Naturalized alien floras still carry the legacy of European colonialism

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Abstract

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 strong evidence that European colonial history is still detectable in alien floras worldwide.

Keywords: Columbian exchange, compositional similarity, European empires, legacy effects, network, plant invasion

Introduction

Naturalized alien plant species, i.e., species that form 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 [2–5]. Globally, North America has received most naturalized alien plant species, followed by Europe and Australasia [4,6], with hotspots being located in coastal mainland regions and on islands [7,8]. These large-scale 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 plants and other taxa is inextricably linked to human movement which has accelerated with the onset of European exploration and colonialism in the late 15th 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 subsequent spread of alien species, such as animals, plants, and pathogens [16–18]. While many of these species were important for the economies of European powers, their naturalization and spread resulted in the alteration and deterioration of ecosystems in occupied lands [15–20]. The first trans-continental 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 and became bidirectional in the 19th and early 20th centuries through the institutionalization of species exchange. 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 the occupied regions as well as to support the growing fashion for introduced ("exotic") ornamental plants and gardening in Europe [24,25]. Finally, governmental departments also played a substantial role in alien plant introductions, mainly for economic purposes (e.g., the US Department of Agriculture; [26]). The British Empire alone maintained around 50 Acclimatization societies and a network of 100 botanical gardens by around 1900 [25,27]. The fascination for "exotic" plants led to a peak in demand for new species in the European horticultural market, fostering innovation for live specimen transport and an economy around "plant hunters", who explicitly searched for and imported attractive plants [28,29]. All these factors drove the global exchange of plant species, but with major exchange routes often constrained within each European empire [21-29]. Trade and transport were further strengthened among regions occupied by one European power via market policies (for example, import duties) designed to favor the power in question; this resulted in up to 2.5 times greater trade volumes for occupied regions compared to unoccupied regions [30]. At the same time, different colonial powers followed different market strategies across the full or parts of their empire. The Dutch Empire had open door policies overall, whereas the others had both open-door policies and preferential trading within their empires[30]. These trade networks and policies should lead to alien plant species being predominantly exchanged and redistributed among regions occupied by the same European power with some variation associated with the different market strategies as well as 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. Additionally, the volume of global trade increased 30-fold in value since 1950 [31]. This reorganization of global trade has 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 time span [33], the centuries of imperial occupation and organization of trade relations may still leave a lasting imprint on the global patterns of naturalized 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) despite more recent changes in global trade and introduction networks. To this end, we reconstructed the spatial and temporal extent of regions occupied by the four European powers by determining the time of colonial occupation for regions worldwide. Using the Global Naturalized Alien Flora (GloNAF) database [3,35] to obtain naturalized alien floras for the formerly occupied regions (see Methods for details), we compiled a data set covering a total of 1183 regions (779 mainland regions, 404 islands). We then used zeta diversity (i.e., 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 the following hypotheses H1 & H2 and qualitatively investigate H3 (Figure 1):

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

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

H3. Regions with an important historical strategic role for the occupying power (e.g., as trade hubs, and administrative centers) share more of their naturalized alien flora with other regions than less strategically important ones.

Results

Similarity of naturalized alien floras among regions occupied by the same European power

Across all four empires, the average number of species shared between regions (i.e., zeta [ζ] diversity, Figure 1) rapidly declined with an increasing number of regions considered (i.e., 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 (Figure 2, Table 1). Regions occupied by the British and the Dutch had floras with greater similarity than random collections of regions, while regions occupied by the Spanish and Portuguese had floras that were not more similar than random region collections (Figure 2, Table 1). We also calculated the retention rate (zeta ratio) of species as the probability that any given species remains within the naturalized flora of each region sequentially added to the collection occupied by a particular European power. When comparing these retention rates to randomly constructed collections of regions, the observed retention rates were always higher than random, for all four European powers (Figure 2). This supports our assumption that alien floristic similarity is overall higher among regions occupied by the observed, historic empire compared to the random collection of regions of similar extent and spatial configuration due to the more frequent presence of widespread species across regions.

Drivers of regional alien plant species turnover

Multi-site generalized dissimilarity models revealed the importance of how different geographic, environmental, and socio-economic drivers shape naturalized alien floras across regions occupied by the same empire. The selected set of variables (Table S1) explained the turnover of species between any two naturalized floras reasonably well for all four empires ($0.32 < R^2 < 0.54$ at ζ_2), but the explained variance decreased with increasing numbers of regions compared ($0.07 < R^2 < 0.20$ at ζ_5; see Figure S11 and Table S2). The decrease in explained variance across zeta orders indicates a decrease in explanatory power of the selected geographic, environmental and socio-economic drivers for the turnover of widespread alien species (i.e. species occurring in many regions). Below we discuss the importance of the selected drivers on species turnover for rare (ζ_2) and widespread (ζ_5) alien plants for the European empires, with a special focus on occupation time.

