

RESEARCH ARTICLE

An ecological and evolutionary perspective of the historical US nursery flora

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Societal Impact Statement

The plants sold in nurseries directly influence urban landscapes by providing habitat that supports humans and other organisms and indirectly influence the natural landscape by acting as a major source of invasive species. We analyzed the ornamental plants sold in US nurseries from 1719 to 1946 and found broad patterns of increasing diversity occurring in step with an increase in species relatedness, a switch from native to alien species, and a decrease in regional distinctness. Patterns like these, which have been observed recently in urban areas, thus have a basis in cultivation/horticultural history.

Summary

- Cultivated plants are foundational species in urban areas, where they simultaneously provide essential ecosystem services while posing a risk of invasion into natural communities. We sought to characterize the spatial and temporal patterns of taxonomic and phylogenetic diversity of cultivated plants using historical data to better understand the origins of the patterns of diversity observed in present-day human-dominated landscapes.
- Using records of 5098 ornamental vascular plant species available in 319 US nursery catalogs published from 1719 to 1946, we quantified the taxonomic and phylogenetic α -diversity, phylogenetic structure, and β -diversity of the historical US nursery flora in cultural regions, biomes, latitudinal bands, and longitudinal zones.
- We showed a peaked increase in taxonomic and phylogenetic diversity of the US nursery flora over time, concurrent with the proliferation of nurseries and the addition of new species to nursery offerings. However, standardized phylogenetic diversity showed a convex pattern, with a trough during a time of peak growth and connectivity in the nursery industry, and diversity actually decreased at the end of the time series. We also showed a pattern of increasing homogenization of regional nursery floras, as well as a shift from offering predominately native to predominately alien species.

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- Echos of the history of the US nursery industry can be found today in patterns with great ecological relevance. Previous reports of high alien plant diversity in urban areas, phylogenetic clustering and overdispersion among naturalized alien plants, and homogenization of urban plant communities are all consistent with the historical availability of these plants in the nursery flora.

KEYWORDS

historical ecology, horticulture, homogenization, introduced species, nursery industry, ornamental plants, phylogenetic diversity, phylogenetic structure

1 | INTRODUCTION

The horticultural flora is a source of historical and cultural insight into a region. Plants are propagated and distributed by nurseries, which supply a large portion of the plants humans cultivate (Avolio et al., 2020; Cavender-Bares et al., 2020). At the same time, cultivated plants constitute the ecological backdrop of human-dominated landscapes, providing resources for pollinators, microclimate regulation, and water retention, among other ecosystem services (Cook et al., 2012). However, many cultivated plants spread without human assistance and invade natural habitats (van Kleunen et al., 2018), often negatively impacting community structure and ecosystem functioning (Vilà et al., 2011). The ecological and evolutionary background of the historical horticultural flora outlines the trajectory of ecosystem service provision and the threat of invasion over time. Thus, there are ecological insights that can be gained by knowing whether horticultural plant diversity continually increased over time, with new species being added to a growing roster of cultivated species, or whether diversity remained constant, with turnover in the species available. The likelihood of either of these scenarios can be informed by using the horticultural history of a region as a prior. The United States (US) is an appropriate setting for this characterization, as its horticultural history is well-described (e.g., Adams, 1998; Pauly, 2007).

The earliest commercial horticulture in the United States involved Eurasian fruit trees; sales of pear, quince, and apple trees were known from the mid-17th century in English America (Adams, 1998) and were concurrent with horticultural developments in Western Europe (Pauly, 2007). Ornamental horticulture became popular later with the establishment of Prince Nurseries in 1732 in Flushing, New York, which was followed by several additional nurseries in New York, Philadelphia, and Massachusetts (Adams, 1998). Thus, the US nursery industry originated under British colonial possession. For this reason, Old World nursery stock and seeds that were originally or directly imported from Europe were cultivated, fostered by individual relationships between US nurserymen and European contacts (Del Tredici, 2017).

The historical trajectory of the US nursery and seed industry was highly regional. Nurseries proliferated in the 1820s and became particularly concentrated in the population centers of the Atlantic coast (Adams, 1998; Lyon-Jenness, 2004). After this, nurseries extended westward, generally tracking the settlement patterns of Euro-

Americans (Adams, 1998). In the mid-19th century, aided by developments in transportation infrastructure (steamboats, canals, and highways) and improved mail service, established northeastern nurseries shipped stock to nurseries further west, and the expansion of rail lines connected nurseries from coast to coast by the 1870s (Burd, 2019; Lyon-Jenness, 2004). In particular, Rochester, New York, was the hub of the US nursery industry from the mid-19th to the early 20th century, shipping plants to other nurseries, farmers, and private customers throughout the continent (Burd, 2019), while a handful of other nursery and seed companies were regionally dominant (Adams, 1998; Lyon-Jenness, 2004). This boom was fueled by the increasing influence of horticultural and agricultural societies, the development of new ornamental varieties, heightened marketing tactics by nurseries and seed companies, and the general rise of consumer culture (Lyon-Jenness, 2004). By 1890, there were over 4500 US nurseries (Adams, 1998).

Parallel with the growth of the nursery industry was an increase in the diversity of plants to trade and sell. Throughout the 19th and 20th centuries, plants from new regions of the world with unique genetic lineages became available in the US. Exotic ornamentals became more popular in the post-Civil War period, in response to trends inspired by gardening publications (e.g., *The Wild Garden*, Robinson, 1870) and amplified by the first wave of suburb proliferation (Jenkins, 1994; Del Tredici, 2017). Plants from East Asia were particularly desirable because of climatic similarities with the eastern United States (Guo, 1999), a shared evolutionary history with North America (popular ornamental genera had higher species richness in East Asia, Olsen, 2013), as well as Western fascination with Japanese- and Chinese-style gardens (Missingham, 2007). East Asian plants were available via Europe, especially after Western access to China was compelled by the Opium Wars (Holway, 2018). Collections sponsored by the Horticultural Society of London, Royal Botanic Gardens, and private nurseries (e.g., Veitch nurseries) took place in East Asia and other regions (e.g., South America, South Africa) from the 1840s onward (Holway, 2018). The direct introduction of East Asian plants became possible after Japan opened to the United States for trade in 1858 (Del Tredici, 2017) and collections in China, Japan, and Korea sponsored by Harvard University's Arnold Arboretum took place in the early 20th century (Howard, 1980). In 1898, the US Department of Agriculture (USDA) established the Section of Seed and Plant Introduction with the goal of collecting and cultivating economically useful

alien plants from throughout South America and Asia (Williams et al., 2020).

However, there is good reason to expect that there would have been disruptions influencing the diversity of the nursery flora. In the 1890s, many US states implemented laws requiring inspection of imported plant materials following economically disastrous plant disease outbreaks in the eastern US caused by San Jose scale, a scale insect pest primarily of ornamental and orchard trees in the Rosaceae family, likely introduced via contaminated nursery stock from California (Burd, 2019; Pauly, 2007). The Plant Quarantine Act was passed by Congress in 1912 and Quarantine 37 was issued by the Secretary of Agriculture in 1919; both regulated international and interstate imports of nursery stock with the goal of preventing the entry and limiting the spread of agricultural pests (Pauly, 2007). Additionally, imports of seeds and nursery stock from Europe to US nurseries were interrupted during World War I and II. Following American involvement in the world wars, US nurseries supplied seeds that were used in Victory Gardens, where families grew their own vegetables at home to reduce nonmilitary demand on food supplies, with demand for ornamentals declining accordingly (Burd, 2019). The post-war period, a time of resurgent economic globalization, was characterized by the proliferation of modern garden centers (where stock originates from wholesale nurseries) and the reinstatement of plant collection and global exchange via botanic gardens and nurseries (Reichard & White, 2001). Today, the United States supports a mature horticultural industry characterized by a mixture of regional and international trade (Hall et al., 2020; Knuth et al., 2021).

