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Research Article

Naturalization of ornamental plants in the United States depends on cultivation and historical land cover context

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Cultivation by humans is the primary mode of introduction for naturalized plants and an important driver of naturalization, a critical step in the invasion process. Historical records of cultivated plants can represent introduced species pools and propagule pressure, allowing for tests of how species' traits and environmental context affect naturalization while accounting for human influence. Ruderal traits, which generally promote naturalization, may not be universally advantageous across closed versus open landscapes (forest versus grassland/shrubland) or different agricultural land use conversion types, though such context dependence has not yet been demonstrated at a broad scale. We analyzed the naturalization of 3949 cultivated ornamental non-native plant taxa that were for sale in nursery and seed catalogs in the conterminous United States during a period over 200 years to test for context dependence between traits associated with ruderality (short lifespan, shade intolerance, and self-compatibility) and estimates of historical forest/grassland cover and agricultural land use change. We found that present-day naturalization was closely tied to longer cultivation duration and greater cultivation extent. While ruderal traits tended to promote naturalization, perennial lifespan and shade tolerance favored naturalization in US states with higher forest cover, which is consistent with an alternative invasion strategy in closed-canopy systems. Land use conversion to pasture and succession of abandoned agricultural land promoted naturalization of disturbance-adapted plants in both forest and grassland landscapes. Our results emphasize the central role of cultivation in plant invasion and

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provide spatially and temporally extensive evidence that, while ruderal traits are important predictors of naturalization, they are dependent on the landscape context into which plants are introduced. Our work demonstrates the importance of integrating historical cultivation and land use/cover data for a nuanced understanding of the ecological factors that drive plant naturalization.

Keywords: biological invasion, context dependence, forest/grassland landscapes, land use history, ornamental plants, ruderal traits

Introduction

Cultivated plants, which are planted and maintained by humans for food, medicine, materials, ornamental purposes, or other uses, are important features of human-inhabited landscapes, which have covered an increasingly large part of Earth's surface over the past several thousand years (Ellis et al. 2021). As long as human migration and exchange networks have existed, so too has the desire to cultivate plants from elsewhere, often distantly so (e.g. seeds were exchanged between societies in India and Africa by ca 2000 BCE, Fuller et al. 2011). Non-native plants introduced for cultivation may, however, reproduce and persist in the new habitat independently of human aid, that is, they may become naturalized (sensu Richardson et al. 2000). In fact, cultivation, particularly for ornamental horticulture, is the primary mode of introduction for naturalized plants (Reichard and White 2001, Mack and Erneberg 2002, Lehan et al. 2013, van Kleunen et al. 2018). Naturalized plants can change the composition of resident communities and ecosystems, and some may become invasive, meaning they can spread widely into new habitats and have the potential to negatively impact native biodiversity and ecosystem functioning (Pyšek et al. 2012).

Historical records of cultivation show which species were introduced into a particular region, making it possible to test hypotheses about why particular non-native plants naturalize or fail to naturalize there. First, introduction and subsequent cultivation can influence which species naturalize, as longer, more extensive cultivation history can promote naturalization (Blackburn et al. 2020, Pyšek et al. 2020). Species that have been cultivated somewhere for a longer time have more opportunities to naturalize (Pyšek et al. 2015), and species cultivated in more places are more likely to persist (Mack 2000, Minton and Mack 2010) and disperse more propagules in the landscape (Pemberton and Liu 2009, Pyšek et al. 2009), increasing the probability of naturalization. Despite the importance of accounting for cultivation history, few studies have included historical records of species' introduction and cultivation in analyses of invasion (Dehnen-Schmutz et al. 2007, Hanspach et al. 2008, Diez et al. 2009, Kinlock et al. 2022b).

Environmental context also influences which species naturalize. Disturbance, an integral aspect of land use, promotes naturalization generally and can favor naturalization of species with distinct traits. Disturbance creates open physical and niche space with discordant abiotic and biotic conditions, which can then be colonized (Davis et al. 2000, Lake and Leishman 2004, Lembrechts et al. 2016). For plants, adaptation to disturbance involves a suite of traits that allow species to quickly grow and reproduce before the next round of disturbance, such as rapid growth rate, short lifespan, short-lived leaves, high resource allocation to reproduction, and seed bank persistence (Grime 1977, Pierce et al. 2017). Plants that are well-adapted to disturbance, that is, ruderal plants, are more likely to be capable of selfing (Munoz et al. 2016), as self-compatibility provides reproductive assurance despite mate limitation and a selective advantage for individuals adapted to temporary habitats (Baker 1955, Stebbins 1957). Shade intolerance is also common among ruderal species, because there is a trade-off between shade tolerance and growth rate in high-light environments (Valladares and Niinemets 2008). Ruderality has long been associated with the successful establishment of non-native species (Baker's 'ideal weed', Baker 1965), and broad-scale studies have found that plants with ruderal strategies are more likely to have naturalized somewhere in the world (Hamilton et al. 2005, Guo et al. 2018, 2022, Montesinos 2021). Similarly, naturalization and invasiveness have been associated with disturbance-adapted traits including rapid growth and resource turnover (Leishman et al. 2007, van Kleunen et al. 2010), short lifespan (Monnet et al. 2020, Dong et al. 2024), seed bank persistence (Pyšek et al. 2015), and self-compatibility (van Kleunen and Johnson 2007, van Kleunen et al. 2008, Razanajatovo et al. 2016) (note that traits not necessarily associated with ruderality have also been associated with naturalization and invasiveness, e.g. dispersal ability (Richardson and Pyšek 2012) and clonality (Milbau and Stout 2008)). Global naturalization success may be higher for plants with disturbance-adapted traits because disturbance is so ubiquitous. In particular, disturbance because of agricultural land use is uniquely extensive (covering more than a third of Earth's ice-free land area, Ramankutty et al. 2008), intensive, and leaves a long-lasting legacy (McLauchlan 2006, Maloney et al. 2008, Parker et al. 2010).

However, the fitness consequences of traits depend on the environment, and there may be no universal trait that promotes naturalization (Kueffer et al. 2013). Rather, different traits may favor naturalization in different landscapes. Thus, though ruderal strategies are overrepresented among naturalized and invasive species, this strategy may only be effective in particular environments, for example, in areas with more frequent and intensive human-induced disturbance (e.g. agricultural land use) or natural disturbance (e.g. open habitats).

Though forests vary considerably in composition and structure (dependent on temperature/precipitation balance, soil, fire, herbivory, etc.), they are generally shaded below the canopy. Grasslands and shrublands, while also highly varied, are relatively open habitats. Under similar climates, natural grasslands and shrublands tend to have more frequent and intensive natural disturbance (fire and/or grazing) than forests (Nerlekar and Veldman 2020). Using a very broad lens, while naturalization in landscapes with more open habitats and more natural disturbance, like grassland landscapes, may favor ruderal traits that confer adaptation to disturbance, non-ruderal traits may be favored in landscapes with more closed habitats and less natural disturbance, like forest landscapes (note that plants may have traits conferring adaptation to particular disturbance agents, e.g. fire (Keeley et al. 2011) or flooding (Perata et al. 2011)). For example, shade tolerant perennial non-native plants have been known to invade both temperate and tropical forests (Huebner 2003, Martin and Marks 2006, Martin et al. 2009, Fridley et al. 2023). Additionally, the traits that promote naturalization under agricultural land use change may depend on land cover context. For example, in successional environments in which agricultural land reverts to forest, certain shade tolerant, non-native species can persist and even increase in abundance following canopy closure (Mosher et al. 2009). Also, succession from abandoned agricultural land to grassland in the western United States (US) is associated with the widespread naturalization of annual non-native species (Yensen 1981, Allen and Knight 1984, Cox et al. 2014). Such patterns are known from habitat-specific research, but have not been previously demonstrated in a unified framework at broad spatial scales.

In order to disentangle the context dependence of the traits promoting naturalization in different landscape types, we conducted a spatially and temporally extensive analysis of cultivated ornamental non-native plants in the conterminous US, some of which have naturalized and others which have not, in relation to the historical land cover and land use changes in the environments in which they were introduced. The conterminous US is an ideal region for such an analysis for several reasons: records of cultivation from the inception of the nursery industry in the 18th century are available, the ecological and phylogenetic patterns of the US ornamental nursery flora have already been characterized (Kinlock et al. 2022a), and the US has extensive forest and grassland cover and distinct patterns of agricultural land use change over time that are relatively well described following nation formation (Ramankutty et al. 2010).

We used historical records of ornamental plant cultivation from conterminous US nurseries and seed houses paired with historical estimates of forest and grassland land cover and agricultural land use conversion to test five hypotheses: 1) species cultivated for longer are more likely to naturalize, 2) species cultivated in more places, i.e. available in more historical nursery/seed catalogs, are more likely to naturalize, and 3) traits that favor naturalization are dependent on land cover and land use context. We selected a small set of disturbance-adapted traits that are binary (short lifespan, shade intolerance, and self-compatibility) in order to facilitate the interpretation of interactions between traits and land cover. Specifically, we hypothesized that: (3a) short lifespan, shade intolerance, and self-compatibility promote naturalization in areas with higher grassland cover, while long lifespan, shade tolerance, and self-incompatibility promote naturalization in areas with higher forest cover; (3b) short lifespan, shade intolerance, and self-compatibility promote naturalization in areas with more conversion to agricultural land use; and (3c) transition from agricultural land back to grassland favors naturalization of short-lived, shade intolerant, or self-compatible species in grassland landscapes, while transition from agricultural land to forest favors naturalization of long-lived, shade tolerant, or self-incompatible species in forest landscapes.

