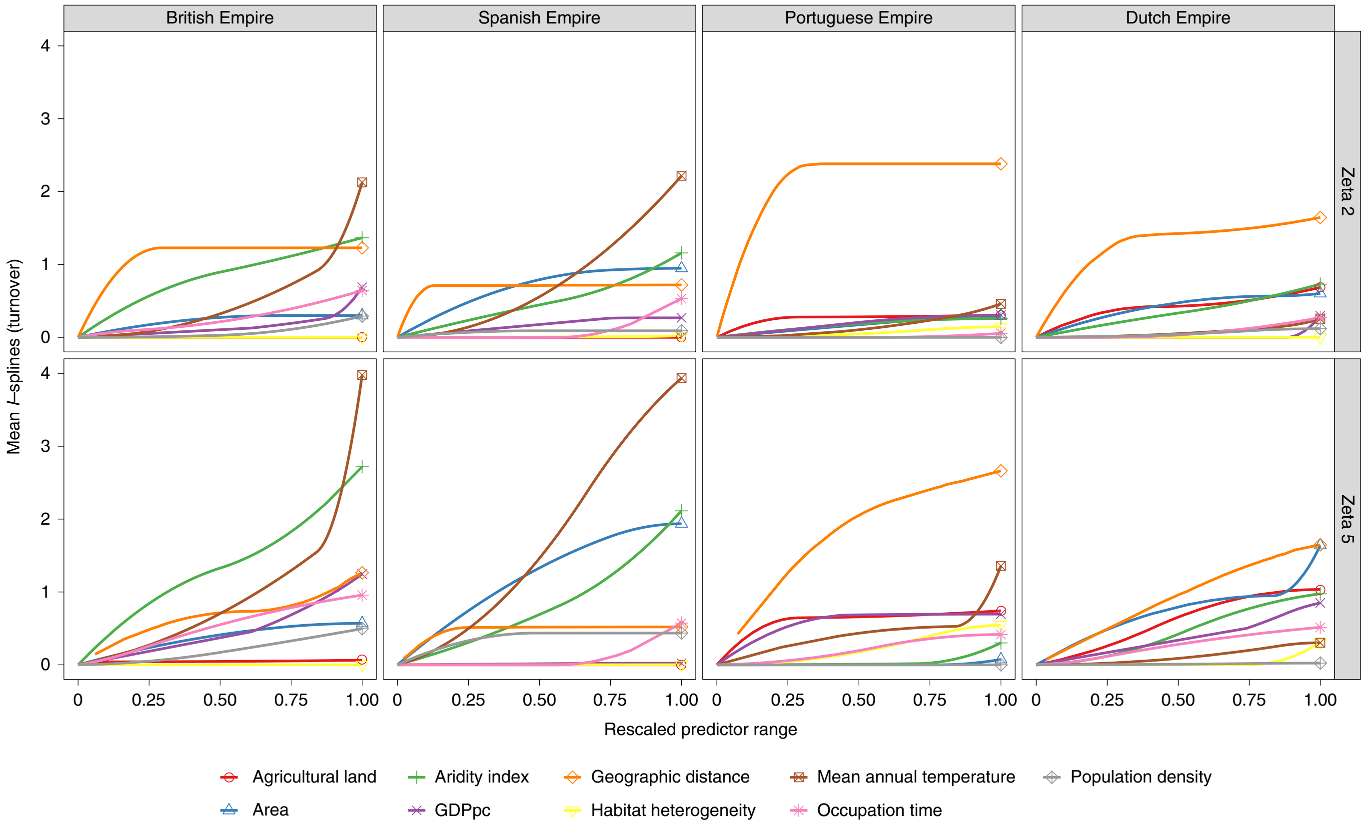

Fig. 2 | Drivers of alien species turnover in the different European empires. Relative importance (amplitude of the mean *I*-splines) and contribution to turnover (slope of the mean *I*-splines) of geographic, environmental and socio-economic drivers of compositional similarity of the alien flora for occupied regions within an empire. Results are shown for ζ_2 (rare alien species) and ζ_5 (common alien species). Mean *I*-splines are derived from the multi-site generalized dissimilarity models for the four European empires and are based on six repetitions with a sampling size of 8,000 region combinations per empire.

Empire affiliation increases similarity of alien floras (H1). Across the European empires, compositional similarity showed distinct patterns compared to a random collection of regions of similar geographic distribution and extent. These patterns might be driven by processes relevant at different invasion stages. Established alien species first need to be transported to a new region and then they must have self-sustaining populations[37]. Both processes are strongly affected by the number of individuals introduced and the frequency of introduction (propagule and colonization pressure[38–40]), which are strongly related to trade and transportation and to the suitability of the environment (for example, climatic similarity and interactions with native species[5,41,42]).

For the British and Spanish Empires, the absolute number of species shared by multiple regions was higher than expected by chance. Even when the number of shared species was similar to that of random empires, all empires showed higher retention of common species across multiple regions than expected by chance. The higher compositional similarity in the British Empire, especially for widespread species, is probably related to its large area and relatively recent expansion: the British Empire was by far the largest empire, including regions from all continents (except Antarctica) and covering most climatic zones of the world[43]. Further, it was established relatively recently, starting in the early seventeenth century and lasting until the late twentieth century[44]. Given its considerable size, the source pool of species with the potential to be dispersed and ultimately naturalize across the occupied regions was larger compared to other empires. Additionally, during the existence of the British Empire, global trade and transportation had already significantly intensified[31]. With the development of steam-engine boats for transoceanic voyages in the mid-nineteenth century and improved navigation techniques, travel times across the Atlantic were roughly cut by half, resulting in reduced transportation and freight costs[45,46] at a time when the Spanish Empire and the American part of the Portuguese Empire had already largely disintegrated (Extended Data Fig. 2). Consequently, a larger source pool, shorter travelling times and improved transportation made it more likely for biota to survive the journeys, increasing the invasion probability in the former colonies[33,40,45,47,48].