Alien species turnover across regions of the different European empires is driven mainly by climate (mean annual temperature and aridity index) and geographic distance, as indicated by the amplitude of the I-splines (Figure 3 & Table 2). Alien species turnover with respect to climate is high, especially for the British and Spanish empires and to a lesser degree for the Portuguese and Dutch empires, suggesting that differences at high temperatures are more important than at low temperatures (Figure 3), replicating commonly observed differences in alien species compositions between extratropical and (sub-)tropical regions [5]. Geographic distance, on the other hand, shows high turnover at short distances and almost no importance for turnover between distant regions (Figure 3). These dynamics follow the previously shown distance decay where species similarity is high for close regions and decreases for more distant regions [36].

Occupation time (i.e., the 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 main climate variables (amplitude for ζ_2: 0.25 – 2.22 and for ζ_5: 0.30 – 3.98) on the turnover of rare and widespread alien plants across regions once occupied by the former European empires (indicated by the amplitude of the I-splines for occupation time; Figure 3 and Table 2). The only exception was for rare alien species turnover in the Portuguese Empire, for which occupation time had no effect on species turnover. 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 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 (i.e., the shape of the mean I-spline) differed across European empires. For the British Empire, turnover increased and slightly accelerated across the entire range of occupation time values, indicating small turnover between regions that were occupied for similar time periods regardless of how long these regions were occupied (and independent of when this time was), and high turnover for regions that were occupied for different time periods (Figure 3). 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 only, and effects were apparent for regions with long occupation times (> 290 years; approx. 0.6 × max. occupation time; Figure 3). We found a similar trend for the Dutch Empire as for the Spanish Empire for rare species, although the effect of differences in occupation time on turnover started to appear earlier (> 140 years; approx. 0.4 × max occupation time; Figure 3). For widespread alien species, differences in occupation time had the same effect on turnover regardless of the value of occupation time, as shown by the steady increase of the spline (Figure 3). Finally, in the Portuguese Empire, the effect of the difference in occupation time on the turnover of widespread species increased across the whole range of occupation time values, but the I-spline showed a deceleration for long occupation times. This indicates that for regions with long occupation times, widespread alien species are likely spread across the Empire to which those regions belong and thus differences in occupation time do not have a substantial effect on turnover anymore (Figure 3).

Identifying central regions via network analysis

Based on the compositional similarity of the alien floras, modularity analyses identified three or four regional clusters (for the British and Spanish empire and the Portuguese and Dutch empire, respectively) and the five regions per cluster that were most similar (i.e., have the highest centrality in their cluster) to other regions in the network (see Figure 4 and Table 2).

For the British Empire three clusters emerged, with the first one including the tropics and subtropics (185 regions), the second one consisting of northern and southern extratropical regions (159 regions) and the third one mainly located on the Indian subcontinent (56 regions) (Figure 4). Regions with the most similar floras per cluster were located in Northern Australia, China and India (centrality between 0.96-0.91; cluster 1), eastern Australia and South Africa (centrality between 1.00-0.93; cluster 2) and India (centrality between 0.94-0.90; cluster 3) (Figure 4).

In the Spanish Empire, the first cluster (117 regions) was located mainly in Central America (including the Caribbean) with few regions at the West African coast and in the west Pacific (Figure 4). The second cluster is mainly situated in southern South America and Northern America (106 regions) and the third cluster includes mainly Mexican regions, Macaronesian and Mediterranean islands (33 regions). Most central regions (i.e., regions with highest centrality scores indicating high compositional similarity to many regions within the empire; see Methods section) are located in Mexico (centrality between 0.85-0.71; cluster 1), Mexico and Colombia (centrality between 0.95-0.84; cluster 2) and Mexico and Chile (centrality between 1.00-0.96; cluster 3) (Figure 4).

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

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

Discussion

We find strong evidence that the legacy of European empires is still detectable in today's patterns of 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 (Figure 2). Within a historical empire, occupation time had a significant impact on alien species turnover among regions (Figure 3, Table 2). Furthermore, network analysis suggests that regional hubs of floristic similarity within historical empires may coincide with regions known to be of greater economic or strategic importance within the respective empire (e.g., important trade hubs, administration centers; Figure 4).