Material and methods

Cultivated species pool

Our pool of cultivated taxa comprised ornamental vascular plants listed in 319 US nursery catalogs, seed catalogs, and newspaper advertisements published between 1719 and 1946, compiled for the book *Restoring American Gardens* (Adams 2004). The data were subset to include only taxa non-native to the conterminous US (including intracontinental non-native taxa, which are native to part of the conterminous US but have been introduced to other parts of the country where they are not native). The total pool comprised 3949 cultivated ornamental non-native taxa available in historical US nursery/seed catalogs (3498 species-level and 451 infraspecific-level taxa, hereafter referred to as species for simplicity). Native status was determined using the Biota of North America Program (BONAP) database (Kartesz 2018). Present-day naturalization status in conterminous US states came from the Global Naturalized Alien Flora (GloNAF) database, ver. 2 (van Kleunen et al. 2019, Davis et al. 2024), which includes data compiled from the BONAP database, http://www.cabi.org/isc/, Weber (2017), Jones et al. (2019), and Fehr et al. (2020). Naturalization status in each state was a binary variable indicating whether non-native species have established self-sustaining populations, including both non-invasive and invasive naturalized species. For intracontinental non-native species, naturalization status was only included for states in which they were not native.

Trait data compilation and imputation

Trait data on lifespan, in which plants were categorized as short-lived (annual or biennial) or long-lived (perennial), came from Cullen et al. (2011), the World Checklist of Vascular Plants (WCVP) database (Govaerts et al. 2021), the GIFT database (Weigelt et al. 2020), and https://www.garden.org. Trait data on shade tolerance, in which plants were categorized as partial/full shade tolerant or shade intolerant (primarily based on the environmental conditions in which species grew well), were compiled from Hill et al. (1999), Ellenberg et al. (2001), Böhling et al. (2002), Pignatti et al. (2005), Niinemets and Valladares (2006), Humbert et al.

(2007), Landolt (2010), Guarino et al. (2012), Chytrý et al. (2018), Domina et al. (2018), Jones et al. (2019), Szakacs et al. (2022), https://pfaf.org, https://www.garden.org, https://davesgarden.com, and http://navigate.botanicgardens.org. Self-compatibility data, in which plants were categorized as self-compatible, i.e. reproducing sexually or apomictically as an individual, or self-incompatible, came from Fryxell (1957), Clements et al. (2004), Cullen et al. (2011), Razanajatovo et al. (2016), Grossenbacher et al. (2017), Moeller et al. (2017), Walas et al. (2018), Jones et al. (2019), and Wang et al. (2021). Lifespan data were available for 94.8%, shade tolerance data for 80.9%, and self-compatibility data for 23.7% of the cultivated species pool. Further details about compiling trait data are in the Supporting information. Taxon names from all sources were standardized according to the WCVP taxonomic backbone (Govaerts et al. 2021) via the 'rWCVP' R package (Brown et al. 2023). Synonyms from Adams (2004) or the GBIF backbone taxonomy (GBIF Secretariat 2023) were included to replace incorrect fuzzy matches or missing matches. Only taxon names that were matched in the WCVP backbone were retained.

We imputed missing trait data using nonmissing trait data and the phylogenetic relationships among species in order to avoid reducing statistical power and biasing parameter estimates (Nakagawa 2015). We pruned a megaphylogeny of vascular plants from Zanne et al. (2014) and Smith and Brown (2018) to the cultivated species pool using the 'U.Phylomaker' R package (Jin and Qian 2023). In the resulting phylogeny, 94% of genera and 71% of species from our dataset were present. Species and genera that were missing were attached to the nearest genus or family branch under Scenario 3 in 'U.Phylomaker.' Missing trait data were imputed by fitting a restricted maximum likelihood evolutionary model assuming Brownian motion to estimate phylogenetic trait covariance via the 'Rphylopars' R package (Goolsby et al. 2016).

Historical land cover data

Modeled annual historical land cover data in the conterminous US starting in 1770 came from Meiyappan and Jain (2012), which incorporated data from multiple sources, including a potential vegetation map in the absence of human land use from Ramankutty and Foley (1999), historical wood harvest data from Hurtt et al. (2011), historical urban land area data from Klein Goldewijk et al. (2010), and historical cropland and pasture land use cover data from Ramankutty and Foley (1999) (note that land use estimates relied on historical US governmental sources and thus underestimated indigenous American agricultural land use, Doolittle 2004). Land cover data were area fractions of 28 land cover types and 92 land use transition types in 0.5° × 0.5° grid cells. We constructed ecologically relevant groupings from the land cover types: 1) forest, which included all forest land cover types; 2) grassland, which included natural grassland and shrubland land cover types (and savanna, which was uncommon in our region); 3) cropland; and 4) pasture. In the Meiyappan and Jain (2012) model, pasture land cover is characterized by land use involving grazing of domestic animals, while grassland land cover is dominated by herbaceous plants in the absence of human activities. We used this same classification to recategorize land use transition types into forest–cropland, forest–pasture, cropland–forest, grassland–cropland, grassland–pasture, cropland–grassland, and pasture–grassland transitions (pasture–forest transitions were not incorporated in the model). There were some unrealistic nonzero estimates of pasture conversion from before 1870 in the western US (noted also by Pongratz et al. 2008). Therefore, we replaced estimates of grassland and pasture percent cover in New Mexico before 1870 with estimates from Arizona and estimates in Wyoming before 1860 with estimates from Utah, both analogous states with similar initial grassland percent cover. To smooth estimates of land use transitions, 10-year windowed means were calculated. The coarse resolution of the historical land cover estimates necessitated that we conduct the analysis at the present-day state-level scale, but note that states were annexed and borders shifted during the study period. We calculated the land cover fractions of forest, grassland, and land use transitions for each year in each state using the 'terra' (Hijmans 2022) and 'exactextractr' R packages (Baston 2022). Because we used coarse-grained cumulative estimates of land cover in states, our land cover metrics reflect the probability that plant populations encountered particular land cover types and land use transitions. Present-day state boundaries came from the 'USAboundaries' R package (Mullen and Bratt 2018). All previously described analyses were carried out in the R environment, ver. 4.4 (www.r-project.org).

Statistical analyses

We modeled the naturalization status of all 3949 species in each of the 48 conterminous US states where they were not native as a Bernoulli response variable (outcomes $Y = 0$ or 1) in a generalized additive mixed model (GAMM) with a logit link function for a total of 182 348 species × state observations. This assumes that all species available in nursery/seed catalogs had the chance to naturalize in all US states, representing a high degree of connectivity within the nursery industry (historically, species were available extra-regionally via traveling nursery agents or mail, Lyon-Jenness 2004, Burd 2019). Explanatory variables included minimum time in cultivation (MTC), estimated as the number of years since the species' first appearance in a nursery/seed catalog in the conterminous US; the total number of historical nursery/seed catalogs listing the species ('Cat', natural log transformed to improve linearity); the interaction between MTC and the log number of catalogs; imputed traits ('T'), including shade tolerance (whether the species is shade intolerant), lifespan (whether the species is short-lived), and self-compatibility (whether the species is self-compatible); land use/cover characteristics of the state at the time of the species' first appearance in catalogs, including the proportion of land cover ('LC') and the proportion of cover undergoing land use transitions ('LU'); and the interactions between traits and land cover variables. To account for shared variation, we included species identity as a simple scalar random effect.

To account for spatial autocorrelation, we fitted a Markov random field (MRF) smoother to the adjacency matrix of US states via the *smooth.construct* function in the ‘mgcv’ R package (basis dimension = 11), and then included the resulting basis functions in the models (Wood 2017). To focus on land cover and trait interactions, we fitted six separate models for each combination of land cover type (forest versus grassland) and trait. The model can be expressed generally using Wilkinson notation as $\mathrm{logit}^{-1}(Y) \sim 1 + \mathrm{MTC} \times \mathrm{Cat} + \mathrm{T} \times \mathrm{LC} + \mathrm{T} \times \mathrm{LU} + (1|\mathrm{Sp}) + f(\mathrm{St})$, where $(1|\mathrm{Sp})$ is the species’ random effect and $f(\mathrm{St})$ is the MRF smoother of US states (see the Supporting information for more details). Land cover variables were not strongly correlated with one another within models (all Pearson’s correlation coefficients $r < 0.37$). For the 38 species with first appearances in catalogs before 1770, land cover estimates were assumed to be equal to their values in 1770, the first year with available data. All continuous variables were centered and standardized by two standard deviations to facilitate comparison with binary trait variables (Gelman 2008).

We fitted models by maximum likelihood using the ‘MixedModels’ package, ver. 4.33 (Bates et al. 2023) in the Julia programming language, ver. 1.10 (Bezanson et al. 2017). Model fit was assessed by comparing models with and without land cover and trait variables using Akaike’s information criterion (AIC) and the marginal and conditional coefficients of determination (R^2) (using distribution-specific variance, Nakagawa et al. 2017). Coefficient estimates were maximum likelihood estimates and their standard errors with Wald-type 95% confidence intervals (CIs). Significance was evaluated using Wald Z-tests with a significance threshold of 0.05. We assessed spatial autocorrelation of mean state-level deviance residuals using a permutation test of Moran’s I statistic (9999 permutations) via the *moran.mc* function in the ‘spdep’ R package (Bivand 2022). Models fitted with the subset of species that had nonmissing trait data showed similar parameter estimates to models fitted with all species (mean difference in parameter estimates = 0.10; Supporting information), and we show results only for analyses with the entire cultivated species pool.