For the Spanish Empire, we observed similar trends that probably emerged for different reasons. The Spanish Empire reached its full extent much earlier, lasted longer and was much more geographically focused on the Americas compared to other empires[49] (Extended Data Fig. 2). High retention rates are probably the result of this spatial aggregation, where many naturalized alien species were introduced to the continent and might have subsequently spread intentionally or unintentionally across the empire[19]. While the secondary spread is probably less important across the entire Americas, spread via trade and transport within a contiguous part of the empire has probably been more intensive than between regions separated by oceans. This follows established knowledge that bilateral trade decreases with distance[50]. Additionally, subsequent establishment after the introduction was probably facilitated by climatic and environmental similarity of the regions on the basis of their proximity.

Patterns of the Portuguese and Dutch Empires indicate that widespread species are less prevalent than in the other two empires, shown by a more pronounced drop in retention rate for higher zeta orders. For the Portuguese Empire, the drop is less pronounced,

Table 2 | Relative importance (amplitude of the *I*-spline) of all drivers based on the results of the MS-GDMs for each empire

Driver	ζ_2	ζ_5
British Empire		
Area	0.30	0.57
Geographic distance	1.23	1.26
Habitat heterogeneity	0	0
Aridity index	1.37	2.72
Mean annual temperature	2.13	3.98
Agricultural land	*0*	*0.06*
GDPpc	*0.69*	*1.25*
Occupation time	***0.64***	***0.96***
Population density	*0.29*	*0.50*
Spanish Empire		
Area	0.95	1.94
Geographic distance	0.72	0.52
Habitat heterogeneity	0.02	0
Aridity index	1.16	2.11
Mean annual temperature	2.22	3.93
Agricultural land	*0*	*0*
GDPpc	*0.27*	*0.02*
Occupation time	***0.53***	***0.57***
Population density	*0.09*	*0.44*
Portuguese Empire		
Area	0.30	0.07
Geographic distance	2.38	2.66
Habitat heterogeneity	0.15	0.55
Aridity index	0.26	0.30
Mean annual temperature	0.46	1.36
Agricultural land	*0.31*	*0.74*
GDPpc	*0.30*	*0.70*
Occupation time	***0.05***	***0.42***
Population density	*0*	*0*
Dutch Empire		
Area	0.60	1.64
Geographic distance	1.64	1.65
Habitat heterogeneity	0	0.31
Aridity index	0.73	0.98
Mean annual temperature	0.25	0.30
Agricultural land	*0.68*	*1.03*
GDPpc	*0.30*	*0.85*
Occupation time	***0.27***	***0.51***
Population density	*0.12*	*0.02*

Results are shown for ζ_2 (rare alien species) and ζ_5 (common alien species). Socio-economic drivers are highlighted in italic and the empire variable (occupation time) is highlighted in bold.

probably due to the higher regional clustering. Here, floras in geographically close and climatically similar regions are similar but as soon as regions from different parts of the empire are compared the number of common species sharply decreases (for example, zeta orders >13). For the Dutch Empire the pronounced drop in the retention rate is probably a result of the small size and the even higher dispersion of formerly occupied regions. Consequently, high initial retention rates at low zeta orders can mainly be attributed to the high concentration of regions in the East Indies but decline quickly when considering more regions of other geographic locations and climatic zones.

Drivers of turnover of naturalized floras in empires (H2). Compositional turnover within the four European empires is strongly driven by climate (mean annual temperature and aridity index) and geography (geographic distance). This is in line with previous findings that show increased compositional similarity of alien floras for regions with more similar climates[5,48,51]. In addition, our results support fundamental assumptions from economic theory, where regions tend to interact more with regions that are nearby[50], facilitating the exchange and thus the spread of alien species across shorter distances leading to homogenization of the floras[5].

Importantly, occupation time was among the most important socio-economic drivers of alien species turnover across all European empires, providing robust evidence for long-lasting imprints of colonial history on alien floras in formerly occupied regions. We found that short occupation times (<140 years) had little relevance for compositional turnover and this started to become more important for longer occupation times. This leads to high turnover when comparing regions with short occupation times to regions with longer occupation times. For longer occupation times, the decreasing effect on turnover indicates that many alien plants might have already been introduced and established, making the alien floras of these regions more dissimilar to regions with shorter occupation times. We use occupation time as a proxy for trade and transport intensity among regions, in the absence of reliable trade data across the full time period considered here (below). One process behind the importance of occupation time on floristic similarity may be the 2.5-fold increase in the exchange of commodities (based on observations from 1870–1913) and people among regions occupied by the same empire compared to unoccupied regions[30]. Consequently, colonization and propagule pressure from regions occupied by the same empire are higher. The longer this increased influx of species and individuals draws from the empire source pool, the more similar the alien flora of that region gets to other occupied regions.

Here, we investigate imprints of historical processes using descriptors of historic and contemporary societies and environmental conditions. The discrepancy in time periods is unavoidable, as predictor selection for such studies is constrained by data availability. For most socio-economic predictors, comprehensive data for such a long time period (1492 to present) are not available. Consequently, we used contemporary data with the best-available spatial coverage and quality in our models based on identified important drivers from recent studies[7,8] that explain current naturalized alien plant species distributions globally. Hence, we include contemporary and historic predictors (occupation time) in our models, to disentangle their importance on current compositional similarities of alien floras.