Empire affiliation increases compositional similarity of regional alien floras (H1)

Across the four European empires, compositional similarity showed distinct patterns compared to a random collection of regions of the same 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 (i.e., propagule and colonization pressure; [38–40]), which are strongly related to trade and transportation, and to the suitability of the environment (e.g., the climatic similarity between regions, 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 (zeta ratio) across multiple regions than expected by chance. The higher compositional similarity in the British Empire, especially for widespread species, is likely 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 [44]. Further, it was established relatively recently, starting in the early 17th century and lasting until the late 20th century with its greatest extent in the early 20th century [45]. 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. In addition, during the existence of the British Empire, global trade and transportation had already significantly intensified [31]. With the development of steam-engine boats for trans-oceanic voyages in the mid-19th century and improved navigation techniques, travel times across the Atlantic were roughly cut by half, resulting in reduced transportation and freight costs [46,47] at a time when the Spanish Empire and the American part of the Portuguese Empire had already largely disintegrated (Figure S10). Consequently, a larger source pool, shorter traveling times, and improved transportation made it more likely for biota to survive the journeys, increasing the invasion probability in the former colonies [33,40,43,46,48].

For the Spanish Empire, we observed similar trends that, however, likely 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] (Figure S10). High retention rates are likely 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 likely less important across the entire Americas given the vast distances between regions and existing geographic and climatic barriers, spread via trade and transport within a contiguous part of the empire has likely been more intensive than between regions separated by the oceans. This follows established knowledge that bilateral trade decreases with distance [50]. Thus, the close proximity of the regions occupied by the Spanish Empire likely facilitated the spread of introduced alien species via more intense bilateral trade and easier trade and transport of species across shorter distances. Additionally, subsequent establishment after the introduction was likely facilitated by climatic and environmental similarity of the regions based on 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, likely due to the regional clustering represented by Brazil and then the East Indies. 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 (e.g., zeta orders > 13). For the Dutch Empire the pronounced drop in the retention rate is likely 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 within empires (H2)

Compositional turnover within the four European empires is strongly driven by climate (i.e., mean annual temperature and aridity index) and geography (i.e., 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. This provides robust evidence of the long-lasting imprint of colonial history on alien floras in formerly occupied regions. We found that short occupation times (approx. < 140 years) had low or no relevance for compositional turnover and started to become more important for intermediate to long occupation times. This leads to high turnover when comparing regions with short occupation times to regions with intermediate to long occupation times. From intermediate to long 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 than for regions with shorter occupation times. Essentially, we use occupation time as a proxy for trade and transport intensity among regions, due to the absence of reliable trade data across the full time period of the European empires considered here (see below for further discussion). 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 exchange with regions not occupied by the empire in question [30]. Consequently, colonization and propagule pressure from regions occupied by the same empire are higher compared to other regions. 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.

In this study, we aim to understand 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 (if not all) socio-economic predictors, comprehensive data for such a long time period (i.e., 1492 – present) is not available. Consequently, we decided to use contemporary data that have the best available spatial coverage and quality in our models. As outlined in the methods section, we base our selection of drivers on recent studies [7,8] showing that contemporary socio-economic predictors are important for explaining naturalized alien plant species distributions globally. Hence, we include both contemporary predictors and historic predictors (i.e., occupation time) in our models, to disentangle the importance of these socio-economic predictors on current compositional similarities of naturalized 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 on longer journeys, commodity exchange or to bring new people. These activities likely resulted in higher propagule pressure and the subsequent establishment of species from across the respective empire compared to less-frequented regions. Introductions occurred intentionally (e.g., horticultural and otherwise economically relevant plants) but also unintentionally (e.g., as seed contaminations). 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 (e.g. [46,52]). Interestingly, in our study, the relationship between the number of colonial powers 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 any of the other empires (Figure S12, 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 to disentangle historical and more recent dynamics, further studies, e.g., focusing on one empire (or a specific region of an empire) 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 [45]. The deliberate exchange of plants and plant material across the British Empire was well developed, with large networks of botanical gardens and Acclimatization societies that aimed to "enrich" the native flora with European plants [25,27]. Together with increased trade and long-lasting imperial exploitation of these regions, high degrees of alien plant species introduction and establishment within these regions 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, in order to control the Atlantic trade and especially for its gold resources [53]. Hence, the Portuguese exploitation and trade in these regions were well developed and thus likely facilitated the accidental and deliberate exchange of alien plants. The Portuguese Empire had important economic regions, especially for the international spice trade from and to the Indo Malay realm (e.g., East Timor, Tamil Nadu, Kerala; [54]) with frequent shipping between and strategic trading posts in these regions. Mozambique, on the other hand, was an important colony for the production of e.g., cotton, sugar, sisal, and in Brazil, the city of Salvador in Bahia was the administrative center of the Portuguese colonies in the Americas, which highlights the importance of these regions in the empire [54]. Finally, the Azores as well as St. Helena emerged as central regions and both were important stopover destinations for trans-oceanic voyages [16,54] and thus likely had high vessel visitation rates. Invasion success on islands has been shown to be especially high given their ecology and eco-evolutionary history, which further explains high compositional similarity of the alien floras of these regions [10]. For the Dutch Empire, central regions in the Indo-Malay realm (especially, West Bengal, Tamil Nadu, Andhra Pradesh, Sumatra, Java & peninsular Malaysia) coincide strongly with trade activities by the Dutch East India Trading Company (VOC), which dominated the European trade with Asia from the mid-17th century to the late 18th century [55,56]. South Africa (as part of the former Cape Colony) was also an important region for the Dutch Empire, as it was one of the few regions where the Dutch established extensive settlements and it was an important stopover of the VOC between the Netherlands and Java [56]. For the regions in the Americas, the Virgin Islands (e.g., St John; Table 3) were an important transshipment place for the exchange of goods and slaves by the Dutch West India