Results

Of the 3949 non-native ornamental plant species introduced into the US for cultivation, 1603 (40.6%) have naturalized somewhere in the conterminous US, with higher instances in the northeastern US and the Pacific West and lower instances in central and non-coastal western regions (Fig. 1A). Species with earlier initial appearances in a nursery/seed catalog (i.e. longer MTCs) and species that were available in more historical nursery/seed catalogs were significantly more likely to naturalize (Fig. 1B–C).

The influence of traits on naturalization was context dependent, meaning that there were significant interactions between species’ traits and the land cover and land use transitions that they experienced at the time they were first

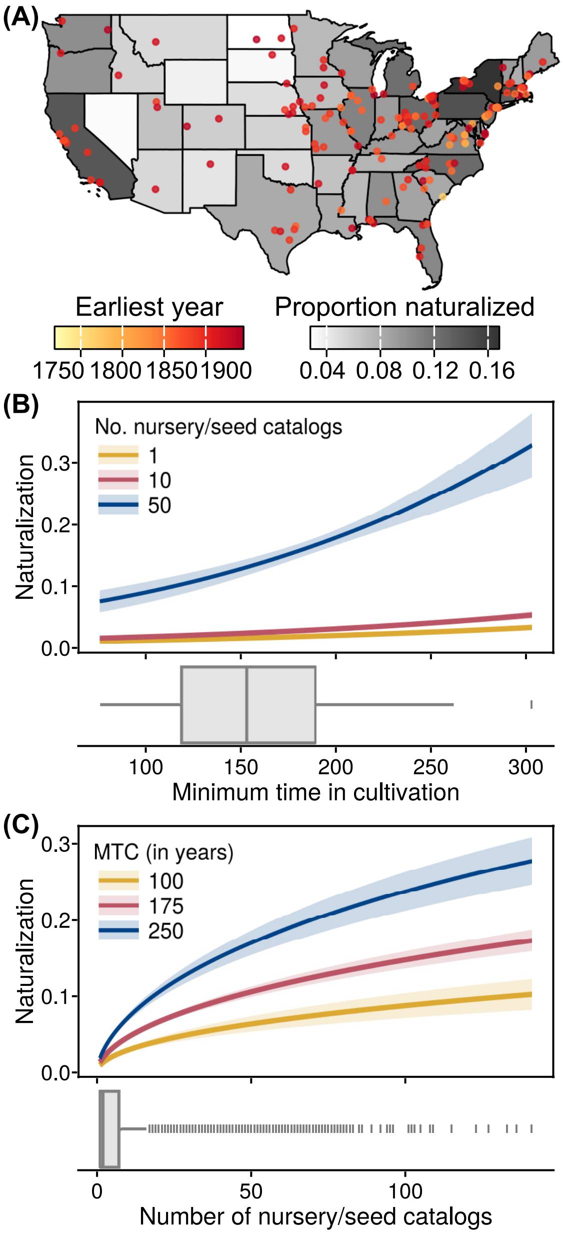

Figure 1. The influence of cultivation history on ornamental plant naturalization in the conterminous US. (A) Map showing locations of historical nurseries/seed houses whose catalogs were used to compile the introduced species pool. Point color shows the earliest year a catalog was published at that location. State shade represents the proportion of the total introduced plant species pool that naturalized. (B, C) Naturalization probability in US states as a function of (B) minimum time in cultivation (MTC, in years) and (C) number of nursery/seed catalogs in which a species was available (back-transformed from natural log) from models including only these main and interaction effects. Relationships with MTC are shown for three different numbers of nursery/seed catalogs, and relationships with number of nursery/seed catalogs are shown for three different MTC values. Lines are means and bands are Wald-type 95% CIs of partial regression estimates. Tukey-style boxplots of the distribution of the data are at the bottom, with outliers shown as vertical stripes.

available in nursery/seed catalogs. In forest cover models, species were more likely to naturalize in states with proportionally higher forest cover, and this relationship was significantly stronger for shade tolerant or long-lived species (Fig. 2A). The relationship between forest conversion to agriculture and naturalization depended on species' traits and agriculture type (Fig. 2B). Specifically, in states with proportionally more forest to pasture transitions, shade intolerant or short-lived species were more likely to naturalize. In contrast, species were generally less likely to naturalize in states with more forest to cropland conversion. Land use transition from agriculture to forest favored species with ruderal traits, meaning that though species were generally less likely to naturalize in states with more land use transitions from cropland to forest, the negative relationship was significantly weaker for shade intolerant, short-lived, or self-compatible species (Fig. 2C).

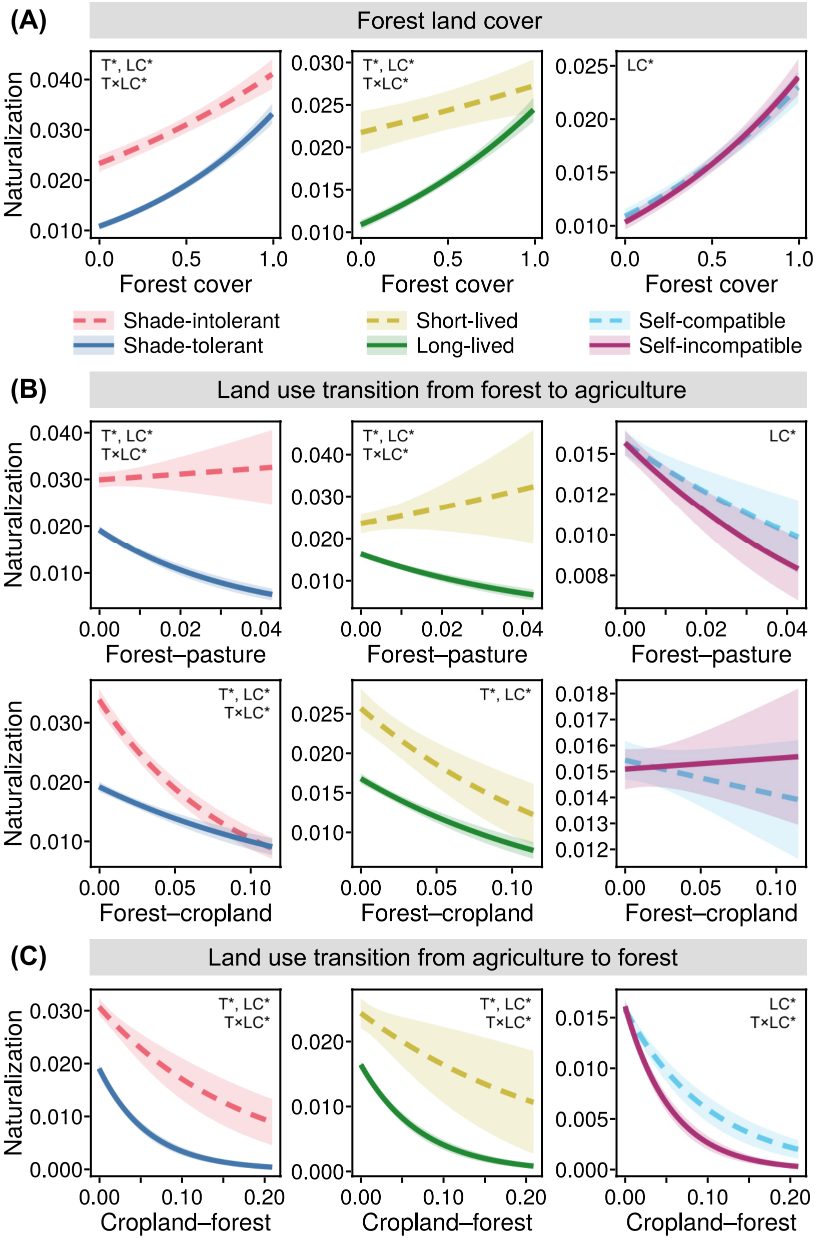

Figure 2. The effects of non-native cultivated ornamental species' traits on naturalization probability in US states depends on forest land cover fractions in states at the time species first appeared in historical nursery/seed catalogs. Lines are means and bands are Wald-type 95% CIs of partial regression estimates. Traits include shade tolerance, lifespan, and self-compatibility. Land cover fractions include (A) forest land cover, (B) land use transition from forest to agriculture (pasture and cropland), and (C) transition from agriculture to forest. Significant effects of traits (T), land cover (LC), or interaction effects (T × LC) are indicated with an asterisk. Minimum time in cultivation (MTC) and log number of nursery/seed catalogs are set to their mean values. Species' random effects and the Markov random field smoother function are set to zero.

In grassland cover models, species were less likely to naturalize in states with proportionally higher grassland cover at the time they were first available in nursery/seed catalogs, mostly independently of traits (Fig. 3A). The relationship between agricultural disturbance in grassland and naturalization depended on species' traits. Land use transitions both from grassland to agriculture and from agriculture back to grassland tended to favor species with disturbance-adapted traits, meaning that in states with proportionally more agricultural land use transitions, shade intolerant, short-lived, or self-compatible species were more likely to naturalize (Fig. 3B, C). This pattern was stronger and more consistent for conversion from grassland to pasture rather than to cropland.

Models including only MTC, log number of catalogs, and their interaction had moderate explanatory power (marginal $R^2 = 0.131$, Table 1). Adding trait and land use/cover variables greatly improved model fit ($\Delta \text{AIC} \geq 215$) and slightly increased explanatory power (marginal R^2 ranged between 0.136 and 0.189, Table 1). Species-specific random effects were large in magnitude and added explanatory power (conditional R^2 ranged between 0.477 and 0.517, Table 1). There was no significant spatial autocorrelation in the residuals for all models after including the spatial basis functions (Table 1).