Central regions within an empire (H3). Regions identified here as central within an empire largely coincide with administratively, economically or strategically important regions within the regional clusters of the empires. Presumably, ships (and other means of transport) visited such regions more frequently, whether for stopovers, commodity exchange or to bring new people. These activities probably resulted in higher propagule pressure from intentional and unintentional introductions and the subsequent establishment of species from across the respective empire compared to less-frequented regions. This link between alien species introduction and subsequent higher probability of establishment and economic, administrative and strategic relevance of a region is also evident in the literature (for example, refs. [45,52]). Interestingly, in our study, the relationship between the number of colonial powers

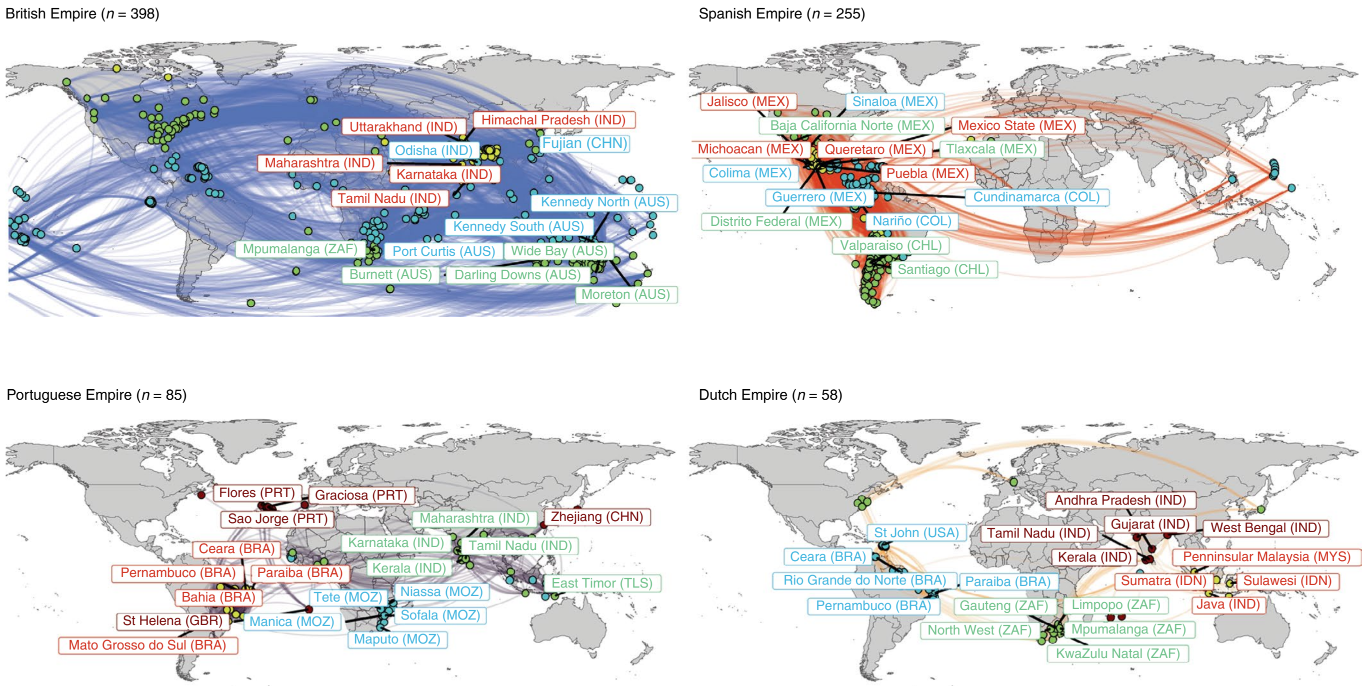

Fig. 3 | Networks of the four empires with nodes placed at the region centroids and edges (links) between the regions. For the analyses, edges were weighted by the pairwise similarity between regions, which is not displayed here for better readability of the figure. Node colours indicate clusters identified by the modularity analysis based on the full network including all pairwise similarities (Methods). For each cluster (indicated by the same colour as the edges) the five regions with the highest centrality score are given. Only edges with a pairwise similarity (beta diversity) >0.2 of the alien naturalized floras between two regions are shown for readability reasons.

having occupied a region and its centrality within the corresponding cluster was only weakly significantly negative for the Spanish Empire and showed no significant trend for the other empires (Supplementary Fig. 11 and Table 3). Note that we did not establish a formal test of this relationship given the absence of comprehensive historical data on bilateral trade and transportation or quantitative measures of regional importance of regions within an empire for the full investigated time period. To empirically test this relationship and disentangle historical and recent dynamics, further studies, for example, focusing on one empire (or specific regions) or a specific time period, are needed. Nevertheless, we argue that a qualitative examination of the results from the network analysis provides a basis for more quantitative analyses in the future.

Central regions of the British Empire emerged mainly in Australia and India, which both have a comparatively long history of British occupation[44]. The deliberate exchange of plants and plant material across the British Empire was well developed, with large networks of botanical gardens and acclimatization societies[25,29]. Together with increased trade and long-lasting imperial exploitation of these regions, high degrees of alien plant species introduction and establishment can be expected. Across all clusters of compositional similarity identified for the Spanish Empire, Mexican regions emerge as most central. Mexico was of strategic importance in the Spanish Empire, to control the Atlantic trade and especially for its gold resources[53]. The Portuguese Empire had important economic regions, especially for the international spice trade with the Indo-Malay realm (for example, East Timor, Tamil Nadu and Kerala[54]). Mozambique, was an important colony for cotton, sugar and sisal production and in Brazil, Bahia was the administrative centre of the colonies in the Americas[54]. Finally, the Azores and St. Helena emerged as central regions and both were important stopover destinations for transoceanic voyages[16,54]. Invasion success on islands has been shown to be especially high given their ecology and eco-evolutionary history explaining high compositional similarity of the alien floras of these regions[10]. For the Dutch Empire, central regions in the Indo-Malay realm coincide strongly with trade activities by the Dutch East India Trading Company, which dominated the European trade with Asia from the mid-seventeenth century to the late eighteenth century[55,56]. South Africa was also an important region for the Dutch Empire, as it was one of the few regions where the Dutch established extensive settlements and an important stopover between the Netherlands and Java[56]. In the Americas, the Virgin Islands (Table 3) were an important trans-shipment place for the trade between New Holland, Brazilian colonies (Table 3) and the African Gold Coast[56].

While many regions identified as central in our network of compositional similarity have been important regions in the European empires, there are other plausible reasons why their compositional similarity is high. Given that our analysis is based on current alien floras and the network is built on compositional similarity between regions, recent dynamics may as well have shaped the results. For example, the British Empire had concessions in Zhejiang and Fujian in China but today these regions are economically well connected with Ningbo-Zhoushan in Zhejiang as the third largest container port worldwide (worldshipping.org). As well, the region around Brisbane (central nodes in the British Empire) holds the third largest port in Australia. Finally, despite the disintegration of the European empires, dependencies still remain (for example, as overseas territories like the British Virgin Islands) and native and common languages (for example, Spanish in Latin America) as a legacy of the empires still lead to increased bilateral trade[57].