The phylogenetic structure of the US nursery flora may contain signatures of history, reflecting whether taxa were selected that were adapted or preadapted to local conditions or to cultivation more generally. Climate suitability can be reflected in the tendency of an assemblage to include taxa that are more related to one another than expected by chance (phylogenetically clustered) versus taxa that are less related than expected by chance (phylogenetically overdispersed). Because related species tend to retain their niche (phylogenetic niche conservatism, reviewed in Wiens & Graham, 2005), and because most plant lineages (i.e., angiosperms) evolved under warmer climates than today (Ramírez-Barahona et al., 2020), traits that confer adaptation to cold and temperature seasonality tend to be limited to a relatively small number of clades with ancestors that were able to pass through these ecological filters (Hawkins et al., 2014; Kerkhoff et al., 2014). Thus, plants in cold climates tend to be phylogenetically clustered groups of species (Qian et al., 2013). This is the explanation for the latitudinal gradient of phylogenetic clustering among native North American angiosperms, in which northern assemblages were increasingly clustered (Qian et al., 2013; Qian & Sandel, 2017). Aridity can act as an environmental filter for drought tolerance, which is also an evolutionarily conserved trait (Rueda et al., 2016). Environmental filtering for drought tolerance can explain why western North American angiosperm assemblages have been found to be more phylogenetically clustered than eastern assemblages (though high endemism in the West from mountain uplift is also influential, Qian & Sandel, 2017). In contrast to the native flora, patterns of phylogenetic

clustering in the nursery flora would be attributable to human selection for cold tolerance, drought tolerance, or filters typical of cultivated habitats (e.g., disturbance, Aronson et al., 2016) rather than millions of years of evolution and migration. Alternatively, phylogenetic overdispersion in the nursery flora would reflect the removal of barriers posed by biogeography and the environment via cultivation (Sandel & Tsirogiannis, 2016). Evidence for phylogenetic structure in present-day human-dominated landscapes is mixed; though some studies have found that spontaneously occurring plants in yards and cities were phylogenetically clustered (Knapp et al., 2012; Knapp et al., 2017), another study showed that cultivated plants in yards were more distantly related to one another than spontaneous plants in yards or plants in natural areas (Pearse et al., 2018).

We used a uniquely extensive database of historical ornamental plant trade lists to characterize the US nursery flora from the mid-18th to the mid-20th century. We split the flora by time periods, cultural regions, biomes, latitudinal bands, and longitudinal zones and estimated taxonomic α -diversity or species richness; phylogenetic α -diversity or the sum of phylogenetic differences among species; and phylogenetic structure or the average phylogenetic difference between species. We also estimated taxonomic and phylogenetic β -diversity to compare regional heterogeneity in species composition and phylogenetic diversity across time periods. We had five hypotheses regarding these patterns: (1) the taxonomic and phylogenetic diversity of the historical US nursery flora increased over time; (2) the proportion of alien species in the nursery flora increased over time and composition likewise shifted from being predominately European/Eurasian in origin to including species with different native origins; (3) the nursery flora was phylogenetically clustered; (4) the degree of phylogenetic clustering among nursery species varied regionally: it was higher in northern regions relative to southern regions and higher in western regions relative to eastern regions; and (5) the taxonomic and phylogenetic β -diversity of the nursery flora across regions exhibited a U-shaped pattern with time, with the lowest regional heterogeneity occurring between the 1870s and the 1890s.

2 | MATERIALS AND METHODS

The main data source for the analysis was *Restoring American Gardens* (Adams, 2004), a compilation of ornamental vascular plant taxa in US plant trade lists, including nursery catalogs, seed catalogs, and newspaper advertisements, for over 200 years, from 1719 (the earliest written commercial horticultural records in the United States) to 1946. Individual lists were too disparate to analyze independently: (i) different nurseries and seed companies had different capacities (relating to their setting, specialization in certain types of plants, leadership, funds, etc.), and (ii) the historical record was limited, meaning that not all relevant catalogs were available and some were incomplete (Adams, 2004). For these reasons, we pooled plant trade lists to form larger groupings representative of the nursery flora for regions and time periods. Regions (from Adams, 2004) were based on the

state in which the nursery, seed company, or seller was located, and were primarily cultural and historical in nature (see Table S1). The latitude and longitude for each list was estimated based on information in catalogs, newspaper advertisements, or other online sources. Lists were grouped by 4° latitudinal bands from 28° to 48° N (and two lists outside these bounds, at 27.45° and 48.45° N, were added to the lowest and highest bands, respectively), and into eastern, central, and western longitudinal zones based on the categorization of states by Qian and Sandel (2017). The biome in which each list was located was determined using maps from the WWF Terrestrial Ecoregions of the World project (Olson et al., 2001).

Taxon names were standardized with The Plant List (TPL) backbone (<https://www.theplantlist.org/> accessed on 2021-11-03) using the Taxonomic Name Resolution Service (TNRS) version 4.0 (Boyle et al., 2013). All unmatched taxa and taxa with warnings raised by TNRS were checked manually. Synonyms were consolidated, and all infraspecific taxa and cultivars were brought to the species level (cultivars without specific epithets were removed). The species list was then matched to the tips of a phylogeny assembled from a megaphylogeny of spermatophytes (Smith & Brown, 2018) and a phylogeny of pteridophytes (Zanne et al., 2014) using the GBOTB.extended tree in the ‘V.Phylo-maker’ R package (Jin & Qian, 2019). In the resulting phylogeny, 92% of all genera and 65% of all species were resolved. Unplaced genera or species were added as polytomies to the middle of the family or genus branch, respectively (scenario 3 in ‘V.Phylo-maker’). For the phylogenetic metrics used in this study, estimates using a phylogeny resolved to the genus level have been shown to be highly correlated with those resolved to the species level, and thus, phylogenetic metrics estimated using pruned megaphylogenies in which the vast majority of genera and many species are resolved are robust (Qian & Jin, 2021).