Discussion

We found that cultivation history was tied to the naturalization of non-native plants introduced into the US for cultivation as ornamentals; plants that were cultivated longer or were for sale in more historical nursery/seed catalogs were more likely to naturalize, corroborating hypotheses (1) and (2). This suggests that patterns of ornamental plant naturalization across the conterminous US can be traced to the increase in the diversity of nursery offerings and the proliferation of nurseries and seed houses from the late 18th to the early 20th century (Kinlock et al. 2022a). This adds to mounting evidence of the close relationship between cultivation and naturalization and emphasizes the need to account for human cultivation in ecological studies of invasion (Dehnen-Schmutz et al. 2007, Hanspach et al. 2008, Maurel et al. 2016, Kinlock et al. 2022b). We found that the number of catalogs in which a species was for sale, a proxy of historical propagule pressure, had particularly strong effects, which aligns with the findings of a recent study of ornamental plant naturalization in the US (Fertakos and Bradley 2024).

The land cover and land use context dependence of species' traits with naturalization success was apparent in our analysis even after accounting for cultivation duration, propagule pressure, and taxonomic and spatial dependencies. Ours is one of few studies investigating context dependence in trait–naturalization relationships (Pearson et al. 2023). We found that ruderal traits conferring adaptation to disturbance, including shade intolerance, short lifespan, and self-compatibility, were positively associated with naturalization in some, but not all, landscape contexts. When natural grassland cover was high – suggesting open landscapes with relatively frequent and intensive natural disturbance – short-lived, shade intolerant non-native species were more likely to naturalize, as expected. In contrast, when forest cover was high – suggesting closed landscapes with relatively lower natural disturbance – shade tolerant, long-lived non-native species were increasingly likely to naturalize, supporting hypothesis (3a). This is consistent with an alternative invasion strategy in forests necessitated by canopy shading, as has been observed in smaller-scale studies in US forests (Huebner 2003, Martin and Marks 2006, Gavier-Pizarro et al. 2010, Kuhman et al. 2011, Matlack and Schaub 2011). Beyond the small set of binary traits we analyzed, a recent review of highly invasive forest species hypothesized that invasiveness in forests involves a combination of shade tolerance, high maximum growth rate, and high fecundity (Fridley et al. 2023). Contrary to our expectations, we found that self-compatible species had lower naturalization in states with high grassland cover. This may be because open habitats like grasslands have higher pollinator diversity (Grundel et al. 2010) and are more conducive to wind pollination (wind-pollinated species have either low or high selfing rates, Culley et al. 2002), both of which could favor self-incompatible non-native species.

Non-native species richness and abundance tend to be higher in areas with frequent or more intensive disturbance, particularly agricultural disturbance (Chytrý et al. 2008, Polce et al. 2011, Jauni et al. 2015). In our study, the relationship between disturbance and naturalization depended on non-native species' traits and the type of agricultural disturbance. We found that land use conversion to agriculture favored the naturalization of ruderal species when land was converted to pasture, but not necessarily when land was converted to cropland, providing mixed evidence for hypothesis (3b). Pasture itself provides suitable habitat for disturbance-adapted species, which may be lacking when land is converted to cropland (particularly in the eastern forests of North America, which may lack native grassland-adapted species, Marks 1983). Pasture may have the optimal intensity and frequency of disturbance for naturalization, in contrast to crop cultivation involving more intensive tilling (Holmes and Matlack 2019), and ruderal non-native species may be better able to take advantage of this optimal disturbance regime. Also, non-native grassland species were historically seeded for fodder in both the eastern and western US (sometimes unintentionally via seed contamination), providing additional propagule sources of ruderal non-native species (Mack 1986, 2003). The ability to naturalize in landscapes with high cropland conversion may instead depend on traits we did not analyze, such as dispersal ability, which has been recognized as a key factor in explaining post-agricultural forest species composition (Matlack 1994, Bellemare et al. 2002).

In our study, land use transitions following the abandonment of agricultural land tended to favor disturbance-adapted traits in both forest and grassland landscapes. This is in contrast to our expectation (hypothesis 3c) that the traits favored by succession were dependent on land cover context. In forest landscapes, succession after abandonment of cropland is accompanied by a relatively long old field period, an

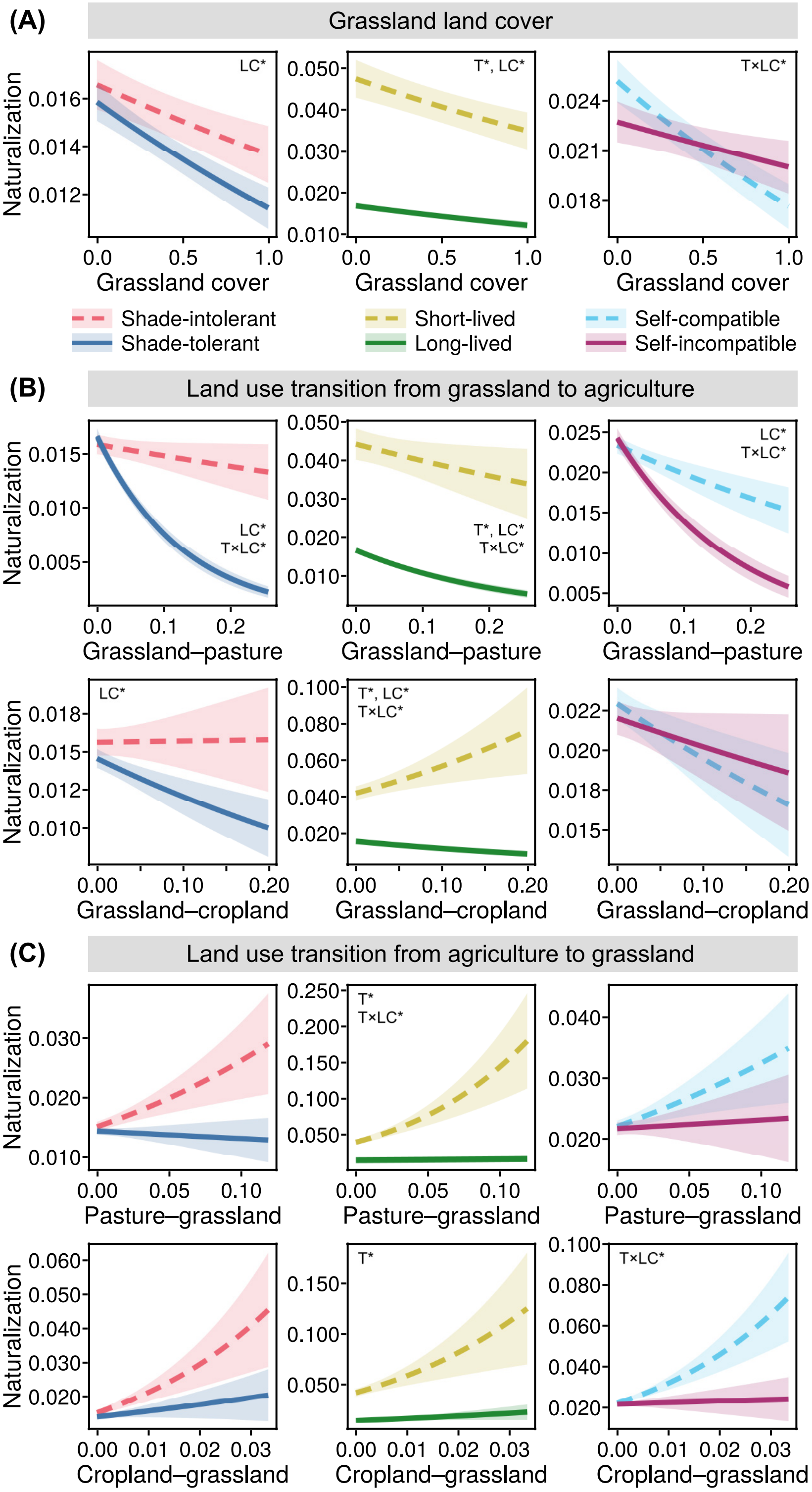

Figure 3. The effects of non-native cultivated ornamental species' traits on naturalization probability in US states depends on grassland land cover fractions in states at the time species first appeared in historical nursery/seed catalogs. Lines are means and bands are Wald-type 95% CIs of partial regression estimates. Traits include shade tolerance, lifespan, and self-compatibility. Land cover fractions include (A) grassland land cover, (B) land use transition from grassland to agriculture (pasture and cropland), and (C) transition from agriculture to grassland. Significant effects of traits (T), land cover (LC), or interaction effects (T × LC) are indicated with an asterisk. Minimum time in cultivation (MTC) and log number of nursery/seed catalogs are set to their mean values. Species' random effects and the Markov random field smoother function are set to zero.

Table 1. Metrics from models of non-native cultivated ornamental plant naturalization in US states, including degrees of freedom (df), AIC, marginal and conditional R^2, species' random effect variance (σ^2), and Moran's *I* test for residual spatial autocorrelation. All models included a species' random effect and all except the null model included a Markov random field spatial smoother for states. Cultivation history variables were minimum time in cultivation (MTC) and log number of nursery/seed catalogs in which species were for sale (Cat). Trait variables were shade tolerance (ST), lifespan (LS), and self-compatibility (SC). Land cover variables were forest or grassland cover and associated agricultural land use transitions.