Conclusion

Our analysis of the similarity of naturalized alien floras reveals that even decades to centuries after the disintegration of European empires, imprints of colonialism can be detected in their regional

Table 3 | Top five regions for each empire with highest centrality scores in their respective cluster based on the network analyses

Region	Modularity	Centrality	No. of empires
British Empire			
Port Curtis (AUS)	1	0.96	1
Fujian (CHN)	1	0.95	1
Odisha (IND)	1	0.93	1
Kennedy South (AUS)	1	0.92	1
Kennedy North (AUS)	1	0.91	1
Darling Downs (AUS)	*2*	*1.00*	*1*
Moreton (AUS)	*2*	*0.97*	*1*
Wide Bay (AUS)	*2*	*0.96*	*1*
Burnett (AUS)	*2*	*0.95*	*1*
Mpumalanga (ZAF)	*2*	*0.93*	*2*
Tamil Nadu (IND)	3	0.94	3
Himachal Pradesh (IND)	3	0.93	1
Maharashtra (IND)	3	0.91	2
Uttarakhand (IND)	3	0.91	1
Karnataka (IND)	3	0.90	2
Spanish Empire			
Guerrero (MEX)	1	0.85	1
Colima (MEX)	1	0.85	1
Sinaloa (MEX)	1	0.82	1
Cundinamarca (COL)	1	0.79	1
Nariño (COL)	1	0.71	1
Distrito Federal (MEX)	*2*	*0.95*	*1*
Tlaxcala (MEX)	*2*	*0.91*	*1*
Baja California Norte (MEX)	*2*	*0.89*	*1*
Santiago (CHL)	*2*	*0.87*	*1*
Valparaiso (CHL)	*2*	*0.84*	*1*
Queretaro (MEX)	3	1.00	1
Jalisco (MEX)	3	0.98	1
Puebla (MEX)	3	0.98	1
Michoacan (MEX)	3	0.98	1
Mexico State (MEX)	3	0.96	1
Portuguese Empire			
Manica (MOZ)	1	0.43	1
Maputo (MOZ)	1	0.41	1
Sofala (MOZ)	1	0.39	1
Tete (MOZ)	1	0.38	1
Niassa (MOZ)	1	0.31	1
Karnataka (IND)	*2*	*0.64*	*2*
Tamil Nadu (IND)	*2*	*0.64*	*3*
Kerala (IND)	*2*	*0.64*	*3*
Maharashtra (IND)	*2*	*0.63*	*2*
East Timor (TLS)	*2*	*0.61*	*1*
Paraiba (BRA)	3	1.00	2
Pernambuco (BRA)	3	0.99	2
Bahia (BRA)	3	0.99	1
Ceara (BRA)	3	0.98	2

Continued

Table 3 | Top five regions for each empire with highest centrality scores in their respective cluster based on the network analysis (continued)

Region	Modularity	Centrality	No. of empires
Mato Grosso do Sul (BRA)	3	0.96	1
Zhejiang (CHN)	*4*	*0.49*	*2*
Flores (PRT)	*4*	*0.42*	*1*
Sao Jorge (PRT)	*4*	*0.42*	*1*
St Helena (GBR)	*4*	*0.42*	*2*
Graciosa (PRT)	*4*	*0.41*	*1*
Dutch Empire			
Paraiba (BRA)	1	1.00	2
Pernambuco (BRA)	1	0.97	2
Ceara (BRA)	1	0.95	2
Rio Grande do Norte (BRA)	1	0.92	2
St John (USA)	1	0.90	1
Mpumalanga (ZAF)	*2*	*0.95*	*2*
Limpopo (ZAF)	*2*	*0.94*	*2*
KwaZulu Natal (ZAF)	*2*	*0.93*	*2*
Gauteng (ZAF)	*2*	*0.89*	*2*
North West (ZAF)	*2*	*0.86*	*2*
Java (IDN)	3	0.59	3
Peninsular Malaysia (MYS)	3	0.54	3
Sulawesi (IDN)	3	0.39	2
Cocos Keeling Islands (AUS)	3	0.38	2
Sumatra (IDN)	3	0.37	2
Kerala (IND)	*4*	*0.84*	*3*
Tamil Nadu (IND)	*4*	*0.84*	*3*
Andhra Pradesh (IND)	*4*	*0.80*	*2*
West Bengal (IND)	*4*	*0.76*	*3*
Gujarat (IND)	*4*	*0.75*	*3*

In brackets, the country the region belongs to is given using ISO Alpha-3 country codes. No. of empires indicates how many of the four empires have occupied the specific region over time.

floras. Regions that were once occupied by an empire are still more similar to each other in terms of their alien floras than expected by chance and the similarity increases with the time the region was occupied by the given empire. Our findings highlight the persistent legacy of human activities on biological invasions over centuries reflected in the compositional similarity and homogenization of their floras. While we can show an effect of European empires on current alien floras and compositional similarity between regions, better data, especially on historical trade volumes and vessel visitation rates might help to disentangle the importance and magnitude of historical and current drivers of alien plant species redistributions and the underlying processes. With an increase in globalization and the connectivity among regions, the exchange of alien species will further increase and the homogenizing effect of species redistributions today will be detectable far into the future.

Methods

Species data. Information about naturalized vascular plant species was extracted from the GloNAF database[3,35], the most comprehensive inventory of regional alien plant species distributions currently available. We included regions with checklists of naturalized plants at the finest available resolution (that is, country or subnational regions such as federal states or islands). This resulted in a selection of 1,183 regions, including 404 island and 779 mainland regions, with a total of 19,250 naturalized plant taxa (including infraspecific taxa and cultivars and known archaeophytes).