Data on species status as native to the state in which they were for sale (native), native to the continental United States but not the state in which they were for sale (adventive), or not native to the continental United States (alien) came from the Biota of North America Program (BONAP) list of the North American Vascular Flora (Kartesz 2018, <https://www.bonap.org/napa> accessed on 2021-11-03). Native range data came from the Kew Plants of the World database (<https://powo.science.kew.org> accessed on 2021-10-06), USDA Germplasm Resources Information Network database (<https://npgsweb.ars-grin.gov/gringlobal/search> accessed on 2021-11-06), Global Compositae Database (Compositae Working Group 2021, <https://www.compositae.org> accessed on 2021-09-10), and the IUCN Red List Database (<https://www.iucnredlist.org> accessed on 2021-07-30), and consisted of the Biodiversity Information Standards (TDWG, Brummitt, 2001) level-3 regions where species are native. Native ranges were then categorized by TDWG level-1 continents, including ranges that consisted of multiple continents: Americas included Northern and Southern America, Eurasia included Europe and Asia-Temperate, and Holarctic included Europe, Asia-Temperate, and Northern America. Species were considered native to a continent if over 80% of their native TDWG level-3 regions were contained within a given TDWG level-1 continent, and if not, to a multiple-continent region. Taxa that did not fulfill these criteria were considered global if

they were native to five or more TDWG level-1 continents, and unclassified otherwise. Taxon names in all databases were standardized using the TPL backbone to enable harmonization across datasets.

Metrics of taxonomic and phylogenetic α -diversity and structure were estimated in quarter-century time periods from 1775 to 1946 (all lists pre-1775 were grouped into a single time period and there were no lists between 1946 and 1949), different regions, different biomes, latitudinal bands, and longitudinal zones. Taxonomic diversity was measured as species richness and PD was measured with Faith's PD metric, which is the sum of branch lengths in the assemblage (Faith, 1992). Phylogenetic structure was calculated as the mean pairwise distance (MPD) metric, which is the mean phylogenetic distance (i.e., branch length) of species pairs in an assemblage (Webb, 2000). PD, MPD, and Unifrac (see below) were calculated using the ‘Phylo-Measures’ R package (Tsirogiannis & Sandel, 2017).

To determine the influence of the number of plant trade lists pooled in each grouping (time period, region, biome, latitudinal band, or longitudinal zone), we also subsampled lists to calculate rarefied taxonomic and phylogenetic α -diversity metrics. We randomly selected a subset of lists from each group level equal to the minimum number of lists found in any group level. We repeated this process 1000 times to generate a distribution of the rarefied metric and calculated the mean and quantiles of this distribution.

Observed values of PD and MPD were compared with null expectations, and the deviations from expectation (observed – expected) and *P*-values from two-tailed randomization quantile tests were calculated from null distributions with 999 iterations. Null distributions were generated by randomizing the labels for the tips of the phylogenetic tree using the “tipShuffle” function in the ‘picante’ R package (Kembel et al., 2010), which holds constant the species richness and occupancy rates within assemblages. Estimates of deviations from expectation effectively remove dependence on species richness (Kalusová et al., 2021). Deviations from expectation for PD (Δ PD) represent a surplus or deficit of PD in the observed assemblage relative to an assemblage with identical species richness but randomized phylogenetic relationships. Deviations from expectation for MPD (Δ MPD) represent patterns of phylogenetic clustering and overdispersion, in which positive values (larger distances than expected) indicate overdispersion and negative values (smaller distances than expected) indicate clustering.

The heterogeneity of diversity in different regions was measured in each time period as β -diversity. Taxonomic β -diversity was measured as Jaccard dissimilarity, which is a measure of the fraction of species that are unique between two assemblages. Jaccard dissimilarity was further decomposed into β -diversity from species turnover, that is, species replacement across assemblages, versus nestedness, that is, species composition in species-poor assemblages as a subset of species-rich assemblages. Jaccard dissimilarity and its components were measured using the ‘betapart’ R package (Baselga et al., 2021). Phylogenetic β -diversity was measured with the UniFrac metric, which is the unique fraction of branch lengths between two assemblages (analogous to PD, Lozupone & Knight, 2005), and the D_{pw} metric, which is the mean phylogenetic distance between species pairs in two assemblages (analogous to MPD). Unifrac is sensitive to turnover

at shallow branching levels, while D_{pw} is reflective of turnover at all phylogenetic scales (Swenson, 2011).

3 | RESULTS

There were 5098 unique ornamental vascular plant species available from 319 US plant trade lists in the period from 1719 to 1946 (hereafter referred to as the US nursery flora). Lists were available from all present-day continental US states except Nevada and Wyoming. Before 1800, lists came from the Mid-Atlantic, New England, and the South (Table 1 and Figure 1a). The majority of lists from this early period were nursery and seed catalogs from the Mid-Atlantic (several listing hundreds of species), while the remainder were newspaper advertisements from the South and New England (each listing few species). After 1800, nearly all lists were nursery or seed catalogs, each with highly variable numbers of species. Lists from the Great Lakes were available from the 1830s onward. After this, a general westward trend was apparent, and all regions had lists by the mid-to-late 19th century (Figure 1a). The number of lists from the Great Plains and West was initially small relative to other regions, but increased after 1875 (Table 1).

3.1 | Taxonomic diversity of the nursery flora

Species richness of the US nursery flora increased steadily before peaking in the early 20th century (Figure 1b). Before 1800, the trend was a consequence of increasing richness within plant trade lists, while after 1800, it was a consequence of the increasing numbers of lists, as rarefied richness (i.e., richness assuming equal numbers of lists in each time period) plateaued by 1800 and dipped slightly in the mid-19th century. The Mid-Atlantic had the highest richness among regions until the mid-19th century, when it declined to a level comparable with other regions (Figure 1c). Richness in the South was initially very low but increased continually until peaking, surpassing other regions, in the period from 1900 to 1924. In the West, richness continually increased until it surpassed other regions in the final quarter century. Richness remained relatively steady in New England, the Great Lakes, and the Great Plains regions.

Across all years, the nursery flora in the Mid-Atlantic had the highest species richness and the Great Plains had the lowest

(Figure 2a). However, the rarefied richness of the West was relatively high (comparable with the Mid-Atlantic), and the rarefied richness of the Great Lakes was relatively low (comparable with the Great Plains). The richness of the nursery flora was higher at middle latitudes, but this was because there were fewer lists from the highest and lowest latitude bands, as rarefied richness did not show a consistent pattern with latitude (Figure 2b). The eastern longitudinal zone had the highest richness because it contained the majority of lists, as the western and eastern zones had comparable rarefied richnesses (Figure 2c). Similarly, the temperate broadleaf forest biome, which encompasses the northeast United States, had the highest overall richness, but the Mediterranean biome had the highest rarefied richness (Figure 2d).

The proportion of native species in the nursery flora was 39% pre-1775, 70% in the period from 1775 to 1799, and thereafter declined considerably to about 30% by the mid-19th century (Figure 1d). A similar proportion of the US nursery flora was adventive (approximately 13%) in all except the earliest time period, in which it was 4%. Representation of European and Eurasian species in the nursery flora increased until the mid-19th century, and representation from additional regions, particularly temperate Asia, Southern America, the Americas, and Africa, became more prevalent for the rest of the time series (Figure 1d). The proportion of the flora from temperate Asia was initially small, but it became the largest donor region of alien flora by the early 20th century (Figure 1d).

Some elements of the nursery flora were consistent across regions; species from the Asteraceae, Rosaceae, and Fabaceae families constituted large proportions of the flora in all regions (Figure S1). Some features were regionally distinctive; for example, Campanulaceae had large representation only in New England, Magnoliaceae only in the South, and Myrtaceae only in the West (Figure S1a). The eight most common families for each time period revealed trends: Ericaceae, Fagaceae, Sapindaceae, and Betulaceae were initially popular but soon faded, while Caprifoliaceae, Brassicaceae, and Oleaceae were only popular in later time periods (Figure S1b). Some species remained popular throughout, including *Alcea rosea*, *Dianthus barbatus*, and *Dianthus caryophyllus* (Table S2). *Hyacinthus orientalis*, *Silene chalconica*, and *Lobelia cardinalis* tended to be more popular in the early 19th century, while *Lamprocapnos spectabilis*, *Thuja occidentalis*, and *Leucanthemum × superbum* were more popular from the late 19th into the 20th century (Table S2).