Company between New Holland, Brazil (Pernambuco, Rio Grande do Norte, Ceara & Paraiba; 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 plant species distributions 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 striving and well-integrated into the current shipping network 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 (e.g., in the form of overseas territories like the British Virgin Islands) and native and common languages (e.g., Spanish in Latin America or Portuguese in Brazil and Mozambique) 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, we can still detect and quantify imprints of colonialism in their regional 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 Global Naturalized Alien Flora (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 (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 (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. Based on 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 likely have a stronger effect on rare (i.e., 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 (i.e., 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 (i.e., 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" (Table S4). Region delineations were based on the GloNAF database and the dataset as outlined above. Information collected includes (i) the colonial affiliation of a region, i.e. the identity of the European empire occupying a specific region, and (ii) the time span a specific European empire occupied that region (i.e. the start and end year).

We used the COLDAT database by [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 (e.g., 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 (i.e. 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, based on slightly different criteria (see Becker et al., 2019, for a thorough discussion on this topic and illustration of differences in start dates across datasets). The dates in COLDAT are expressed as (i) the mean dates over all datasets and (ii) 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 (e.g., 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: (i) as the start of colonial rule, the date of the establishment of permanent settlements of the colonial power (e.g., trading posts, whaling stations, fortifications) was accepted, (ii) for regions without additional information the dates from the country level based on COLDAT were used, and (iii) 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 (i.e. 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, 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 (all regions that have once been occupied by the respective European empire are given in Figure S7).

Null model

To test H1, we established a null model based on 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 (see statistical analysis section below). We assigned all regions within our dataset to the 17 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 archeological research and provides regions that are roughly comparable in size (see Figure S9).

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 based on the minimum geographic distance from the last region (i.e., 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 10 random empires for each colonial empire that each has 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 [7] and refined for plants in [8]. 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). For gridded variables, we calculated the respective metric including all raster cells covered by the respective region (national or sub-national entity).

All datasets are openly available and provide spatially explicit, gridded information and the aggregated data are provided in Table S5. 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 below 0.7 (see Figure S1-S4). 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 MS-GDMs (see description below) two times, 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 (table S4) and explained variance of the drivers between the models (table S5). Additionally, mean trends for each predictor remained consistent across the two models (see Figures S13 & S14). 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 version 4.0.4 [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 (i.e. for order 1) represents the average species richness (i.e., alpha diversity) of an assemblage in a set of regions. ζ_2 is the average pairwise similarity between two regions (i.e., 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 (e.g., beta diversity) is that the suite of zeta values provides information on the contribution of rare (e.g., ζ_2) to more widespread species (e.g., 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 ζi/ζi-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 version 1.2.0 [64,65]. Models were run for all possible combinations of regions up to order 40 (i.e., 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 10 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 (Table S1) to compositional turnover among naturalized regional floras, we ran Multi-Site Generalized Dissimilarity Models (MS-GDM) using the *Zeta.msgdm()*-function from the *zetadiv*-package version 1.2.0 [64,65] for each empire separately. MS-GDM uses a combination of generalized linear models and I-splines to evaluate non-linear 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 (i.e., across rare and common species). The models generate a monotonic I-spline whose features inform about predictor behavior (Figure 1b, i). Two features of the I-spline are of importance: (i) the amplitude of the I-spline indicates the relative importance of a predictor compared to the other predictors and (ii) 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 8000 combinations of i regions (for $\zeta_i \in [2,5]$) and 6 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 based on the observed predictor trends across the different replicates and the deviation from the mean spline across all replicates (Figure S5-S8).

Network analysis

Networks were visualized based on the complete regional naturalized flora of the observed empire, with nodes as the centroids of the regions and edges weighted by the pairwise similarity (i.e., 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 based on the pairwise-similarity weighted empire network. As a metric of modularity, we used the optimized algorithm proposed by [69], which is based on the measure developed by [68] and is implemented in the *igraph* – package version 1.2.8 [70]. Second, we calculated the eigenvector centrality of each node in the network. This metric identifies important nodes within the pairwise-similarity weighted network based on 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, i.e. a region is connected to many other regions that are in turn well connected in the network.