The GloNAF database, like most global databases, has a heterogeneous coverage of regions worldwide, in terms of completeness and quality of the data. On the basis of an expert assessment by the GloNAF core team and regional experts, the coverage of the checklists used in the study is classified as follows: 393 regions are categorized as complete (>90% of taxa included), 691 as incomplete (50–90%) and 99 as very incomplete (<50%), resulting in only 8% classified as very incomplete. For our analyses, we assume that this incompleteness will probably have a stronger effect on rare (less abundant and less widespread) than widespread species in the checklist, as they are more likely overlooked in the absence of extensive surveys, expertise and sampling effort. Consequently, our analyses might be more affected for rare species (lower zeta order, see below) potentially resulting in changes in the slope of the zeta diversity decline and the increase of the zeta ratio for small orders of zeta. For widespread species (high zeta orders), we do not expect a strong effect, which should result in similar trajectories as observed in our models.

Empire database. We compiled a dataset of the colonial affiliation of regions of the four most extensive European empires (today's Great Britain, Spain, Portugal and the Netherlands), hereafter called 'empire database' (Supplementary Table 4). Region delineations were based on the GloNAF database and the dataset as outlined above. Information collected includes (1) the colonial affiliation of a region, that is the identity of the European empire occupying a specific region, and (2) the time span a specific European empire occupied that region (the start and end year).

We used the Colonial Dates Dataset (COLDAT)[58] that merges four older colonial empire datasets, as a baseline dataset for the empire database. COLDAT provides information on the colonial power and the start and end date of colonial rule. Defining the end date of colonial rule (for example, the date of official independence of a region) is generally straightforward. However, defining start dates of colonial rule is less obvious, given that the build-up of colonial occupation in a region often gradually increased (from the establishment of first trade posts to full formal integration of the region into an empire). As a result, different datasets included in COLDAT provide somewhat varying start dates for colonial occupation of regions, on the basis of slightly different criteria (see ref. [58] for a thorough discussion on this topic and illustration of differences in start dates across datasets). The dates in COLDAT are expressed as (1) the mean dates over all datasets and (2) the latest dates of all datasets. We used the mean dates as they provide a consensus date across sources but with the constraint that these dates will not necessarily be tied to a specific event if different sources provide different information (for example, the formal integration of the region into the empire). Further, COLDAT is restricted to the country level, whereas our alien plant dataset includes subnational entities and islands governed by mainland countries. Consequently, we included additional information on colonization dates for subnational mainland regions from the existing literature and online sources. To do so, we used the following criteria: (1) as the start of colonial rule, the date of the establishment of permanent settlements of the colonial power (for example, trading posts, whaling stations and fortifications) was accepted, (2) for regions without additional information the dates from the country level based on COLDAT were used and (3) the end date was used for all subnational regions from COLDAT to be consistent with the baseline data. Finally, for islands, we followed the same procedure as for subnational mainland regions but additionally classified uninhabited islands as not belonging to a specific colonial empire. This was done even when the entire island group was part of an empire because most of these islands include small rocky outcrops or islands without any freshwater source (available groundwater lens) prohibiting permanent settlements.

We restricted the colonial empire dataset to regions that have been incorporated into empires after 1492, the onset of modern ages, which roughly marks the start of global colonial expansion and is also used for the separation of old invaders (archaeophytes) from more recent aliens (neophytes)[59]. We thus excluded medieval expansions in Europe, which have become integrated into the ruling country of the colonial empire. The full spatiotemporal extent of the four empires under consideration resulted in 398 regions (176 islands and 222 mainland regions) for the British Empire, 255 regions (51 islands and 204 mainland regions) for the Spanish Empire, 85 regions (27 islands and 58 mainland regions) for the Portuguese Empire and 58 regions (27 islands and 31 mainland regions) for the Dutch Empire (all regions that have once been occupied by the respective European empire are given in Supplementary Fig. 7).

Null model. To test H1, we established a null model on the basis of the observed number of colonial regions within the investigated empires to assess how compositional similarity of the naturalized flora changes between observed and random empires while accounting for geographic structure and spatial extent (section on Statistical analysis). We assigned all regions within our dataset to the 17 United Nations (UN) geospatial units (provided by the ArchaeoGLOBE project https://dataverse.harvard.edu/file.xhtml?persistentId=doi:10.7910/DVN/CQWUBI/RIFPKR&version=6.0). The dataset provides regions suitable for analysis regarding historical land-use and archaeological research and provides regions that are roughly comparable in size (Supplementary Fig. 9).

To establish the null model, for each UN geospatial region, we drew the same number of mainland and island regions from the GloNAF regions as present in the observed empire. The first region in each UN geospatial unit was chosen randomly and each subsequent region was selected on the basis of the minimum geographic distance from the last region (based on the minimum geographic distance between the centroids of the regions). This way we were able to mirror an actual occupation process, where imperial expansion progressed from one region to the next. For the final analyses we used ten random empires for each colonial empire that each have the same number of mainland and island regions in total and per UN geospatial region as the observed empire.

Driver data. To explain species turnover between naturalized alien floras of regions, we compiled descriptors representing important global drivers of naturalizations as identified in ref. [7] and refined for plants in ref. [8]. We compiled information on geographic (area and habitat heterogeneity and geographic distance between regions), environmental (mean annual temperature and aridity index) and socio-economic (GDPpc, population density and cropland area) drivers (Supplementary Table 1). For gridded variables, we calculated the respective metric including all raster cells covered by the respective region (national or subnational entity).

All datasets are openly available and provide spatially explicit, gridded information and the aggregated data are provided in Supplementary Table 5. Additionally, we computed an empire-specific variable from the empire database indicating the 'occupation time' given as the number of years a region was occupied by a specific European empire. The correlations among all drivers included in the various models were assessed using pairwise Pearson correlation tests with all correlations being <0.7 (Supplementary Figs. 1–4). To improve symmetry and linearity of the drivers and to stabilize variances, the following numerical drivers were natural-log transformed: area, habitat heterogeneity, aridity, human population density, per capita GDP and cropland area. For the British and Dutch Empires, correlation of area and habitat heterogeneity were slightly above the threshold of 0.7 (GBR 0.75 and NED 0.73). For these two empires, we ran the multisite generalized dissimilarity models (MS-GDMs, description below) twice, once including both terms and once excluding habitat heterogeneity, to assess how strongly the collinearity affects the results. Results only marginally differed for the explained variance of the full models across zeta orders (Supplementary Table 6) and explained variance of the drivers between the models (Supplementary Table 7). Additionally, mean trends for each predictor remained consistent across the two models (Supplementary Figs. 12 and 13). To maintain comparability across the different empires, we report the model results including all predictors in the main text.