Model	df	AIC	marg. R^2	cond. R^2	σ^2	Moran's *I*	P(*I*)
Null	2	57675			5.400	0.488	0.0001
MTC, Cat	15	55894	0.131	0.477	2.176	−0.064	0.6580
MTC, Cat, Forest, ST	24	55113	0.174	0.514	2.307	−0.135	0.8909
MTC, Cat, Forest, LS	24	55141	0.149	0.496	2.264	−0.154	0.9261
MTC, Cat, Forest, SC	24	55198	0.189	0.517	2.230	−0.132	0.8820
MTC, Cat, Grassland, ST	26	55553	0.144	0.491	2.236	−0.103	0.8013
MTC, Cat, Grassland, LS	26	55269	0.166	0.504	2.247	−0.167	0.9408
MTC, Cat, Grassland, SC	26	55679	0.136	0.486	2.242	−0.170	0.9457

open habitat with colonization-driven dynamics that may be ideal for the naturalization of disturbance-adapted species (Bartha et al. 2003, Von Holle and Motzkin 2007), but which was not explicitly included in the land use transition model we used. Most forest succession occurred in the eastern US after forests that had been converted to agricultural land in the 18th–19th century were abandoned in the 19th–20th century (Supporting information). Much of the eastern US has had no native grassland analog to act as a species source pool, meaning that non-native disturbance-adapted species would be most likely to colonize the newly open habitat (as has been observed in a long-term study of forest succession in New Jersey, e.g. Meiners et al. 2002). The environmental legacy of intensive agriculture is prolonged, promoting the persistence of established species after canopy closure, well after cultivation or pasturing has ended (Dupouey et al. 2002, Parker et al. 2010, Holmes and Matlack 2019, Holmes et al. 2021, 2022). It should also be noted that US forests are not uniformly shaded (open forests were once common throughout the eastern US and remain common in the southeastern Coastal Plain, Hanberry et al. 2020), and therefore shade tolerance is likely not uniformly adaptive in US forests.

In the grassland landscapes of the central and western US, pasture was being abandoned at the same time as grassland was being converted to pasture during the late 19th–20th centuries (Supporting information), suggesting a mosaic of open habitats with different histories of abandonment and current land use. Disturbance-adapted species are best able to take advantage of open space (Tognetti et al. 2010), and can benefit from the spatial and temporal heterogeneity in the landscape (Cousins 2009, Reitalu et al. 2012). Current issues with the invasion of non-native annuals in the western US have previously been attributed to the widespread abandonment of pasture in the late 19th and early 20th centuries (in response to unsustainable fluctuations in cattle populations permitted by the US Homestead Acts and exacerbated by overgrazing and drought events, Svejcar 2015, Svejcar et al. 2017). Non-native annuals, which had been introduced for forage sometime after livestock pasturing was introduced to the region in the mid-19th century, were able to capitalize on the sudden land use shifts (Allen and Knight 1984, Inouye et al. 1987, Davies et al. 2021; though a more recent increase in nitrogen deposition is also influential, Concilio and Loik 2013). Though most of the serious invasive annuals in the western US have been non-ornamental grasses (and thus not included in the dataset used in this study), the broad-scale pattern of increased non-native ruderal plant naturalization with succession of agricultural land to grassland that we demonstrate is consistent with this well-documented regional observation.

We found a significant relationship between self-compatibility and cropland abandonment, but not pasture abandonment, which may relate to historical patterns of cropland abandonment in the US. Grassland in the Great Plains was converted to agricultural land extensively following the US Homestead Act of 1862; at first, cropland, pasture, and remnant grassland coexisted in a patchy landscape, but in the early 20th century, grassland that was initially deemed unsuitable was converted to cropland to meet high demand brought about by World War I (Fite 1977, Samson et al. 2004). After cropland abandonment in the 1930s, which was caused by drought and unsustainable agricultural practices (Fite 1977), the limited distribution of remaining natural grassland and limited availability of native grassland species' propagules may have made self-compatibility a particularly effective strategy for establishment of non-native species to isolated successional patches (Baker 1955, Stebbins 1957).

There are several caveats that must be considered when interpreting our results. First, our study involves simplifying generalizations – we used a coarse spatial grain that averaged over heterogeneous land cover (necessary because high-resolution land cover estimates are not available for time periods predating satellite technology), and we considered only binary species' traits, simplifying complex aspects of plant life history and physiology. Despite these generalizations, we found broad-scale context dependence in the traits that were associated with naturalization under different land cover types. If our study were carried out at a finer grain or with more complex traits, we would expect that heterogeneity would be better accounted for and thus the estimated probabilities of naturalization (which are currently small, i.e. ≤ 0.04) would be larger under certain combinations of variables. Second, we did not account for species' spread from one state to another. This was because historical data on non-native species' spread are limited, making it impossible to incorporate a process-based model of species' spread into our observational model. It is thus likely that some of the patterns we observed relate to species' spread from another region in which it is already naturalized rather than independent naturalization from cultivation. Last, we did not incorporate climate in our analyses, which has a foundational role in structuring the distribution of ecoregions (Mucina 2019). Accordingly, we found that naturalization probability was higher in states with higher forest cover, which may partly be because forest ecoregions tend to receive more precipitation than grasslands or shrublands. Also, we observed patterns of naturalized cultivated plant diversity similar to previously described patterns of native and non-native plant diversity in the US (Jarnevich et al. 2006, Stohlgren et al. 2006), which suggests that the climatic drivers of native plant diversity can influence cultivated plant naturalization directly and/or indirectly (i.e. by supporting human settlement, Luck and Smallbone 2010). Though including climatic variables could reduce the unexplained variation in our models, we intentionally focused on a small set of trait–land cover interactions to characterize context dependence in naturalization.

Conclusions

Key species' traits influencing ruderal life history strategies are important predictors of naturalization. We showed that the tendency for disturbance-adapted traits to promote naturalization depended on land cover, specifically whether landscapes were relatively closed with lower natural disturbance (forests) or more open with higher natural disturbance (grasslands/shrubland), and the agricultural land use context into which plants were introduced and cultivated. We found that shade tolerant, non-native species were more likely to naturalize in US states with higher forest cover at the time of their introduction into the nursery industry, which provides broad-scale evidence supporting observations of shade tolerant, non-native species invading landscapes dominated by closed-canopy forests (in the northeastern US, Martin et al. 2009; and in the tropics, Fine 2002). We also showed that land use conversion between pasture and grassland favored the naturalization of disturbance-adapted species, which is consistent with the observation that naturalized and invasive annual species, especially annual grasses, have transformed a large portion of the western US (Davies et al. 2021). Historical cultivation records are a valuable tool to establish which species were present in the historical landscape in order to test for the influences of cultivation history and environmental context in shaping present-day patterns of plant naturalization. Characterizing environmental context dependence is essential to move beyond unified descriptions of naturalization and to understand alternative naturalization strategies.

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Author contributions

Nicole L. Kinlock: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (equal); Software (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Denise W. Adams**: Data curation (equal); Writing – review and editing (supporting). **Wayne Dawson**: Data curation (supporting); Funding acquisition (supporting); Resources (supporting); Writing – review and editing (supporting). **Franz Essl**: Data curation (supporting); Funding acquisition (supporting); Resources (supporting); Writing – review and editing (supporting). **John Kartesz**: Data curation (equal); Validation (supporting); Writing – review and editing (supporting). **Holger Kreft**: Data curation (supporting); Funding acquisition (supporting); Resources (supporting); Writing – review and editing (supporting). **Misako Nishino**: Data curation (equal); Validation (supporting); Writing – review and editing (supporting). **Jan Pergl**: Data curation (supporting); Funding acquisition (supporting); Resources (supporting); Writing – review and editing (supporting). **Petr Pyšek**: Data curation (supporting); Funding acquisition (supporting); Resources (supporting); Writing – review and editing (supporting). **Patrick Weigelt**: Data curation (supporting); Funding acquisition (supporting); Resources (supporting); Writing – review and editing (supporting). **Mark van Kleunen**: Conceptualization (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (supporting); Resources (lead); Validation (supporting); Writing – review and editing (equal).

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Data availability statement

Data and code are available from Figshare: http://doi.org/10.6084/m9.figshare.25225001 (Kinlock et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Adams, D. W. 2004. Restoring American gardens: an encyclopedia of heirloom ornamental plants, 1640–1940. – Timber Press.

Allen, E. B. and Knight, D. H. 1984. The effects of introduced annuals on secondary succession in sagebrush-grassland, Wyoming. – Southwest. Nat. 29: 407.

Baker, H. G. 1955. Self-compatibility and establishment after 'long-distance' dispersal. – Evolution 9: 347–349.

Baker, H. G. 1965. Characteristics and modes of origin of weeds. – In: Baker, H. G. and Stebbins, G. (eds), The genetics of colonizing species. Academic Press, pp. 147–172.

Bartha, S., Meiners, S. J., Pickett, S. T. A. and Cadenasso, M. L. 2003. Plant colonization windows in a mesic old field succession. – Appl. Veg. Sci. 6: 205–212.

Baston, D. 2022. exactextractr: fast extraction from raster datasets using polygons. – https://CRAN.R-project.org/package=exactextractr.

Bates, D. et al. 2023. JuliaStats/MixedModels.jl, v4.8.2. – Zenodo, https://doi.org/10.5281/zenodo.596435.

Bellemare, J., Motzkin, G. and Foster, D. R. 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. – J. Biogeogr. 29: 1401–1420.

Bezanson, J., Edelman, A., Karpinski, S. and Shah, V. B. 2017. Julia: a fresh approach to numerical computing. – SIAM Rev. 59: 65–98.

Bivand, R. 2022. R packages for analyzing spatial data: a comparative case study with areal data. – Geogr. Anal. 54: 488–518.