TABLE 1 Number of plant trade lists from each US region, grouped by time period

Region	Pre-1775	1775–1799	1800–1824	1825–1849	1850–1874	1875–1899	1900–1924	1925–1946
New England	3			14	15	20	6	5
Mid-Atlantic	1	5	10	17	16	7	8	6
South	2	3	2	1	16	15	12	6
Great Lakes				6	23	19	12	10
Great Plains					6	13	8	5
West					2	7	10	8

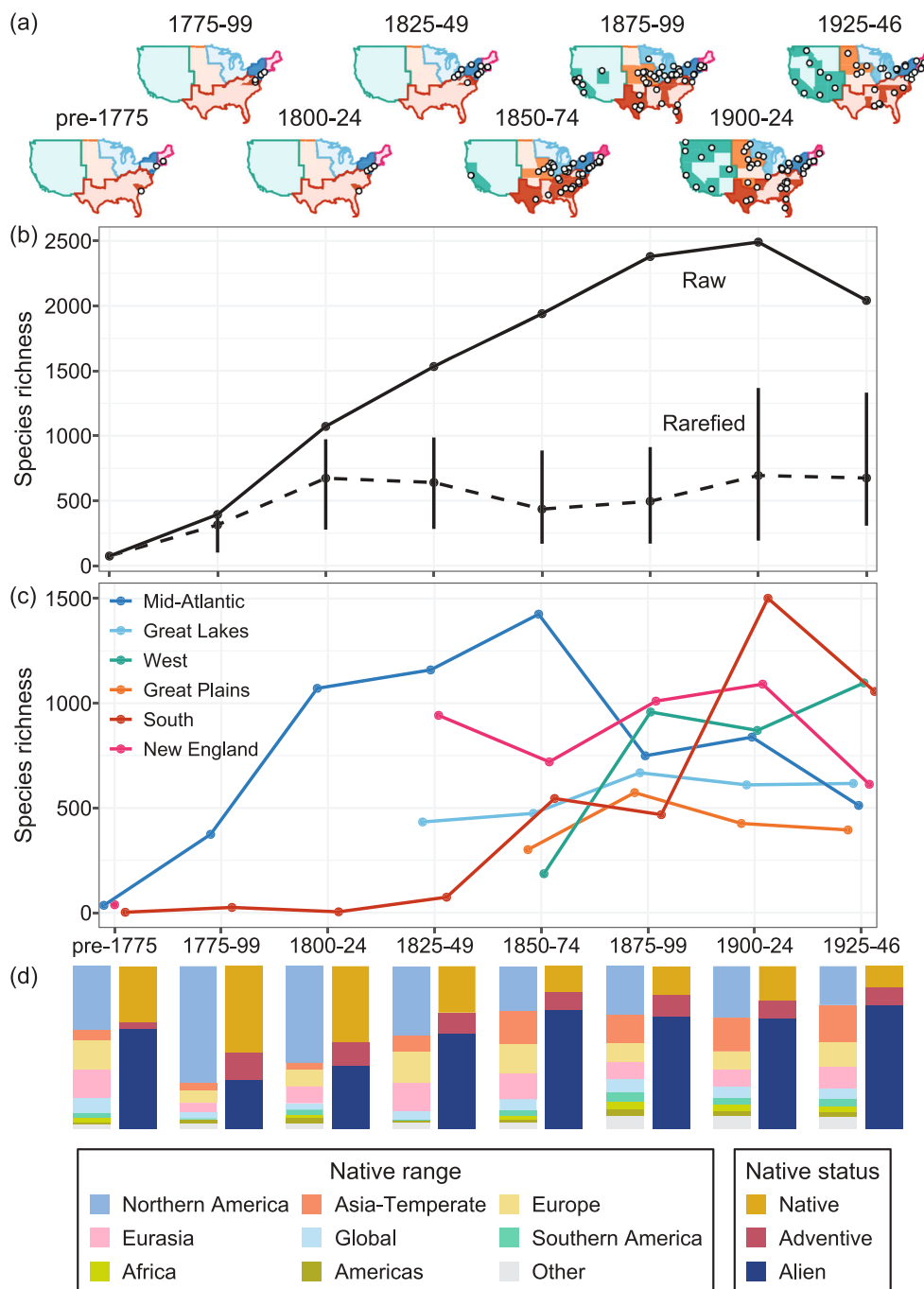


FIGURE 1 Composition of the historical US ornamental nursery flora in quarter-century time periods. (a) Locations of nurseries are shown as white points, and states with nurseries are highlighted with present-day boundaries. (b) Taxonomic α -diversity, measured as raw species richness (solid line) and rarefied species richness (dashed line). For rarefied richness, the number of plant trade lists in each time period was subsampled to equal the minimum number of lists in any time period (six), and error bars are .025 and .975 quantiles from the random rarefaction distribution. (c) Regional species richness of the nursery flora. (d) Breakdown of native regions (bars on left; “Other” includes Australasia, Asia-Tropical, Holarctic, Pacific, and unclassified) and native status (bars on right) for the nursery flora in each time period. The period from 1719 to 1774 is combined in the “pre-1775” category

3.2 | Phylogenetic diversity of the nursery flora

Like richness, PD increased to a peak over time and rarefied PD plateaued after 1800 with a dip in the mid-19th century (Figure S2). However, Δ PD was negative at all times except the period from 1900 to 1924 ($P = .311$;

Table S3 and Figure 3a), meaning that the PD observed in a given region or time period was lower than expected if phylogenetic relationships were randomized within the nursery flora as a whole. Additionally, Δ PD had a U-shaped relationship with time, in which the lowest value occurred in the mid-19th century and was higher both

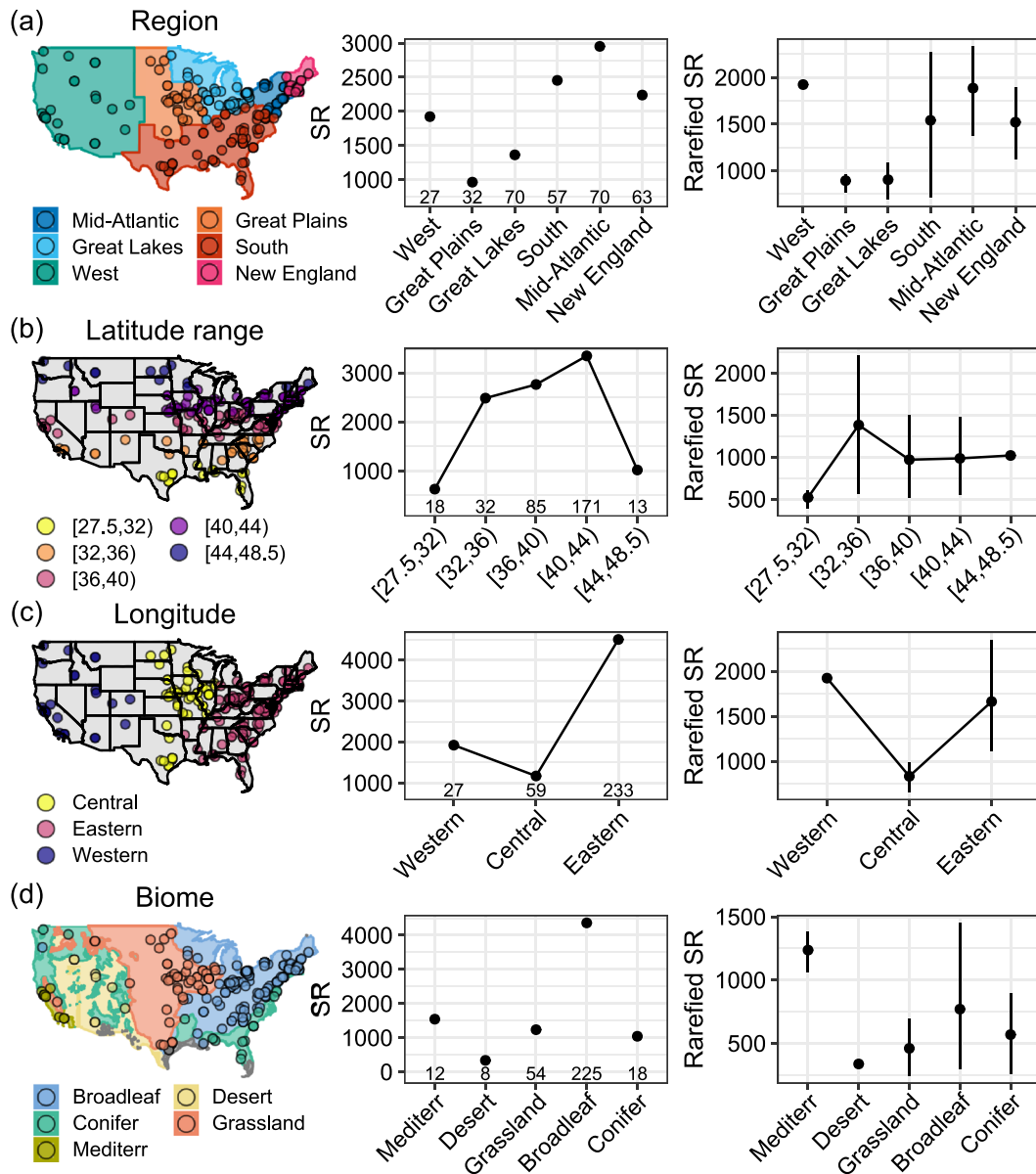


FIGURE 2 Taxonomic α -diversity of the US nursery flora, measured as raw species richness (SR, middle column) and rarefied SR (right column). Species were grouped by (a) region, (b) latitudinal band, (c) longitudinal zone, and (d) biome. Locations of plant trade lists are shown on maps of the continental United States in the left column. To calculate rarefied SR, the number of lists in each group level was subsampled to equal the minimum number of lists in any group level. Numbers of lists are shown along the x-axis of raw SR plots. In rarefied SR plots, points are means and error bars are .025 and .975 quantiles from the random rarefaction distribution (n.b., the group level with the minimum number of lists has no error bars). Mediterr = Mediterranean forests, woodlands, and scrub; Grassland = temperate grasslands, savannas, and shrubland; Broadleaf = temperate broadleaf and mixed forests; Conifer = temperate coniferous forests

before and after this period, though it decreased in the final time period. Initially, Δ PD among regions was disparate; the South had the highest Δ PD, and New England and the Mid-Atlantic had the lowest Δ PD, but all regions converged on a similar Δ PD in the final time period (Figure 3b). These patterns were not strongly influenced by variation in the number of plant trade lists across regions and time periods (i.e., rarefied Δ PD showed similar patterns; Figure S3).

Across all time periods, the South was the only region where the PD of the nursery flora was not lower than expected (Δ PD was not negative, $P = .763$; Figure 3c). At higher latitudes, the deficit between

observed and expected PD was higher than at lower latitudes (more negative Δ PD at higher latitudes; Figure 3e). The lowest PD deficit occurred in the eastern longitudinal zone (Figure 3f). Again, this was because the eastern zone included the most lists, and the rarefied PD deficit was lowest in the western zone (Figure S3). The temperate coniferous forest and Mediterranean nursery floras had the lowest PD deficits among biomes (Figures 3d and S3). The highest PD deficit among biomes was the temperate grassland biome, though the temperate broadleaf forest biome had comparably low rarefied Δ PD (Figure S3).

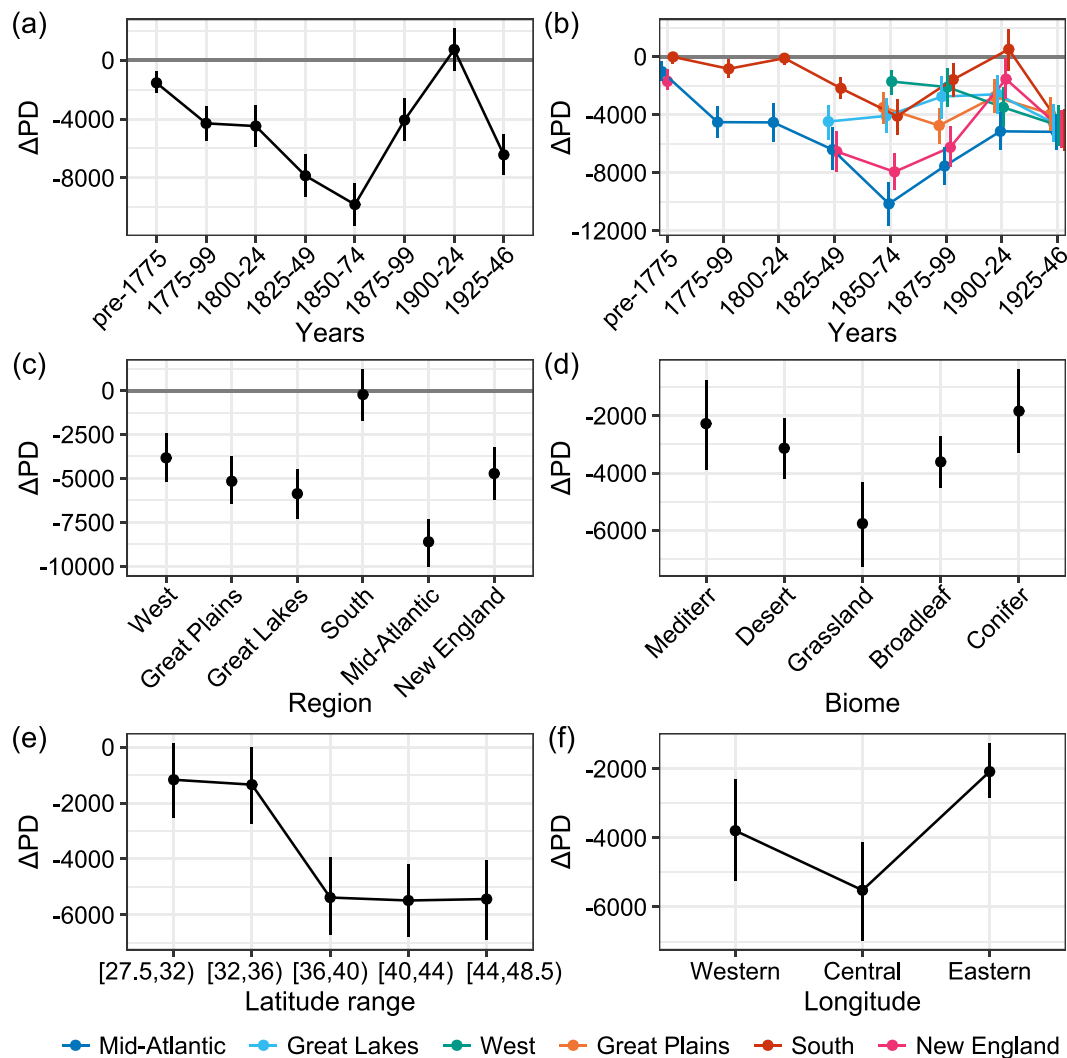


FIGURE 3 Phylogenetic α -diversity of the US nursery flora, measured as the difference between observed and expected Faith's PD (Δ PD). Species were grouped by (a) time period, (b) region and time period, (c) region, (d) biome, (e) latitudinal band, and (f) longitudinal zone. Positive values of Δ PD indicate a surplus of PD relative to an equal-sized community with randomized phylogenetic relationships and negative values indicate a deficit. Points are means, and error bars are .025 and .975 quantiles of the null distribution from randomization tests

3.3 | The phylogenetic structure of the nursery flora

In early time periods, Δ MPPD decreased, indicating that the nursery flora became increasingly phylogenetically clustered (Figure 4a). During the 19th century, the nursery flora went from phylogenetically clustered (having a negative Δ MPPD, $P(1800-1824) = .001$) to phylogenetically overdispersed (having a positive Δ MPPD, $P(1875-1899) = .001$), and then back to phylogenetically clustered in the final time period ($P(1925-1946) = .002$; Figure 4a and Table S3).

As a whole, the nursery flora of the West and the South were phylogenetically overdispersed ($P(\text{West}) = .037$, $P(\text{South}) = .001$; Figure 4b and Table S3). There was a negative relationship between latitude and Δ MPPD that was apparent for all except the highest latitude band (Figure 4d). The nursery flora in the western longitudinal

zone was marginally overdispersed, and the central zone was marginally clustered ($P(\text{western}) = .047$, $P(\text{central}) = .059$; Figure 4e and Table S3). The Mediterranean and temperate coniferous forest biomes had phylogenetically overdispersed nursery floras ($P(\text{Mediterranean}) = .002$, $P(\text{temp. coniferous}) = .008$), while temperate broadleaf forest and desert biome floras were phylogenetically clustered ($P(\text{temp. broadleaf}) = .008$, $P(\text{desert}) = .002$; Figure 4d and Table S3). Rarefied Δ MPPD showed the same general patterns with higher variability (Figure S4).

3.4 | Regional heterogeneity of the nursery flora over time

Taxonomic β -diversity measured as Jaccard dissimilarity tended to decline over time, meaning that the regional nursery floras became

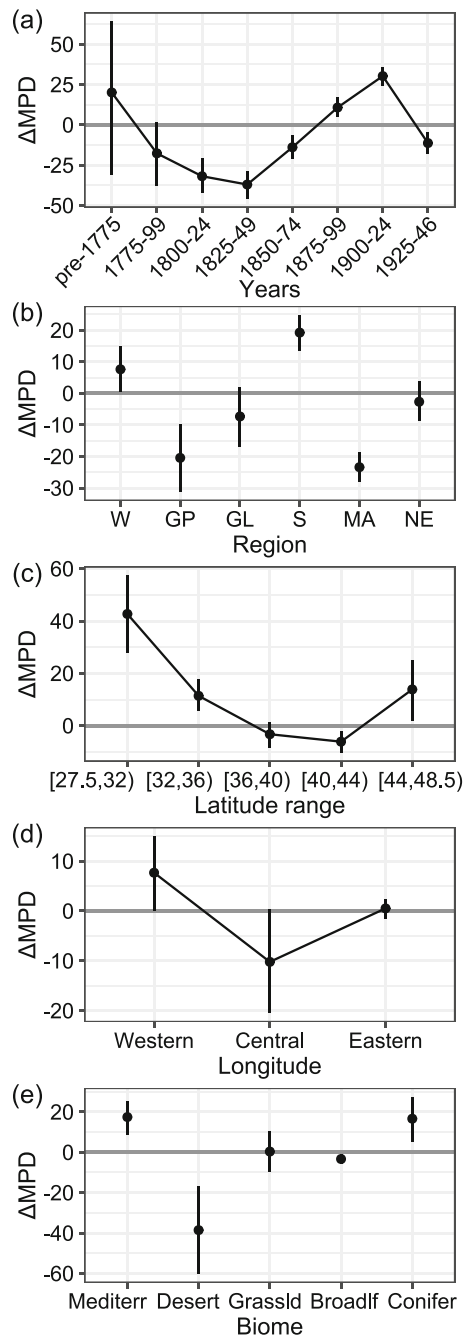


FIGURE 4 Phylogenetic structure of the US nursery flora, measured as the difference between observed and expected mean pairwise distance (ΔMPD). Species were grouped by (a) time period, (b) region, (c) latitudinal band, (d) longitudinal zone, and (e) biome. Negative values of ΔMPD indicate clustering and positive values indicate overdispersion. Points are means and error bars are .025 and .975 quantiles of the null distribution from randomization tests. Regions are abbreviated as initials

more similar to one another from one time period to the next (Figure 5a). In the early 19th century, this was attributable both to an increase in the number of species available (i.e., nestedness had a considerable influence) and species turnover, but the influence of species

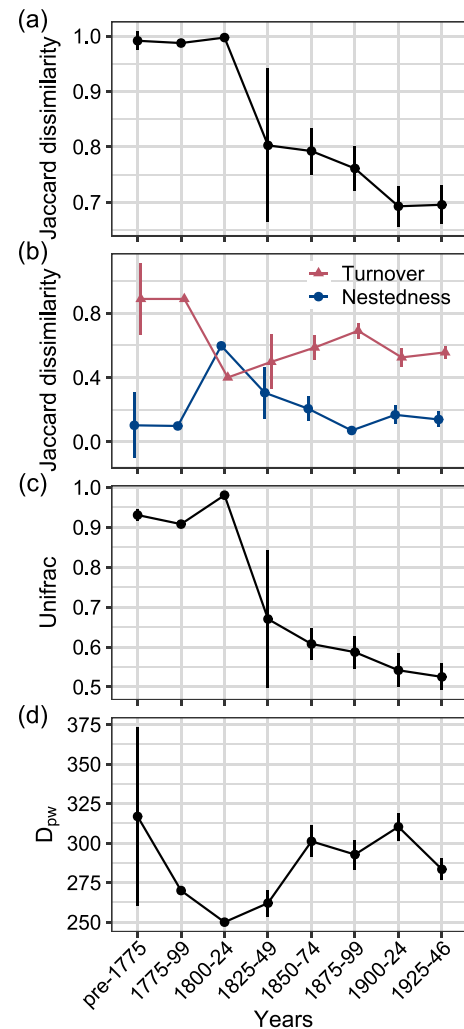


FIGURE 5 Taxonomic and phylogenetic regional β -diversity of the US nursery flora, grouped by time period. Taxonomic β -diversity was measured as (a) Jaccard dissimilarity and (b) fractional Jaccard dissimilarity attributable to species turnover (red triangles) and nestedness (blue circles). Phylogenetic β -diversity was measured using (c) Unifrac and (d) D_{pw} . Points and error bars are means \pm 2 SE of pairwise regional β -diversity estimates (n.b., estimates from 1775 to 1799 and 1800 to 1824 have no error bars because they each include only one region-pair)