Statistical analysis. All analyses were run in R v.4.0.4 (ref. [60]).

Zeta diversity. Zeta (ζ) diversity is a relatively new concept for measuring the compositional similarity among species assemblages and capturing the contribution of rare to widespread species to turnover[61,62]. ζ_1 (for order 1) represents the average species richness (alpha diversity) of an assemblage in a set of regions. ζ_2 is the average pairwise similarity between two regions (1 − beta diversity). More generally, ζ_i is the average number of species shared by i regions. One advantage of using multiple orders of ζ over classical measures of richness and pairwise compositional similarity only (for example, beta diversity) is that the suite of zeta values provides information on the contribution of rare (for example, ζ_2) to more widespread species (for example, ζ_5) to species turnover[63]. To better capture the shape of the zeta diversity decline over increasing orders of zeta, the retention rate was computed as the zeta ratio ζ_i/ζ_i-1. The retention rate represents the rate at which common or widespread species are retained across the landscape[62].

Here, we calculated ζ diversity for each of the four observed empires using the Zeta.decline.ex()-function from the zetadiv package v.1.2.0 (refs. [64,65]). Models were run for all possible combinations of regions up to order 40 (ζ_1 to ζ_{40}), independently of the spatial position of sites to identify the general pattern of compositional diversity across the entire empire[62]. The same analyses were repeated separately for ten null model runs of each respective empire to assess if species turnover for rare to common species differed between colonial empires and regions from the same spatial unit.

MS-GDM. To assess the contribution of geographic, environmental and socio-economic drivers (Supplementary Table 1) to compositional turnover among naturalized regional floras, we ran MS-GDM using the Zeta.msgdm()-function from the zetadiv package v.1.2.0 (refs. [64,65]) for each empire separately. MS-GDM uses a combination of generalized linear models and I-splines to evaluate nonlinear relationships between zeta values and changes in predictor values. As a similarity measure, we again used the Simpson-equivalent of zeta diversity[66,67]. Using MS-GDMs enables the assessment of the importance of different drivers for the explanation of compositional turnover for different zeta orders (across rare and common species). The models generate a monotonic I-spline whose features inform about predictor behaviour (Extended Data Fig. 1b,i). Two features of the

I-spline are of importance: (1) the amplitude of the *I*-spline indicates the relative importance of a predictor compared to the other predictors and (2) changes in the slope of the *I*-spline across predictor values indicate at which values the effect of a predictor is most relevant[63,67].

Models were run for 8,000 combinations of *i* regions (for $\zeta_i \in (2,5)$) and six replicates with different region combinations for each replicate and mean *I*-splines are reported in the study. Number of combinations and replicates were chosen to ensure computational feasibility and assessed on the basis of the observed predictor trends across the different replicates and the deviation from the mean spline across all replicates (Supplementary Figs. 5–8).

Network analysis. Networks were visualized on the basis of the complete regional naturalized flora of the observed empire, with nodes as the centroids of the regions and edges weighted by the pairwise similarity (1 − Sørensen pairwise dissimilarity) of the naturalized floras between regions. To assess the network structure and investigate patterns of compositional similarity among regions, we calculated two metrics for the weighted network of each empire separately.

First, we calculated the modularity of the network. This is a metric of the strength of the division within a network and identifies clusters of regions[68]. This way, we can identify clusters of regions that emerge on the basis of the pairwise-similarity weighted empire network. As a metric of modularity, we used the optimized algorithm proposed by ref. [69], which is based on the measure developed by ref. [68] and is implemented in the igraph package v.1.2.8 (ref. [70]). Second, we calculated the eigenvector centrality of each node in the network. This metric identifies important nodes within the pairwise-similarity weighted network on the basis of how many links this node has within the network[71,72], in our case each node represents a region within an empire that is connected to all other regions within this empire and the connection to other regions is weighted by the pairwise compositional similarity of the regions to the others. The higher the eigenvector centrality value is, the more important the nodes are, that is a region is connected to many other regions that are in turn well connected in the network.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All driver datasets used in the study are openly available and provide spatially explicit, gridded information and the aggregated data are provided in Supplementary Table 5. The GloNAF database together with the shapefile that was used to produce the maps have been published in a data paper[35]. All data and code are available on Zenodo and can be found here: https://doi.org/10.5281/zenodo.6640264.

Code availability

All code is available on Zenodo and can be found here: https://doi.org/10.5281/zenodo.6640264.

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Author contributions

B.L. and F.E. designed the study. B.L. performed the analysis with input from G.L. B.L. led the writing with significant input from F.E. and S.D. Species data were provided by the GloNAF core team (F.E., M.v.K., M.W., W.D., P.P., J.P., H.K. and P.W.). All other authors (including A.S., H.S. and Q.Y.) contributed to the discussion and writing.

Competing interests

The authors declare no competing interests.

Additional information

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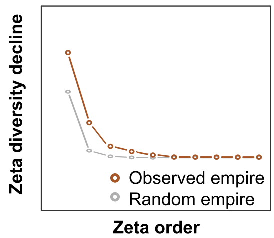
a) Zeta diversity

i) Interpretation

Zeta decline
Number of species shared between sites (= zeta diversity). With increasing number of sites (= zeta orders) zeta diversity declines monotonously and rare species are excluded from the analysis. Changes in the value and slope therefore disentangle the contribution of rare and widespread species to turnover.

Zeta ratio (= retention rate)
Probability of a species remaining in n sites when considering n+1 sites. Allows to better differentiate between the slopes of zeta declines.