Blackburn, T. M., Cassey, P. and Duncan, R. P. 2020. Colonization pressure: a second null model for invasion biology. – Biol. Invasions 22: 1221–1233.

Böhling, N., Greuter, W. and Raus, T. 2002. Zeigerwerte der Gefässpflanzen der Südägäis. – Braun-Blanquetia 32: 3–107.

Brown, M. J. M., Walker, B. E., Black, N., Govaerts, R. H. A., Ondo, I., Turner, R. and Nic Lughadha, E. 2023. rWCVP: a companion R package to the world checklist of vascular plants. – New Phytol. 240: 1355–1365.

Burd, C. 2019. The ornament of empire: plant nurserymen and the making of the American landscape. – PhD thesis, Univ. of Rochester, USA.

Chytrý, M., Maskell, L. C., Pino, J., Pyšek, P., Vilà, M., Font, X. and Smart, S. M. 2008. Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. – J. Appl. Ecol. 45: 448–458.

Chytrý, M., Tichý, L., Dřevojan, P., Sádlo, J. and Zelený, D. 2018. Ellenberg-type indicator values for the Czech flora. – Preslia 90: 83–103.

Clements, D. R., DiTommaso, A., Jordan, N., Booth, B. D., Cardina, J., Doohan, D., Mohler, C. L., Murphy, S. D. and Swanton, C. J. 2004. Adaptability of plants invading North American cropland. – Agric. Ecosyst. Environ. 104: 379–398.

Concilio, A. L. and Loik, M. E. 2013. Elevated nitrogen effects on *Bromus tectorum* dominance and native plant diversity in an arid montane ecosystem. – Appl. Veg. Sci. 16: 598–609.

Cousins, S. A. 2009. Landscape history and soil properties affect grassland decline and plant species richness in rural landscapes. – Biol. Conserv. 142: 2752–2758.

Cox, R. D., Preston, K. L., Johnson, R. F., Minnich, R. A. and Allen, E. B. 2014. Influence of landscape-scale variables on vegetation conversion to exotic annual grassland in southern California, USA. – Global Ecol. Conserv. 2: 190–203.

Cullen, J., Knees, S., Cubey, H. S. and Shaw, J. M. H. (eds) 2011. The European garden flora, flowering plants: a manual for the identification of plants cultivated in Europe, both out-of-doors and under glass, 2nd edn. – Cambridge Univ. Press.

Culley, T. M., Weller, S. G. and Sakai, A. K. 2002. The evolution of wind pollination in angiosperms. – Trends Ecol. Evol. 17: 361–369.

Davies, K. W., Leger, E. A., Boyd, C. S. and Hallett, L. M. 2021. Living with exotic annual grasses in the sagebrush ecosystem. – J. Environ. Manage. 288: 112417.

Davis, A. J., Dawson, W., Essl, F., Kreft, H., Pergl, J., Pyšek, P., Weigelt, P., Winter, M. and van Kleunen, M. 2024. Global naturalized alien flora (GloNAF). Open access data to support research on understanding global plant invasions. – Zenodo, https://doi.org/10.5281/zenodo.13235356.

Davis, M. A., Grime, J. P. and Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. – J. Ecol. 88: 528–534.

Dehnen-Schmutz, K., Touza, J., Perrings, C. and Williamson, M. 2007. A century of the ornamental plant trade and its impact on invasion success. – Divers. Distrib. 13: 527–534.

Diez, J. M., Williams, P. A., Randall, R. P., Sullivan, J. J., Hulme, P. E. and Duncan, R. P. 2009. Learning from failures: testing broad taxonomic hypotheses about plant naturalization. – Ecol. Lett. 12: 1174–1183.

Domina, G., Galasso, G., Bartolucci, F. and Guarino, R. 2018. Ellenberg indicator values for the vascular flora alien to Italy. – Flora Mediterr. 28: 53–61.

Dong, B.-C., Yang, Q., Kinlock, N. L., Pouteau, R., Pyšek, P., Weigelt, P., Yu, F.-H. and Van Kleunen, M. 2024. Naturalization of introduced plants is driven by life-form-dependent cultivation biases. – Divers. Distrib. 30: 55–70.

Doolittle, W. E. 2004. Cultivated landscapes of native North America. – Oxford geographical and environmental studies, reprint edn. – Oxford Univ. Press.

Dupouey, J. L., Dambrine, E., Laffite, J. D. and Moares, C. 2002. Irreversible impact of past land use on forest soils and biodiversity. – Ecology 83: 2978–2984.

Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W. and Paulißen, D. 2001. Zeigerwerte von Pflanzen in Mitteleuropa. – No. 18 in Scripta Geobotanica, 3rd edn. – E. Goltze.

Ellis, E. C., Gauthier, N., Klein Goldewijk, K., Bliege Bird, R., Boivin, N., Díaz, S., Fuller, D. Q., Gill, J. L., Kaplan, J. O., Kingston, N., Locke, H., McMichael, C. N. H., Ranco, D., Rick, T. C., Shaw, M. R., Stephens, L., Svenning, J.-C. and Watson, J. E. M. 2021. People have shaped most of terrestrial nature for at least 12000 years. – Proc. Natl Acad. Sci. USA 118: e2023483118.

Fehr, V., Buitenwerf, R. and Svenning, J.-C. 2020. Non-native palms (Arecaceae) as generators of novel ecosystems: a global assessment. – Divers. Distrib. 26: 1523–1538.

Fertakos, M. E. and Bradley, B. A. 2024. Propagule pressure from historic U.S. plant sales explains establishment but not invasion. – Ecol. Lett. 27: e14494.

Fine, P. V. A. 2002. The invasibility of tropical forests by exotic plants. – J. Trop. Ecol. 18: 687–705.

Fite, G. C. 1977. Great Plains farming: a century of change and adjustment. Agric. Hist. 51: 244–256.

Fridley, J. D., Bellingham, P. J., Closset-Kopp, D., Daehler, C. C., Dechoum, M. S., Martin, P. H., Murphy, H. T., Rojas-Sandoval, J. and Tng, D. 2023. A general hypothesis of forest invasions by woody plants based on whole-plant carbon economics. – J. Ecol. 111: 4–22.

Fryxell, P. A. 1957. Mode of reproduction of higher plants. – Bot. Rev. 23: 135–233.

Fuller, D. Q., Boivin, N., Hoogervorst, T. and Allaby, R. 2011. Across the Indian Ocean: the prehistoric movement of plants and animals. – Antiquity 85: 544–558.

Gavier-Pizarro, G. I., Radeloff, V. C., Stewart, S. I., Huebner, C. D. and Keuler, N. S. 2010. Housing is positively associated with invasive exotic plant species richness in New England, USA. – Ecol. Appl. 20: 1913–1925.

GBIF Secretariat. 2023. GBIF backbone taxonomy. – https://doi.org/10.15468/39omei.

Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. – Stat. Med. 27: 2865–2873.

Goolsby, E. W., Bruggeman, J. and Ané, C. 2016. Rphylopars: fast multivariate phylogenetic comparative methods for missing data and within-species variation. – Methods Ecol. Evol. 8: 22–27.

Govaerts, R., Nic Lughadha, E., Black, N., Turner, R. and Paton, A. 2021. The World Checklist of Vascular Plants, a continuously updated resource for exploring global plant diversity. – Sci. Data 8: 215.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. – Am. Nat. 111: 1169–1194.

Grossenbacher, D. L., Brandvain, Y., Auld, J. R., Burd, M., Cheptou, P.-O., Conner, J. K., Grant, A. G., Hovick, S. M., Pannell, J. R., Pauw, A., Petanidou, T., Randle, A. M., Rubio de Casas, R., Vamosi, J., Winn, A., Igic, B., Busch, J. W., Kalisz, S. and Goldberg, E. E. 2017. Self-compatibility is over-represented on islands. – New Phytol. 215: 469–478.

Grundel, R., Jean, R. P., Frohnapple, K. J., Glowacki, G. A., Scott, P. E. and Pavlovic, N. B. 2010. Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. – Ecol. Appl. 20: 1678–1692.

Guarino, R., Domina, G. and Pignatti, S. 2012. Ellenberg's indicator values for the flora of Italy – first update: Pteridophyta, Gymnospermae and Monocotyledoneae. – Flora Mediterr. 22: 197–209.

Guo, K., Pyšek, P., Chytrý, M., Divíšek, J., Lososová, Z., Van Kleunen, M., Pierce, S. and Guo, W.-Y. 2022. Ruderals naturalize, competitors invade: varying roles of plant adaptive strategies along the invasion continuum. – Funct. Ecol. 36: 2469–2479.

Guo, W.-Y., van Kleunen, M., Winter, M., Weigelt, P., Stein, A., Pierce, S., Pergl, J., Moser, D., Maurel, N., Lenzner, B., Kreft, H., Essl, F., Dawson, W. and Pyšek, P. 2018. The role of adaptive strategies in plant naturalization. – Ecol. Lett. 21: 1380–1389.

Hamilton, M. A., Murray, B. R., Cadotte, M. W., Hose, G. C., Baker, A. C., Harris, C. J. and Licari, D. 2005. Life-history correlates of plant invasiveness at regional and continental scales. – Ecol. Lett. 8: 1066–1074.

Hanberry, B. B., Bragg, D. C. and Alexander, H. D. 2020. Open forest ecosystems: an excluded state. – For. Ecol. Manage. 472: 118256.

Hanspach, J., Kühn, I., Pyšek, P., Boos, E. and Klotz, S. 2008. Correlates of naturalization and occupancy of introduced ornamentals in Germany. – Perspect. Plant Ecol. Evol. Syst. 10: 241–250.

Hijmans, R. J. 2022. terra: spatial data analysis. – https://CRAN.R-project.org/package=terra.

Hill, M. O., Mountford, J. O., Roy, D. B. and Bunce, R. G. H. (eds) 1999. Ellenberg's indicator values for British plants. vol. 2 Technical annex of ECOFACT. – Institute of Terrestrial Ecology.

Holmes, M. A. and Matlack, G. R. 2019. Non-native plant species show a legacy of agricultural history in second-growth forests of southeastern Ohio. – Biol. Invasions 21: 3063–3076.

Holmes, M. A., Whitacre, J. V., Bennion, L. D., Poteet, J. and Kuebbing, S. E. 2021. Land-use history and abiotic gradients drive abundance of non-native shrubs in Appalachian second-growth forests with histories of mining, agriculture, and logging. – For. Ecol. Manage. 494: 119296.

Holmes, M. A., Whitacre, J. V., Bennion, L. D., Poteet, J. and Kuebbing, S. E. 2022. Native-exotic richness relationships in second-growth forests differ along a gradient of land-use history. – Landsc. Ecol. 37: 847–859.

Huebner, C. D. 2003. Vulnerability of oak-dominated forests in West Virginia to invasive exotic plants: temporal and spatial patterns of nine exotic species using herbarium records and land classification data. – Castanea 68: 1–14.

Humbert, L., Gagnon, D., Kneeshaw, D. and Messier, C. 2007. A shade tolerance index for common understory species of northeastern North America. – Ecol. Indic. 7: 195–207.

Hurtt, G. C. et al. 2011. Harmonization of land-use scenarios for the period 1500–2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. – Clim. Change 109: 117–161.

Inouye, R. S., Huntly, N. J., Tilman, D., Tester, J. R., Stillwell, M. and Zinnel, K. C. 1987. Old-field succession on a Minnesota sand plain. – Ecology 68: 12–26.

Jarnevich, C. S., Stohlgren, T. J., Barnett, D. and Kartesz, J. 2006. Filling in the gaps: modelling native species richness and invasions using spatially incomplete data. – Divers. Distrib. 12: 511–520.

Jauni, M., Gripenberg, S. and Ramula, S. 2015. Non-native plant species benefit from disturbance: a meta-analysis. – Oikos 124: 122–129.

Jin, Y. and Qian, H. 2023. U.PhyloMaker: an R package that can generate large phylogenetic trees for plants and animals. – Plant Divers. 45: 347–352.

Jones, E. J., Kraaij, T., Fritz, H. and Moodley, D. 2019. A global assessment of terrestrial alien ferns (Polypodiophyta): species' traits as drivers of naturalisation and invasion. – Biol. Invas. 21: 861–873.

Kartesz, J. 2018. Biota of North America Program (BONAP). – http://www.bonap.org/tdc.

Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J. and Bradstock, R. A. 2011. Fire as an evolutionary pressure shaping plant traits. – Trends Plant Sci. 16: 406–411.

Kinlock, N. L., Adams, D. W. and van Kleunen, M. 2022a. An ecological and evolutionary perspective of the historical US nursery flora. – Plants People Planet 2022: ppp3.10336.

Kinlock, N. L., Dehnen-Schmutz, K., Essl, F., Pergl, J., Pyšek, P., Kreft, H., Weigelt, P., Yang, Q. and van Kleunen, M. 2022b. Introduction history mediates naturalization and invasiveness of cultivated plants. – Global Ecol. Biogeogr. 31: 1104–1119.

Kinlock, N. L., Adams, D. W., Dawson, W., Essl, F., Kartesz, J., Kreft, H., Nishino, M., Pergl, J., Pyšek, P., Weigelt, P. and van Kleunen, M. 2025. Data from: Naturalization of ornamental plants in the United States depends on cultivation and historical land cover context. – Figshare, http://doi.org/10.6084/m9.figshare.25225001.

Klein Goldewijk, K., Beusen, A. and Janssen, P. 2010. Long-term dynamic modeling of global population and built-up area in a spatially explicit way: HYDE 3.1. – Holocene 20: 565–573.

Kueffer, C., Pyšek, P. and Richardson, D. M. 2013. Integrative invasion science: model systems, multi-site studies, focused meta-analysis and invasion syndromes. – New Phytol. 200: 615–633.

Kuhman, T. R., Pearson, S. M. and Turner, M. G. 2011. Agricultural land-use history increases non-native plant invasion in a southern Appalachian forest a century after abandonment. – Can. J. For. Res. 41: 920–929.

Lake, J. C. and Leishman, M. R. 2004. Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. – Biol. Conserv. 117: 215–226.

Landolt, E. 2010. Flora indicativa: ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen, 2nd edn. – Haupt.

Lehan, N. E., Murphy, J. R., Thorburn, L. P. and Bradley, B. A. 2013. Accidental introductions are an important source of invasive plants in the continental United States. – Am. J. Bot. 100: 1287–1293.

Leishman, M. R., Haslehurst, T., Ares, A. and Baruch, Z. 2007. Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. – New Phytol. 176: 635–643.

Lembrechts, J. J., Pauchard, A., Lenoir, J., Nuñez, M. A., Geron, C., Ven, A., Bravo-Monasterio, P., Teneb, E., Nijs, I. and Milbau, A. 2016. Disturbance is the key to plant invasions in cold environments. – Proc. Natl Acad. Sci. USA 113: 14061–14066.

Luck, G. W. and Smallbone, L. 2010. Species diversity in urban landscapes: patterns, drivers and implications. – In: Gaston, K. J. (ed.), Urban ecology. Cambridge Univ. Press, pp. 88–119.

Lyon-Jenness, C. 2004. Planting a seed: the nineteenth-century horticultural boom in America. – Bus. Hist. Rev. 78: 381–421.

Mack, R. N. 1986. Alien plant invasion into the intermountain west: a case history. – In: Mooney, H. A. and Drake, J. A. (eds), Ecology of biological invasions of North America and Hawaii vol. 58. Springer-Verlag, pp. 191–213.

Mack, R. N. 2000. Cultivation fosters plant naturalization by reducing environmental stochasticity. – Biol. Invasions 2: 111–122.

Mack, R. N. 2003. Plant naturalizations and invasions in the eastern United States: 1634–1860. – Ann. Mo. Bot. Gard. 90: 77.

Mack, R. N. and Erneberg, M. 2002. The United States naturalized flora: largely the product of deliberate introductions. – Ann. Mo. Bot. Gard. 89: 176–189.

Maloney, K. O., Garten, C. T. and Ashwood, T. L. 2008. Changes in soil properties following 55 years of secondary forest succession at Fort Benning, Georgia, U.S.A. – Restor. Ecol. 16: 503–510.

Marks, P. L. 1983. On the origin of the field plants of the northeastern United States. – Am. Nat. 122: 210–228.

Martin, P. H. and Marks, P. L. 2006. Intact forests provide only weak resistance to a shade-tolerant invasive Norway maple (*Acer platanoides* L.). – J. Ecol. 94: 1070–1079.

Martin, P. H., Canham, C. D. and Marks, P. L. 2009. Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. – Front. Ecol. Environ. 7: 142–149.

Matlack, G. R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. – Ecology 75: 1491–1502.

Matlack, G. R. and Schaub, J. R. 2011. Long-term persistence and spatial assortment of nonnative plant species in second-growth forests. – Ecography 34: 649–658.

Maurel, N., Hanspach, J., Kühn, I., Pyšek, P. and van Kleunen, M. 2016. Introduction bias affects relationships between the characteristics of ornamental alien plants and their naturalization success. – Global Ecol. Biogeogr. 25: 1500–1509.

McLauchlan, K. 2006. The nature and longevity of agricultural impacts on soil carbon and nutrients: a review. – Ecosystems 9: 1364–1382.

Meiners, S. J., Pickett, S. T. A. and Cadenasso, M. L. 2002. Exotic plant invasions over 40 years of old field successions: community patterns and associations. – Ecography 25: 215–223.

Meiyappan, P. and Jain, A. K. 2012. Three distinct global estimates of historical land-cover change and land-use conversions for over 200 years. – Front. Earth Sci. 6: 122–139.

Milbau, A. and Stout, J. C. 2008. Factors associated with alien plants transitioning from casual, to naturalized, to invasive. – Conserv. Biol. 22: 308–317.

Minton, M. S. and Mack, R. N. 2010. Naturalization of plant populations: the role of cultivation and population size and density. – Oecologia 164: 399–409.

Moeller, D. A., Briscoe Runquist, R. D., Moe, A. M., Geber, M. A., Goodwillie, C., Cheptou, P. O., Eckert, C. G., Elle, E., Johnston, M. O., Kalisz, S., Ree, R. H., Sargent, R. D., Vallejo-Marin, M. and Winn, A. A. 2017. Global biogeography of mating system variation in seed plants. – Ecol. Lett. 20: 375–384.

Monnet, A.-C., Vorontsova, M. S., Govaerts, R. H. A., Svenning, J.-C. and Sandel, B. 2020. Historical legacies and ecological determinants of grass naturalizations worldwide. – Ecography 43: 1373–1385.

Montesinos, D. 2021. Fast invasives fastly become faster: invasive plants align largely with the fast side of the plant economics spectrum. – J. Ecol. 2021: 1365-2745.13616.

Mosher, E. S., Silander, J. A. and Latimer, A. M. 2009. The role of land-use history in major invasions by woody plant species in the northeastern North American landscape. – Biol. Invasions 11: 2317.

Mucina, L. 2019. Biome: evolution of a crucial ecological and biogeographical concept. – New Phytol. 222: 97–114.

Mullen, L. A. and Bratt, J. 2018. USA boundaries: historical and contemporary boundaries of the United States of America. – J. Open Source Softw. 3: 314.

Munoz, F., Violle, C. and Cheptou, P.-O. 2016. CSR ecological strategies and plant mating systems: outcrossing increases with competitiveness but stress-tolerance is related to mixed mating. – Oikos 125: 1296–1303.

Nakagawa, S. 2015. Missing data: mechanisms, methods and messages. – In: Fox, G. A., Negrete-Yankelevich, S. and Sosa, V. J. (eds), Ecological statistics: contemporary theory and application. Oxford Univ. Press, pp. 81–105.

Nakagawa, S., Johnson, P. C. D. and Schielzeth, H. 2017. The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. – J. R. Soc. Interface 14: 20170213.

Nerlekar, A. N. and Veldman, J. W. 2020. High plant diversity and slow assembly of old-growth grasslands. – Proc. Natl Acad. Sci. USA 117: 18550–18556.

Niinemets, Ü. and Valladares, F. 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. – Ecol. Monogr. 76: 521–547.

Parker, J. D., Richie, L. J., Lind, E. M. and Maloney, K. O. 2010. Land use history alters the relationship between native and exotic plants: the rich don't always get richer. – Biol. Invasions 12: 1557–1571.

Pearson, D. E., Ortega, Y. K., Eren, Ö., Villarreal, D., Lekberg, Y. and Hierro, J. 2023. Exotic success following disturbance explained by weak native resilience and ruderal exotic bias. – J. Ecol. 111: 2412–2423.

Pemberton, R. W. and Liu, H. 2009. Marketing time predicts naturalization of horticultural plants. – Ecology 90: 69–80.

Perata, P., Armstrong, W. and Voesenek, L. A. C. J. 2011. Plants and flooding stress. – New Phytol. 190: 269–273.

Pierce, S. et al. 2017. A global method for calculating plant CSR ecological strategies applied across biomes world-wide. – Funct. Ecol. 31: 444–457.

Pignatti, S., Menegoni, P. and Pietrosanti, S. 2005. Biondicazione attraverso le piante vascolari. Valori di indicazione secondo Ellenberg (Zeigerwerte) per le specie della Flora d'Italia. – Braun-Blanquetia 39: 1–97.

Polce, C., Kunin, W. E., Biesmeijer, J. C., Dauber, J., Phillips, O. L. and The ALARM Field Site Network 2011. Alien and native plants show contrasting responses to climate and land use in Europe. – Global Ecol. Biogeogr. 20: 367–379.

Pongratz, J., Reick, C., Raddatz, T. and Claussen, M. 2008. A reconstruction of global agricultural areas and land cover for the last millennium. – Global Biogeochem. Cycles 22: GB3018.

Pyšek, P., Křivánek, M. and Jarošík, V. 2009. Planting intensity, residence time, and species traits determine invasion success of alien woody species. – Ecology 90: 2734–2744.

Pyšek, P., Jarošík, V., Hulme, P. E., Pergl, J., Hejda, M., Schaffner, U. and Vilà, M. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. – Global Change Biol. 18: 1725–1737.

Pyšek, P., Manceur, A. M., Alba, C., McGregor, K. F., Pergl, J., Štajerová, K., Chytrý, M., Danihelka, J., Kartesz, J., Klimešová, J., Lucanova, M., Moravcová, L., Nishino, M., Sadlo, J., Suda, J., Tichy, L. and Kühn, I. 2015. Naturalization of central European plants in North America: species traits, habitats, propagule pressure, residence time. – Ecology 96: 762–774.

Pyšek, P., Bacher, S., Kühn, I., Novoa, A., Catford, J. A., Hulme, P. E., Pergl, J., Richardson, D. M., Wilson, J. R. U. and Blackburn, T. M. 2020. MAcroecological Framework for Invasive Aliens (MAFIA): disentangling large-scale context dependence in biological invasions. – NeoBiota 62: 407–461.

Ramankutty, N. and Foley, J. A. 1999. Estimating historical changes in global land cover: croplands from 1700 to 1992. – Global Biogeochem. Cycles 13: 997–1027.

Ramankutty, N., Evan, A. T., Monfreda, C. and Foley, J. A. 2008. Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. – Global Biogeochem. Cycles 22: GB1003.

Ramankutty, N., Heller, E. and Rhemtulla, J. 2010. Prevailing myths about agricultural abandonment and forest regrowth in the United States. – Ann. Assoc. Am. Geogr. 100: 502–512.

Razanajatovo, M., Maurel, N., Dawson, W., Essl, F., Kreft, H., Pergl, J., Pyšek, P., Weigelt, P., Winter, M. and van Kleunen, M. 2016. Plants capable of selfing are more likely to become naturalized. – Nat. Commun. 7: 13313.

Reichard, S. H. and White, P. 2001. Horticulture as a pathway of invasive plant introductions in the United States. – BioScience 51: 103–113.

Reitalu, T., Purschke, O., Johansson, L. J., Hall, K., Sykes, M. T. and Prentice, H. C. 2012. Responses of grassland species richness to local and landscape factors depend on spatial scale and habitat specialization. – J. Veg. Sci. 23: 41–51.

Richardson, D. M. and Pyšek, P. 2012. Naturalization of introduced plants: ecological drivers of biogeographical patterns. – New Phytol. 196: 383–396.

Richardson, D. M., Pyšek, P., Rejmánek, M., Barbour, M. G., Panetta, F. D. and West, C. J. 2000. Naturalization and invasion of alien plants: concepts and definitions. – Divers. Distrib. 6: 93–107.

Samson, F. B., Knopf, F. L. and Ostlie, W. R. 2004. Great Plains ecosystems: past, present, and future. – Wildl. Soc. Bull. 32: 6–15.

Smith, S. A. and Brown, J. W. 2018. Constructing a broadly inclusive seed plant phylogeny. – Am. J. Bot. 105: 302–314.

Stebbins, G. L. 1957. Self fertilization and population variability in the higher plants. – Am. Nat. 91: 337–354.

Stohlgren, T. J., Barnett, D., Flather, C., Fuller, P., Peterjohn, B., Kartesz, J. and Master, L. L. 2006. Species richness and patterns of invasion in plants, birds, and fishes in the United States. – Biol. Invasions 8: 427–447.

Svejcar, T. 2015. The northern Great Basin: a region of continual change. – Rangelands 37: 114–118.

Svejcar, T., Boyd, C., Davies, K., Hamerlynck, E. and Svejcar, L. 2017. Challenges and limitations to native species restoration in the Great Basin, USA. – Plant Ecol. 218: 81–94.

Szakacs, A. D., Krings, A. and Wentworth, T. R. 2022. Shade-tolerance classification of the upland herbaceous flora of the Carolina and Virginia Piedmont. – Am. Midl. Nat. 187: 113–147.

Tognetti, P. M., Chaneton, E. J., Omacini, M., Trebino, H. J. and León, R. J. 2010. Exotic vs. native plant dominance over 20 years of old-field succession on set-aside farmland in Argentina. – Biol. Conserv. 143: 2494–2503.

Valladares, F. and Niinemets, Ü. 2008. Shade tolerance, a key plant feature of complex nature and consequences. – Annu. Rev. Ecol. Evol. Syst. 39: 237–257.

van Kleunen, M. and Johnson, S. D. 2007. Effects of self-compatibility on the distribution range of invasive European plants in North America. – Conserv. Biol. 21: 1537–1544.

van Kleunen, M., Manning, J. C., Pasqualetto, V. and Johnson, S. D. 2008. Phylogenetically independent associations between autonomous self-fertilization and plant invasiveness. – Am. Nat. 171: 195–201.

van Kleunen, M., Weber, E. and Fischer, M. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. – Ecol. Lett. 13: 235–245.

van Kleunen, M. et al. 2018. The changing role of ornamental horticulture in alien plant invasions. – Biol. Rev. 93: 1421–1437.

van Kleunen, M. et al. 2019. The Global Naturalized Alien Flora (GloNAF) database. – Ecology 100: e02542.

Von Holle, B. and Motzkin, G. 2007. Historical land use and environmental determinants of nonnative plant distribution in coastal southern New England. – Biol. Conserv. 136: 33–43.

Walas, Ł., Mandryk, W., Thomas, P. A., Tyrała-Wierucka, Ż. and Iszkuło, G. 2018. Sexual systems in gymnosperms: a review. – Basic Appl. Ecol. 31: 1–9.

Wang, Y., Luo, A., Lyu, T., Dimitrov, D., Xu, X., Freckleton, R. P., Li, Y., Su, X., Li, Y., Liu, Y., Sandanov, D., Li, Q., Hao, Z., Liu, S. and Wang, Z. 2021. Global distribution and evolutionary transitions of angiosperm sexual systems. – Ecol. Lett. 24: 1835–1847.

Weber, E. 2017. Invasive plant species of the world: a reference guide to environmental weeds, 2nd edn. – CABI.

Weigelt, P., König, C. and Kreft, H. 2020. GIFT – a global inventory of floras and traits for macroecology and biogeography. – J. Biogeogr. 47: 16–43.

Wood, S. 2017. Generalized additive models: an introduction with R, 2nd edn. – Chapman and Hall/CRC.

Yensen, D. L. 1981. The 1900 invasion of alien plants into southern Idaho. – Gr. Basin Nat. 41: 176–183.

Zanne, A. E. et al. 2014. Three keys to the radiation of angiosperms into freezing environments. – Nature 506: 89–92.