turnover came to dominate with time and was particularly dominant during the period from 1875 to 1899 (Figure 5b). Phylogenetic β -diversity measured as Unifrac also tended to decrease with time (Figure 5c). In contrast, phylogenetic β -diversity measured as D_{pw} , which is more reflective of deeper branching than Unifrac, tended to increase through the 19th century and peaked in the period from 1900 to 1924 (Figure 5d).

Early in the history of the US nursery industry, the nursery flora from other regions differed strongly from the South, that is, had high pairwise β -diversities, but became more similar to the South over time (with the exception of the Great Plains; Figure S5). Though the West did not have nurseries until the mid-19th century, a similar

pattern was observed; initially, most regions differed strongly from the West, and differences tended to decrease with time (Figure S5). The nursery floras of the Mid-Atlantic, New England, and the Great Lakes tended to be relatively similar to one another (though the Mid-Atlantic and New England differed strongly pre-1775), and the nursery floras of the Great Lakes and Great Plains were consistently similar (Figure S5).

4 | DISCUSSION

The taxonomic and phylogenetic diversity of the US ornamental nursery flora increased continually from the 18th to the early 20th century. On the whole, the mid-to-late 19th century was a period with diverse horticultural resources in the United States. This pattern is consistent with the increase in number and the westward proliferation of nurseries and seed houses (Adams, 1998), as well as the increasingly globalized importation of plant species (Holway, 2018; Williams et al., 2020). However, the early-to-mid 19th century, a time of booming trade and connectivity for the nursery industry (Burd, 2019), was characterized by a trough in standardized PD and pairwise phylogenetic distances, as the phylogenetic scope of nursery offerings was relatively narrow and new species were related to those already available. During the same time period, the species richness within nurseries plateaued and dipped slightly, which could reflect the phenomenon in which entrepreneurs, inspired by the boom, established nurseries despite having little horticultural knowledge (and thus began with relatively few resources, Lyon-Jenness, 2004). Diversity reached a peak in the 20th century concurrent with the first wave of US-sponsored plant collections, and indeed, 70 species that were first listed after 1911 in our dataset were known to have been introduced by the USDA Office of Foreign Seed and Plant Introduction between 1912 and 1942 (Office of Foreign Seed and Plant Introduction, 1912). Diversity actually decreased in the final period between 1925 and 1946, which may be attributable to some combination of interrupted trade and shifted focus away from ornamentals during the world wars, and the regulation of international and interstate nursery trade in the early 20th century (Pauly, 2007). After the period covered by our study, it is likely that the diversity of the US nursery flora once again increased; a study of the nursery flora in Los Angeles, California showed a slight decrease in richness from the period 1900–1929 to 1930–1959 (which aligns with our findings) and the largest increase in richness in the period from 1990–2011 (Pincetl et al., 2013). This increase is probably not limited to Los Angeles, as global plant collection and importation mediated by botanical gardens and nurseries in the United States remains active (Reichard & White, 2001). Trade restrictions became less of a barrier once the strictest limitations of Quarantine 37 were relaxed during the 1930s (Liebhold & Griffin, 2016), excepting particular species or regions based on pest risk assessment (Simberloff, 2005).

Regionally, the Mid-Atlantic had the most diverse nursery flora until the mid-19th century, as expected given that the first US nurseries and seed houses were established there. However, the West

and the South surpassed other regions in the 20th century. This switch from domination by the Mid-Atlantic to domination by the West and South has not shifted after the 1940s, as California, Florida, and Oregon were the states with the most horticultural operations and the highest nursery stock sales in 2019 (USDA-NASS, 2020).

The large proportion of native species in the nursery flora during the late 18th and early 19th centuries relates to the cultivation of native North American plants for the purpose of sending to Europe (Parrish, 2006), a number of which became popular ornamentals. For example, Bernard M'Mahon's Philadelphia seed house, one of the first in the United States, specialized in native plants and 70% of the stock in their 1804 catalog was native. The raw number of available native species increased only slightly over time, 417 native species were available from 1800 to 1824 and 579 were available from 1900 to 1924. Of these, 272 species were shared between the two time periods, including many species that were initially sent by the plant collector John Bartram to contacts in England in the 18th century, for example, *Acer saccharum*, *Panax quinquefolius*, and *Rhododendron maximum* (Barnhart, 1930). However, of all species in the historical US nursery flora, 3587 (70%) were alien to the continental United States, a substantial number when compared with the approximately 18,000 species that comprise the native vascular flora (Qian & Ricklefs, 1999). The proportion of alien species in the nursery flora increased over time, as expected, which can be attributed to several factors, including trade relationships between US and European nurserymen, collections funded by European horticultural societies and nurseries (Holway, 2018), and collections funded by US horticultural institutions and the USDA (Williams et al., 2020). After the period covered by our study, the number of alien species in the US nursery flora likely continued increasing; for example, 91% of tree species sold in southern Californian nurseries during the 20th and early 21st century were alien to California (Pincetl et al., 2013), and 77% of plant species sold in a nursery and 66% of species cultivated in yards in Minneapolis–Saint Paul, Minnesota, were alien (Cavender-Bares et al., 2020). Present-day cultivated landscapes in other regions vary in composition: Similar to the United States, 70% of species cultivated in yards in five cities in the United Kingdom were alien (Loram et al., 2008), while only 23% of cultivated plants in 18 Chinese cities were alien (Zhu et al., 2019). Some alien species in the historical US nursery flora have since altered native ecosystems; two species that are currently invasive in the US were among the most common species available in historical nurseries, including *Lonicera japonica* (available in 78 nurseries after the first record in 1832) and *Berberis thunbergii* (available in 46 nurseries after 1859; Table S3).

As predicted, the native origins of alien species shifted from being predominately European/Eurasian (50% of the nursery flora from 1800 to 1824) to including other global regions. In fact, beginning in 1850, plants native to temperate Asia composed the largest percentage of the alien nursery flora. The increased representation from temperate Asia reflects the popularity of East Asian plants in US horticulture (Olsen, 2013) and can be explained by the onset of botanical collections in East Asia during the 1840s (Holway, 2018).

Though a smaller proportion of the alien nursery flora, plants native to Central America, South America, and Africa became increasingly available over time. Notably, the nursery flora in the West had a much higher proportion of species native to Australasia (15% in the West compared with about 2% in other regions). California, where the majority of western nurseries were located, contains the only Mediterranean climate zone in the United States. In this study, 17 *Acacia* species and 45 *Eucalyptus* species native to Australasia were sold in Californian nurseries. These genera, which have been especially important in Californian horticulture (Butterfield, 1935, 1938), are recognized as problematic invaders in Mediterranean zones worldwide (Badalamenti et al., 2018; Ritter & Yost, 2009; Souza-Alonso et al., 2017).

The nursery flora was variably phylogenetically clustered or overdispersed depending on the time period and region. From the late 18th to the mid-19th century, the nursery flora was phylogenetically clustered, and the structure switched to phylogenetic overdispersion coincidental with the peak in diversity. The phylogenetic clustering that we observed is consistent with human selection for species desirable for cultivation; a recent study showed that seed plants introduced for cultivation in southern Africa were a phylogenetically clustered subset of the global seed plant flora (Omer et al., 2021). The extent to which this pattern is attributable to human selection of phylogenetically clustered traits, as opposed to human selection for species with particular native origins and habitat associations (which vary in phylogenetic structure, Kalusová et al., 2021), depends on the traits being conserved rather than labile (Cavender-Bares et al., 2004). Though not well characterized, traits associated with cultivation may be labile; domestication had a minimal phylogenetic signal in a study of angiosperms (Milla et al., 2018), and showiness, which is related to flower/fruit size and color, is associated with convergent pollination and dispersal syndromes (Fenster et al., 2004). The overdispersion we observed at later time periods may result from the addition of distantly related species to the nursery flora (thus overcoming biogeographic barriers, Sandel & Tsirogianis, 2016). Generally, we found that the nursery floras in the West and the South were phylogenetically overdispersed, while other regions had clustered floras. In a study of naturalized aliens in the United States and Canada, assemblages in the southeast were phylogenetically overdispersed, while assemblages in northern regions were phylogenetically clustered (Qian & Sandel, 2021). Because we found similar regional patterns in the US nursery flora, our results suggest that this phylogenetic structure was already present in the pool of introduced species before naturalization took place (the nursery flora being a proxy of the introduced species pool).

We found a pattern of increased phylogenetic clustering at more northern latitudes, as hypothesized, for all except the most northern latitudinal band. In our study, the inferred pattern-generating mechanism does not involve the evolution of cold tolerance and migration of cold-tolerant species (as for native angiosperms in the United States and Canada, Qian et al., 2013; Qian & Sandel, 2017), but rather, human selection for cultivated plants that are cold-tolerant. Similarly, a study of 72 present-day globally distributed urban

floras found that the taxonomic composition of cultivated plant assemblages was closely associated with temperature (though phylogenetic structure was not assessed, Kendal et al., 2012).

We did not observe a pattern of increased phylogenetic clustering in the western US relative to the eastern United States, as has been observed for the native angiosperm flora (Qian & Sandel, 2017). In fact, the opposite pattern was observed; the nursery flora in the West was phylogenetically overdispersed, while central and eastern regions tended to be clustered. While adaptation to Mediterranean climates, characterized by hot dry summers, was a noted influence in Californian horticulture (Pauly, 2007), species were selected from entirely new global regions (i.e., Australasia) likely contributing more to phylogenetic overdispersion. Also, the irrigation of cultivated landscapes has been practiced in the western United States since canal irrigation systems were developed by indigenous people in the second century (Doolittle, 1992), and became ubiquitous following extensive development by private corporations and the federal government in the late 19th and early 20th century (Akhter & Ormerod, 2015). In the present-day Southwest, mesic yards are common and desirable (e.g., Larson et al., 2009). Thus, irrigation may have reduced the potential for drought to act as a filter for cultivated species. Nevertheless, the nursery flora in the desert biome was the most phylogenetically clustered among biomes, which is consistent with environmental filtering for drought, and it included a number of species that are today recognized as xeriscape plants, for example, *Eschscholzia californica*, *Portulaca grandiflora*, and *Pinus mugo*.

Regional heterogeneity in taxonomic and phylogenetic composition tended to decrease over time, meaning that the regional nursery floras became more similar to one another. Increasing homogenization could be attributed to developments in transportation infrastructure, increased regulation of international imports, and interrupted international trade during the world wars (Pauly, 2007). Today, cultivated plant assemblages in US urban yards are relatively homogenized, that is, more similar to one another than to analogous natural areas (Pearse et al., 2018). Present-day homogenization could therefore be a result of the historical homogenization of the US nursery flora. In our study, the nursery floras of the Mid-Atlantic, New England, and Great Lakes were particularly similar to one another, and the nursery flora of the Great Lakes was initially a nested subset of the Mid-Atlantic. These patterns are in accordance with well-established northeastern nurseries providing stock for newly establishing nurseries in the Great Lakes region (Adams, 1998; Burd, 2019). In contrast, the South and the West maintained more independent nursery floras. Consistent with the regional patterns we observed in the historical cultivated flora, a recent study found that cultivated alien plants in southern and southwestern US cities contributed more to phylogenetic differentiation in yards, while cultivated alien plants in northern cities contributed to homogenization (Padullés Cubino et al., 2019). Despite increasing homogenization of taxonomic and phylogenetic composition in the historical US nursery flora, species turnover across regions remained relatively high and the regional heterogeneity of PD weighted by deeper branching patterns (D_{pw}) continued increasing into the 20th century.

5 | CONCLUSIONS

The nursery flora of a region has a direct influence on the composition of urban plant communities by creating the habitat supporting humans, birds, insects, and other organisms (Avolio et al., 2018). The ability of human-dominated landscapes to provide these services is dependent on the plants present there, and the species cultivated in present-day US urban yards have been found to be diverse, predominantly alien, and homogeneous in composition (e.g., Avolio et al., 2020; Cavender-Bares et al., 2020; Pearse et al., 2018). In this study, we show an increase in the taxonomic and phylogenetic diversity of the ornamental US nursery flora from the beginning of the US nursery industry in the 18th century to the early 20th century, occurring in step with the proliferation of nurseries throughout the country and the addition of species to nursery offerings via plant collection and trade. The increase in diversity was not continual, however; there was a trough in standardized PD during the mid-19th century, and there was a decrease in taxonomic and phylogenetic diversity in the mid-20th century. There was also an increase in the number and proportion of alien species available over time, and a shift in alien species being of predominantly European/Eurasian origin to including multiple global origins, with temperate Asia having the highest representation. The phylogenetic structure of the nursery flora varied regionally, with phylogenetically clustered communities in the Northeast and phylogenetically overdispersed communities in the Southeast and West, which may reflect human selection for related groups of species (potentially because they share desirable traits, e.g., cold tolerance) and the addition of species from new biogeographic regions, respectively. Last, the regional nursery floras, which were initially relatively distinct, became taxonomically and phylogenetically homogenized over time. The patterns of α - and β -diversity that have been observed in present-day urban areas have a basis in history, and patterns of phylogenetic structure and homogenization observed among naturalized alien plants today were already present in historical nursery offerings.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

NLK and MvK designed the study; DWA, NLK, and MvK collected the data; NLK performed the data analysis, interpreted the results, and wrote the first draft of the manuscript with input from MvK. NLK, MvK, and DWA edited the manuscript.

DATA AVAILABILITY STATEMENT

The code used for the analysis is publicly available in figshare at <https://doi.org/10.6084/m9.figshare.19899415>. The US nursery flora data are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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