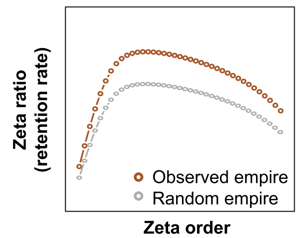
ii) Zeta decline



Expectation

Compositional similarity (zeta diversity values) within the observed empire is higher across combinations of sites (i.e., zeta orders) and decreases more slowly than in the random empire.

iii) Zeta ratio

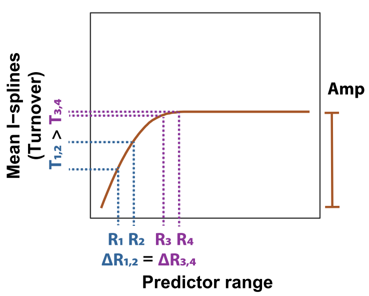


Expectation

The probability of species per combination of sites (i.e., zeta orders) remaing in the observed empire is higher compared to the random empire. This indicates larger contribution of widespread species to flora similarity.

b) Multi-site generalized dissimilarity model

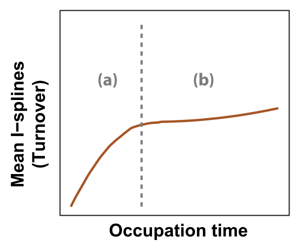
i) I-spline interpretation



Amplitude (Amp)
Indicates the relative importance of a predictor compared to the other predictors.

Slope
Changes in the slope of the I-spline across predictor values indicates differences in the influence of this predictor on turnover across the gradient of values. A steep slope indicates that small differences in predictor values between two regions(e.g., R_1 & R_2) will result in large differences in species composition, whereas the same difference for a more shallow slope (e.g., R_3 & R_4) will have a low effect on species composition.

ii) Low zeta orders (i.e., rare alien species)

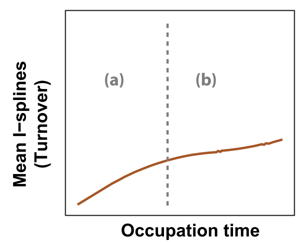


Expectation

High turnover between regions that are occupied for short times (i.e., large slope in section a), because rare alien species do not spread quickly.

Low turnover between regions that are occupied for medium to long times (i.e., small slope in section b), because rare aliens have potentially spread across empire by now.

iii) High zeta orders (i.e., widespread alien species)



Expectation

High turnover between regions that are occupied for short times (i.e., large slope in section a), because common alien species need time to spread across the empire. Turnover is lower compared to rare alien species.

Low turnover between regions that are occupied for medium to long times (i.e., small slope in section b), because common alien species have spread across empire by now.

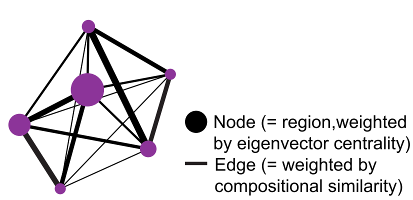
c) Network analysis

i) Interpretation

Network centrality (= eigenvector centrality)
This metric identifies important nodes within the pairwise-similarity weighted network based on how many links this node has within the network and on how important the neighbor nodes are (Bonacich, 1987; Delmas et al., 2019).
The higher the eigenvector centrality value is, as more important the nodes are, i.e. a region is connected to many other regions that are in turn well connected in the network.

Network modularity
Metric of the strength of the division within a network to identify clusters of regions (Newman & Girvan, 2004) based on the pairwise-similarity weighted empire network.

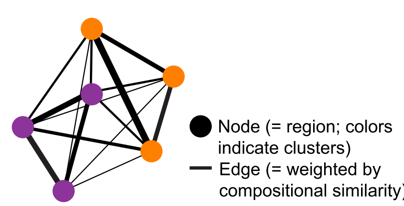
ii) Centrality



Expectation

We expect regions that had a central position in an empire (e.g., trade hubs) to have a more similar naturlized alien flora to other regions occupied by the same empire and thus have a higher centrality in the network.