Author contribution

BL and FE designed the study. BL performed the analysis with input from GL. BL led the writing with significant input from FE and SD. Species data were provided by the GloNAF core team (FE, MvK, MW, WD, PP, JP, HK, PW). All other authors contributed to the discussion and writing.

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Conflict of interest

The authors declare no conflict of interest.

Data availability statement

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. The empire database is currently available in in the supplementary material and will be made available via Zenodo after acceptance of the manuscript.

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Figures

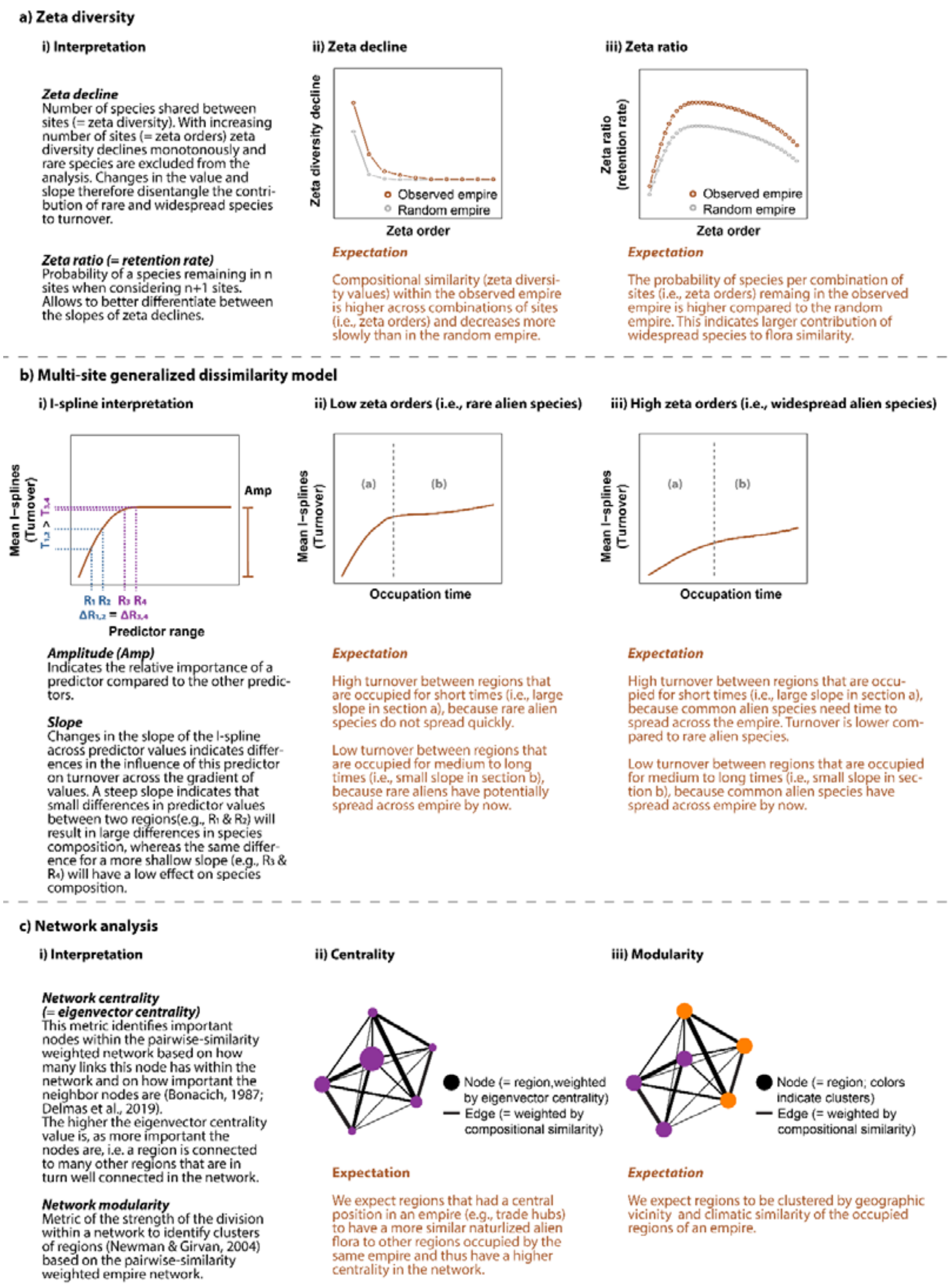
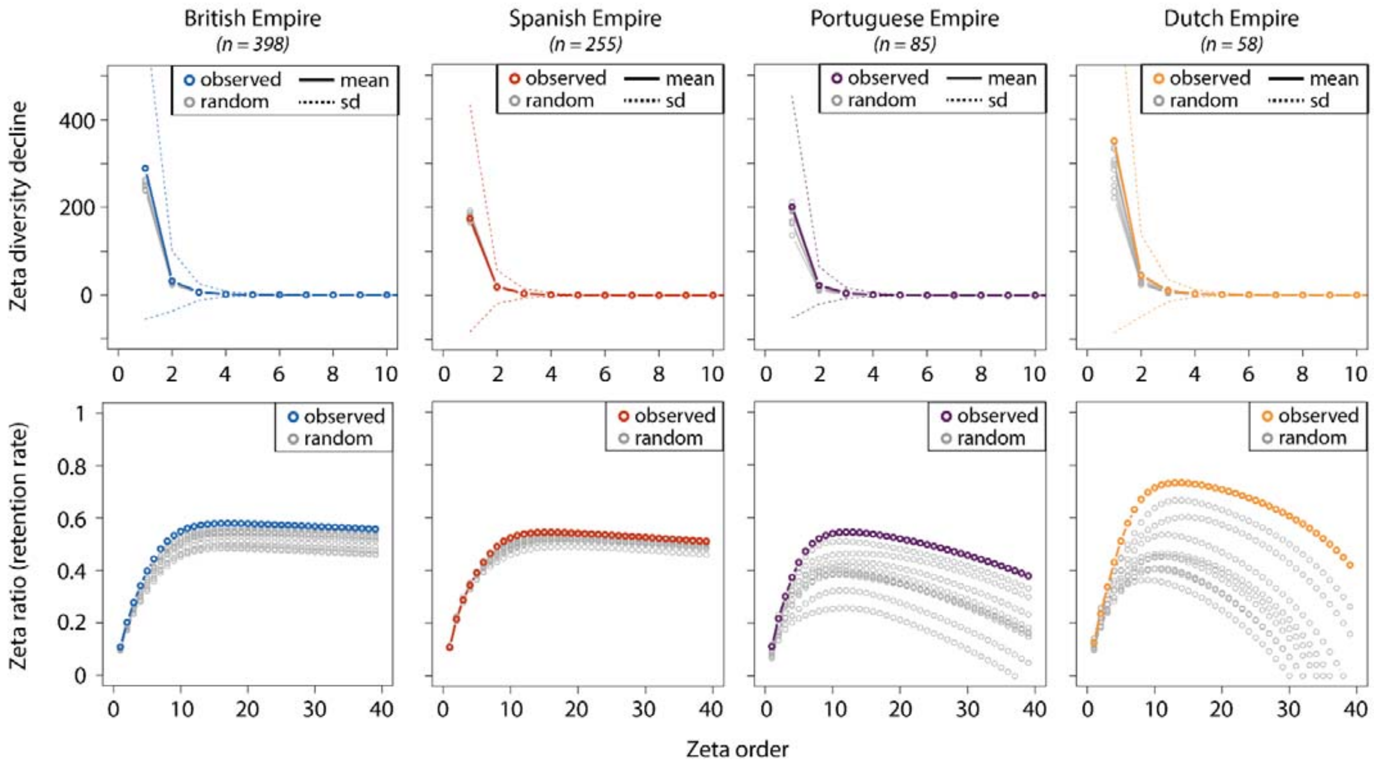


Figure 1: Conceptual overview of the analyses performed in the study. For each analysis, an interpretation of the metrics is provided (a-i; b-i; c-i) and the expectation based on the formulated hypotheses (a-ii & a-iii; b-ii & b-iii; c-ii & c-iii). “Random empire” (a-ii & a-iii) relates to a hypothetical 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 (e.g., county or island).



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853 **Figure 2**: Zeta diversity decline (upper row) for each empire from $\zeta_1 - \zeta_{10}$. Zeta orders indicate the number of regions for which compositional similarities are computed (i.e., ζ_2 indicates mean compositional similarities among all pairwise region combinations). The trend for the observed empire is given in color, including the 95%- confidence interval (broken lines) and the trends for 10 random empire draws are given in grey. The Zeta ratio or retention rate (lower row) is shown for $\zeta_1 - \zeta_{40}$. Again, trends for the observed empire are given in color and for the random draws in grey.

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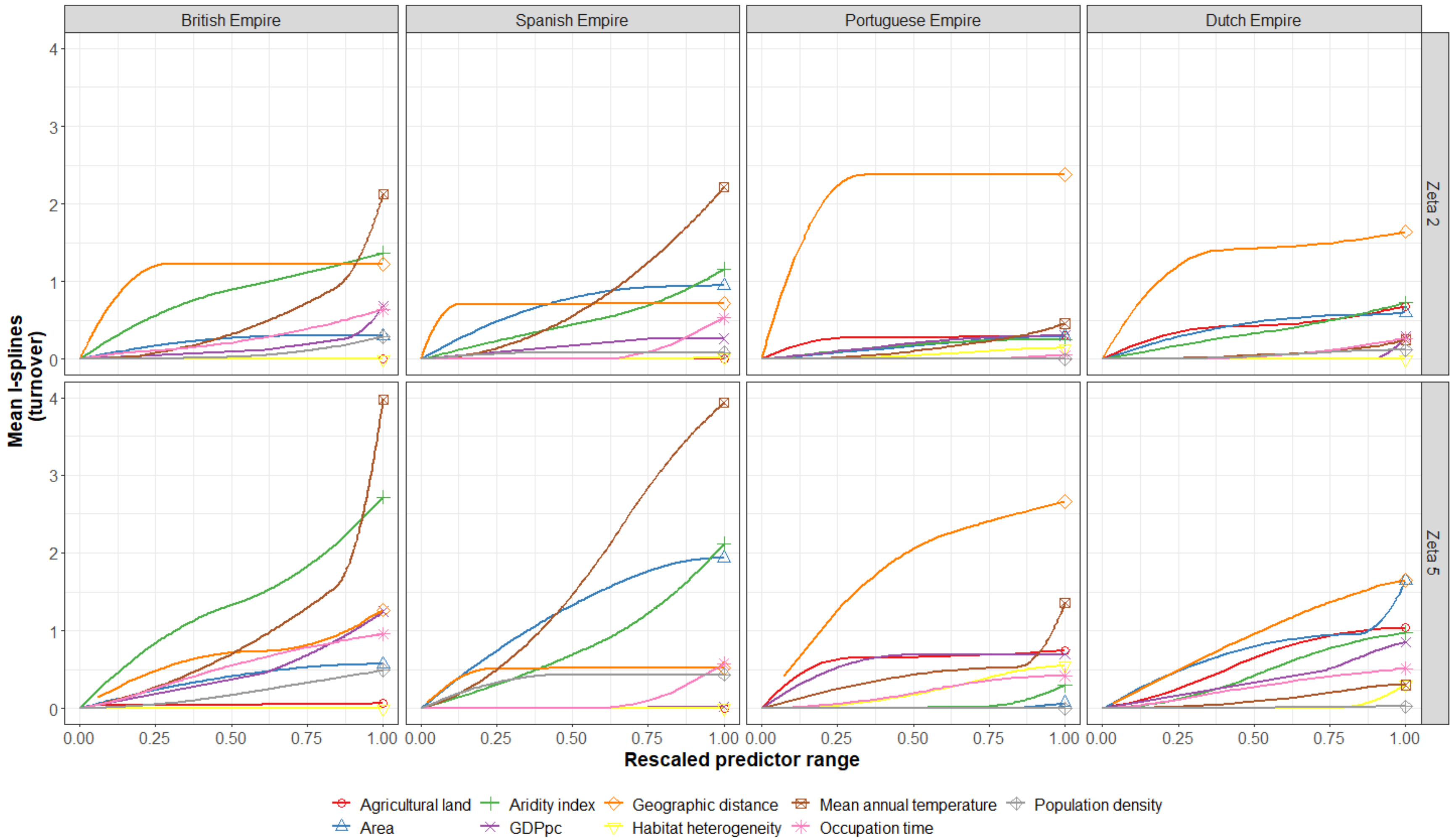

British Empire
Spanish Empire
Portuguese Empire
Dutch Empire
Zeta 2
Zeta 5
Mean I-splines (turnover)
Rescaled predictor range
0
1
2
3
4
0.00
0.25
0.50
0.75
1.00
Agricultural land
Area
Aridity index
GDPpc
Geographic distance
Habitat heterogeneity
Mean annual temperature
Occupation time
Population density

Figure 3: 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 (i.e., rare alien species) and ζ_5 (i.e., common alien species). Mean I-splines are derived from the MS-GDM models for the four European empires and are based on 6 repetitions with a sampling size of 8000 regions combinations per empire.

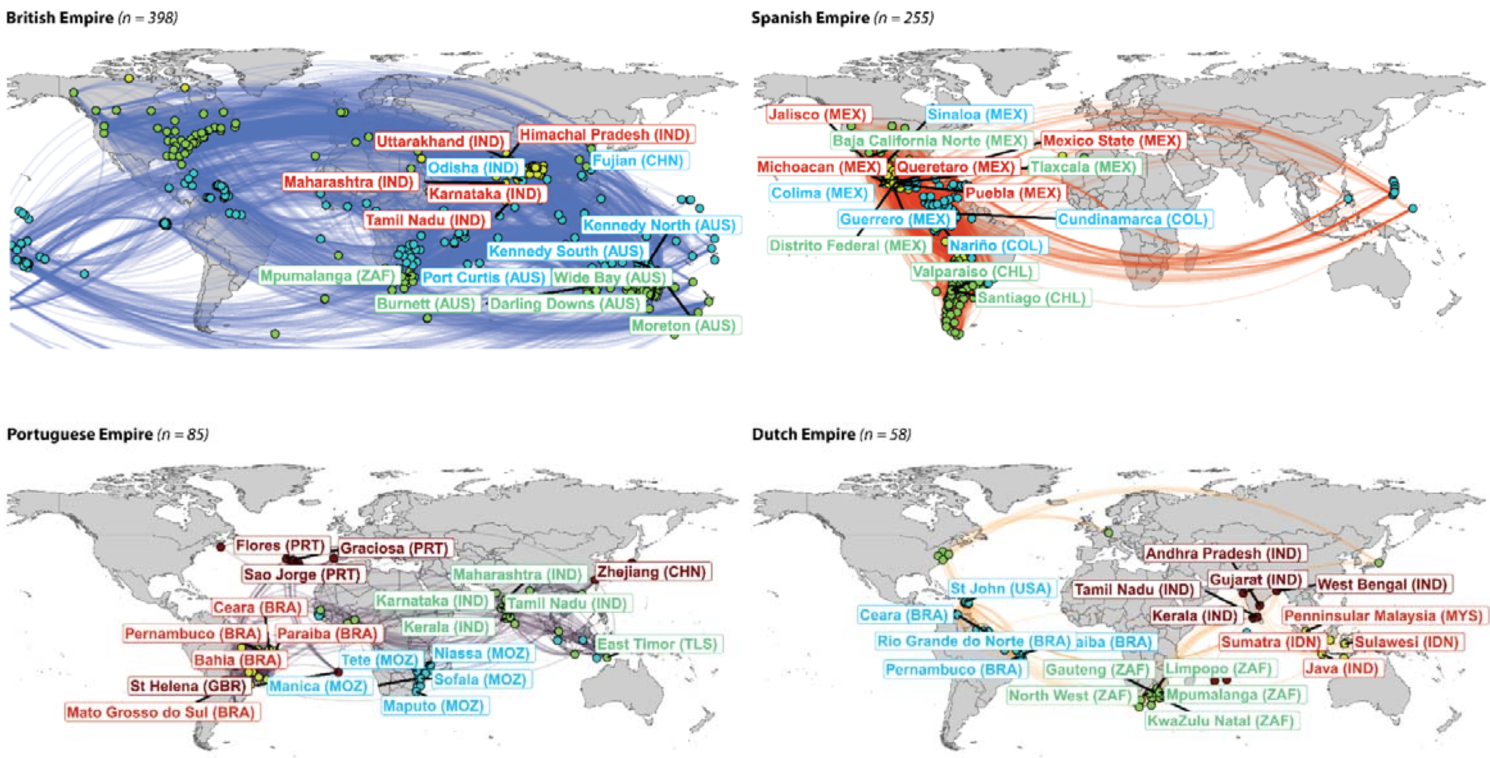

Figure 4. Networks or the four Empires with nodes placed at the region centroids and edges (links) between the regions. For the analysis, edges were weighted by the pairwise similarity between regions, which is not displayed here for better readability of the figure. Node colors indicate clusters identified by the modularity analysis based on the full network including all pairwise similarities (see methods section). For each cluster (indicated by the same color 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.

Tables

Table 1: Model results for the mean estimated compositional similarity (i.e., zeta diversity) across zeta orders 1-5 for the four observed European empires and the random empires. For the random empires, mean values and standard deviations are given across 10 random empires, respectively.

	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)

Table 2: Relative importance (i.e, amplitude of the I-spline) of all drivers based on the results of the MD-GDMs for each empire. Results are shown for ζ_2 (i.e., rare alien species) and ζ_5 (i.e., common alien species). Socio-economic drivers are highlighted by grey shading and the empire variable (i.e., occupation time) is highlighted in bold.

	Driver	ζ_2	ζ_5
British Empire	Area	0.3	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	0.5
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	0.3	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

Table 3: Top 5 regions for each empire with highest centrality scores in their respective cluster based on the network analysis. In brackets, the country the region belongs to is given. # Empires indicates, how many of the 4 empires have occupied the specific region over time.

	Region	Modularity	Centrality	# 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	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	0.9	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	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	2
	Pernambuco (BRA)	3	0.99	2
	Bahia (BRA)	3	0.99	1
	Ceara (BRA)	3	0.98	2
	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	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	0.9	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	0.8	2
	West Bengal (IND)	4	0.76	3
	Gujarat (IND)	4	0.75	3