iii) Modularity

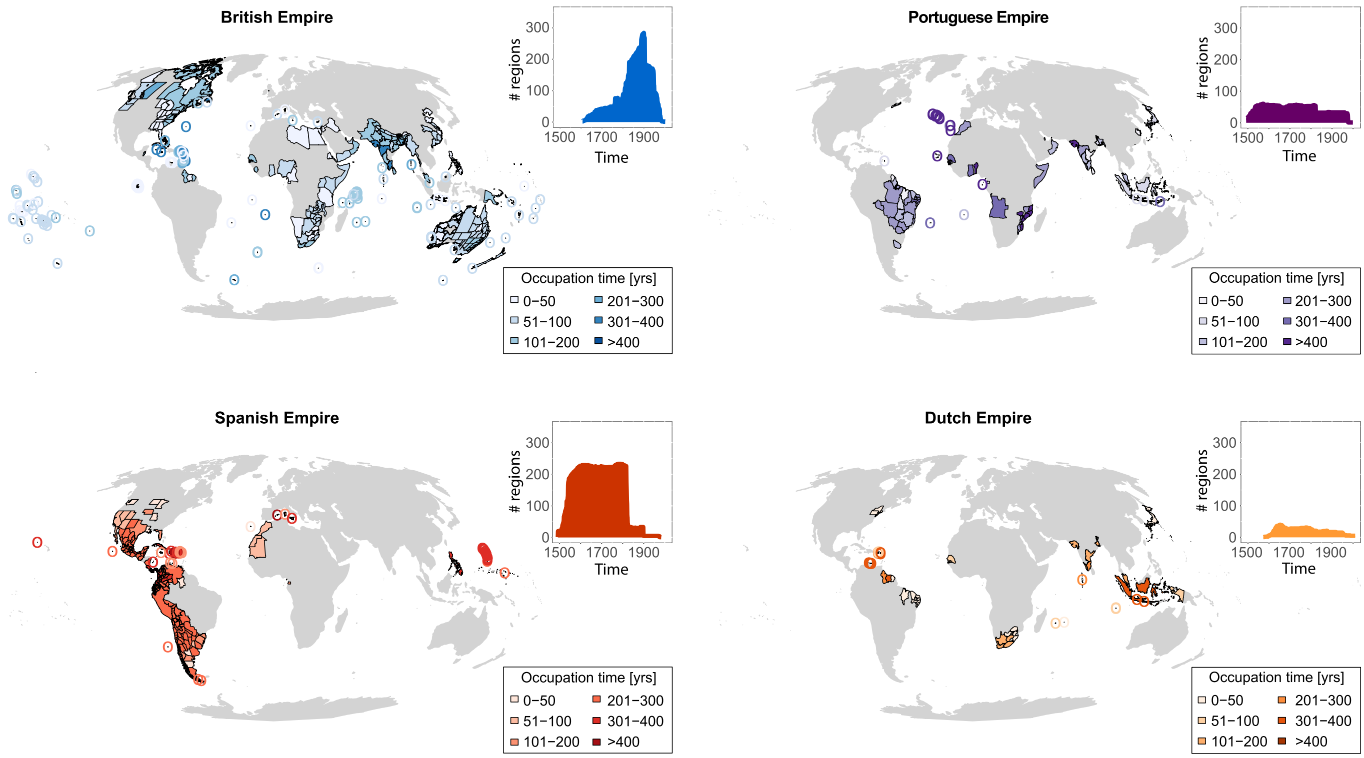


Expectation

We expect regions to be clustered by geographic vicinity and climatic similarity of the occupied regions of an empire.

Extended Data Fig. 1 | See next page for caption.

Extended Data Fig. 1 | Conceptual overview of the analyses performed in the study. Conceptual overview of the analyses performed in the study. For each analysis, an interpretation of the metrics is provided (a-i; b-i; c-i) and the expectation based on the formulated hypotheses (a-ii & a-iii; b-ii & b-iii; c-ii & c-iii). 'Random empire' (a-ii & a-iii) relates to a hypothetical empire associated with a colonial power that has the same number of mainland and island regions in total and per UN geospatial region as the observed empire of that colonial power. 'Sites' refers to the respective spatial unit used in the analysis and can be a country or subnational region (for example, county or island).



Extended Data Fig. 2 | Maximum extent of the four European Empires under consideration independent of the temporal dimension. Maximum extent of the four European Empires under consideration independent of the temporal dimension. All regions have been included at some point in the respective empire. Regions with an area < 50000 km^2 are additionally highlighted by a circle. Saturation of the colour indicates the total time in years the region was occupied by the respective empire. The bar graph shows the extent of the European Empires (that is, number of regions) over time from 1492-2010.

nature portfolio

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Reporting Summary

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☒	☐	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	All driver datasets used in the study are openly available and provide spatially explicit, gridded information and the aggregated data are provided in Table S5. The GloNAF database together with the shapefile that was used to produce the maps have been published in a data paper (van Kleunen et al. 2019). All data and code is available on Zenodo and can be found here: https://doi.org/10.5281/zenodo.6640264.
Data analysis	All analyses were run in R version 4.0.4 R Core Team. R: A language and environment for statistical computing. (2021).

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

All driver datasets used in the study are openly available and provide spatially explicit, gridded information and the aggregated data are provided in Table S5. The

GloNAF database together with the shapefile that was used to produce the maps have been published in a data paper (van Kleunen et al. 2019), and the most recent version is available upon request. All data and code is available on Zenodo and can be found here: https://doi.org/10.5281/zenodo.6640264.

Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	not applicable
Population characteristics	not applicable
Recruitment	not applicable
Ethics oversight	not applicable

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	The redistribution of alien species across the globe accelerated with the start of European colonialism. European powers were responsible for the deliberate and accidental transportation, introduction and establishment of alien species throughout their occupied territories and the motherland. Here, we show that these activities left a lasting imprint on the global distribution of alien plants. Specifically, we investigated how four European empires structure current alien floras worldwide. We found that compositional similarity is higher than expected among regions that once were occupied by the same empire. Further, we provide strong evidence that floristic similarity between regions occupied by the same empire increases with the time a region was occupied. Network analysis suggests that historically more economically or strategically important regions have more similar alien floras across regions occupied by an empire. Overall, we find strong evidence that European colonial history is still detectable in alien floras worldwide.
Research sample	Information about naturalized vascular plant species was extracted from the Global Naturalized Alien Flora (GloNAF) database 3,35433 , the most comprehensive inventory of regional alien plant species distributions currently available. We included regions with checklists of naturalized plants at the finest available resolution (i.e. country or subnational regions like federal states or islands). This resulted in a selection of 1,183 regions, including 404 island and 779 mainland regions with a total of 19,250 naturalized plant taxa. Additionally, we compiled a dataset of the colonial affiliation of regions of the four most extensive European empires (today's Great Britain, Spain, Portugal, and the Netherlands). The full spatiotemporal extent of the four empires under consideration resulted in 398 regions (176 islands, 222 mainland regions) for the British Empire, 255 regions (51 islands, 204 mainland regions) for the Spanish Empire, 85 regions (27 islands, 58 mainland regions) for the Portuguese Empire and 58 regions (27 islands, 31 mainland regions) for the Dutch Empire. To explain species turnover between naturalized alien floras of regions, we compiled descriptors representing important global drivers of naturalizations as identified in and refined for plants in. We compiled information on geographic (area and habitat heterogeneity, geographic distance between regions), environmental (mean annual temperature and aridity index) and socio-economic (GDPpc, population density and cropland area) drivers (Table S1). As empire-specific variable from the empire database we computed the “occupation time” given as the number of years a region was occupied by a specific European empire. All datasets are openly available and provide spatially explicit, gridded information or are provided with the manuscript.
Sampling strategy	No sampling procedure was available. We used all available data based on the available datasets.
Data collection	Data was collected from published online repositories. The Empire database was collected mainly by Bernd Lenzner with help of some students.
Timing and spatial scale	not applicable
Data exclusions	not applicable
Reproducibility	no experiments were conducted
Randomization	not applicable

Blinding | not applicable

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study	
☒	☐	Antibodies
☒	☐	Eukaryotic cell lines
☒	☐	Palaeontology and archaeology
☒	☐	Animals and other organisms
☒	☐	Clinical data
☒	☐	Dual use research of concern

Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging