









RESEARCH ARTICLE

Introduction history mediates naturalization and invasiveness of cultivated plants

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Abstract

Aim: Species characteristics and cultivation are both associated with alien plant naturalization and invasiveness. Particular species characteristics are favoured for cultivation, obscuring the relationship between traits and naturalization success. We sought to better understand the drivers of naturalization and invasiveness by analysing relationships with species characteristics and cultivation and by disentangling the direct effects of characteristics from the indirect effects mediated by cultivation.

Location: Great Britain.

Time period: c. 1000–present.

Major taxa studied: Seed plants.

Methods: We used a comprehensive dataset of 17,396 alien plant taxa introduced to Great Britain before 1850, a country with one of the most well-documented histories of plant introductions. We integrated this with cultivation data from historical and modern records from botanic gardens and commercial nurseries and with trait data. Accounting for time since introduction, we quantified the influences of cultivation and species characteristics on present-day naturalization and invasiveness in Great Britain.

Results: Larger native range size, earlier flowering, long-lived herbaceous growth form, and outdoor cultivated habitat were all associated with naturalization. However,

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these relationships between characteristics and naturalization largely reflected cultivation patterns. The indirect, mediating influence of cultivation on naturalization varied among species characteristics, and was relatively strong for growth form and weak for native range size. Cultivation variables, particularly availability in present-day nurseries, best explained invasiveness, while species characteristics had weaker associations.

Main conclusions: Human influence on species introduction and cultivation is associated with increased probability of naturalization and invasiveness, and it has measurable indirect effects by biasing the distribution of species characteristics in the pool of introduced species. Accounting for human cultivation preferences is necessary to make ecological interpretations of the effects of species characteristics on invasion.

KEYWORDS

alien plants, cultivation, Great Britain, introduction history, invasion, mediation analysis, naturalization, planting frequency, propagule pressure, residence time

1 | INTRODUCTION

The movement of humans and goods around the globe is accompanied by the movement of human-associated organisms. Plants have been cultivated by humans globally for c. 12,000 years as sources of food, medicine, shelter, and ornamentation (Larson et al., 2014; Price & Bar-Yosef, 2011). Throughout this time and especially since the advent of European colonialism in the 15th century, cultivated plants have been introduced to new regions in great numbers (Brockway, 1979; van Kleunen et al., 2015), and about half of the vascular plant species known today are cultivated (van Kleunen et al., 2018). Only a fraction of the plants introduced for cultivation become naturalized, establishing self-sustaining populations in new regions, and a fraction of those go on to become invasive, increasing in abundance and spreading to new areas (Jeschke et al., 2012; Williamson & Fitter, 1996) and often negatively impacting community structure and ecosystem functions (Pyšek, Hulme, et al., 2020; Pyšek et al., 2012; Richardson & Pyšek, 2006; Simberloff et al., 2013). Cultivation is the means by which most currently invasive plants were initially introduced (Hulme et al., 2008; Mack & Erneberg, 2002; Pergl et al., 2020), and the introduction of plants for cultivation has continued to increase over time (Bradley et al., 2012; van Kleunen et al., 2018).

Understanding why certain introduced plants become naturalized or invasive while others do not is of great importance for assessing and managing the risks posed by new introductions and the continued propagation of alien species. Previous work has revealed many associations between naturalization and life history, reproduction biology, competitive ability, native provenance, and evolutionary history (e.g., Lenzner et al., 2021; Pyšek & Richardson, 2007; Rejmánek & Richardson, 1996; van Kleunen et al., 2010). However, the mechanisms that underlie these associations between species' ecology and naturalization are impossible to tease out without accounting for context-dependent anthropogenic effects, including

introduction history and cultivation, that can bias the composition and distribution of traits of introduced species (Pyšek, Bacher, et al., 2020; Pyšek et al., 2015). Introduction history involves (a) colonization pressure, that is, the number of species introduced (Diez et al., 2009; Lockwood et al., 2009); (b) residence time since introduction (Rejmánek, 1995); and (c) propagule pressure, that is, the number of propagules introduced (Lockwood et al., 2005; Simberloff, 2009). Cultivation involves selection of taxa with traits (and selection for traits) that best accommodate human uses or that are best adapted to the cultivated environment (Ensslin & Godefroid, 2019; Martin-Robles et al., 2019; Meyer et al., 2012); therefore, cultivated taxa are more likely to be introduced (higher colonization pressure), introduced earlier (longer residence time), or planted more frequently (higher propagule pressure) (Palma et al., 2021), all of which increase the probability that the taxon will naturalize (Cassey et al., 2018; Kowarik, 1995; Maurel et al., 2016). Additionally, cultivation is linked to naturalization via increased survival, as humans create favourable site conditions for the species they cultivate, adding water and nutrients, tilling the soil, and removing herbivores, pathogens, and/or competitors. This then increases population persistence by dampening the influence of environmental stochasticity and also increases propagule pressure (Mack, 2000; Minton & Mack, 2010). Despite the importance of introduction history, incorporating introduction and cultivation records in studies of invasion is not standard (but see Blackburn et al., 2011; Dehnen-Schmutz et al., 2007a, 2007b; Diez et al., 2009; Hanspach et al., 2008).

Understanding the complete process from introduction to naturalization to invasion requires incorporating introduction and cultivation history, traits, and their interaction. Great Britain is ideal for a comprehensive analysis, as there exist detailed records documenting the nearly complete introduction history of cultivated plants and their naturalization and invasiveness. From the 18th to the mid-20th century, Great Britain was the hub of a global network of 126 botanic gardens throughout its colonies and other dependencies

(McCracken, 1997). Botanic gardens and commercial nurseries mediated the introduction of thousands of plants from these colonies to Great Britain and facilitated their propagation and spread within the country and globally (Alcorn, 2020; Brockway, 1979; Clark, 2012). In order to create a database of alien plant species introduced to Great Britain that was as complete as possible, including taxa that did and did not naturalize, we used all 17,396 alien seed-plant taxa listed in John Claudius Loudon's (1850) *Hortus Britannicus*. We collated data on minimum residence time in cultivation and historical and present-day records of species cultivated in British botanic gardens and sold in commercial nursery and seed catalogues. We merged this with data on species characteristics, including region of origin, native range size, cultivated habitat, height, growth form, and the onset and duration of the flowering period.

To reveal the drivers of invasion, we fit multiple regression models of current naturalization and invasiveness in Great Britain as a function of minimum residence time in cultivation, cultivation variables, and species characteristics. We anticipated a higher probability of naturalization and invasiveness with longer residence time, history of cultivation in historical botanic gardens, availability in historical and modern nurseries, larger native range, taller height, earlier onset of flowering, and longer flowering duration. Furthermore, we expected that residence time, cultivation variables, and species characteristics would be interrelated with one another. Therefore, we used mediation analysis as a modelling framework that incorporates the indirect effect of cultivation on the relationship between species characteristics and naturalization or invasiveness. In this way, we were able to disentangle the direct effects of species characteristics from the indirect effects mediated by introduction history.

2 | METHODS

2.1 | Compiling the database

We used the list of all alien seed-plant taxa in J.C. Loudon's (1850) *Hortus Britannicus*, which provided a relatively complete snapshot of all taxa known to have been introduced to Great Britain by the mid-19th century, including those that naturalized and those that did not, paired with trait data and introduction years. Though more recent sources would list taxa that have naturalized post-1850, it is unlikely that a complete list of introduced species including those that did not naturalize would be available in more recent sources, as introductions to Great Britain in the 19th century were particularly centralized (operating primarily via botanic gardens and an associated small community of collectors and scientists, Brockway, 1979; McCracken, 1997). We considered archaeophytes (i.e., alien taxa introduced and established before 1500 as defined in Preston et al., 2004), neophytes (i.e., aliens introduced and/or established in Great Britain after 1500 in the Euro+Med database, Greuter & Raab-Straube, 2005), and partially native taxa (i.e., taxa native to part of Great Britain and introduced in another part) to be alien in Great

Britain. We repeated the analyses including only neophytes to determine the influence that inclusion of archaeophytes and partially native taxa had on the results. We extracted present-day naturalization status, that is, whether taxa have established and formed self-sustaining populations in Great Britain, from the Global Naturalized Alien Flora (GloNAF) database (van Kleunen et al., 2019; and sources therein: Jones et al., 2019; National Biodiversity Network, 2017; National Biodiversity Network Atlas, 2018; Roy et al., 2012; Zieritz et al., 2019), and present-day invasive status, that is, whether naturalized taxa have spread and become abundant in (semi-)natural habitats in Great Britain, from Stace and Crawley (2015).

Cultivation variables and species characteristics were compiled for the taxa listed in Loudon (1850). Cultivation variables included: the number of botanic gardens in which taxa were planted (using records from four British botanic gardens published between 1796 and 1825, see Supporting Information Appendix S1), whether taxa were available in historical nursery catalogues (using 19 British nursery and seed catalogues published between c. 1375 and 1887; Harvey, 1972, 1974; Supporting Information Appendix S1, Figures S1.1–2), and whether taxa were available in modern nurseries (using the Royal Horticultural Society's online database, The Plant Finder, accessed 13 March 2021, which contains lists from over 530 nurseries, RHS, 2021). Species characteristics included: native region (categorical groupings based on the Taxonomic Databases Working Group, TDWG, level-1 regions, see Supporting Information Appendix S1 and Table S1.1); native range size (number of TDWG level-3 regions); height (in metres); growth form (short-lived herbaceous, long-lived herbaceous, and woody, where short-lived taxa were annual or biennial and long-lived/woody taxa were perennial, Supporting Information Table S1.2); recommended habitat for cultivation in the 19th century (outdoors, indoors in a greenhouse, and indoors with a stove); flowering phenology, that is, first flowering month and flowering duration in months; and whether the taxon was aquatic/terrestrial or a climber/non-climber. We extracted native range data from Kew Plants of the World Online (POWO, 2021), the Germplasm Resource Information Network (GRIN, 2021), the Global Compositae Database (GCD, 2021), the Global Inventory of Floras and Traits (Weigelt et al., 2020), and the Global Biodiversity Information Facility (GBIF, 2021, see Supporting Information Appendix S1). We took data on height, growth form, cultivated habitat, and flowering phenology from Loudon (1850). Flowering phenology data were also extracted from six additional sources and growth form data from 24 additional sources, all detailed in Supporting Information Appendix S1.

We first standardized taxon names from all sources with The Plant List backbone (TPL, 2013) using the 'Taxonstand' R package (Cayuela et al., 2019). Because TPL has not been updated since 2013, we subsequently standardized taxon names with The World Checklist of Vascular Plants backbone (WCVP, 2021) using the 'taxize' R package (Chamberlain et al., 2020). We manually checked taxa missing from these sources for spelling variations using Tropicos (Missouri Botanical Garden, 2021), GBIF, and other online resources. Loudon (1850) includes 27,561 species and

intraspecific taxa, and from these, we removed 291 taxa that were not found in TPL or POWO, 8,399 duplicate taxa (i.e., synonymous names), 1,163 native taxa, and 312 non-spermatophytes, leaving 17,396 taxa (16,724 species and 672 intraspecific taxa) after standardization.

2.2 | Statistical analyses

We conducted all analyses in the R environment, version 4.0.4 (R Core Team, 2021). We first modelled naturalization as a function of individual cultivation variables and species characteristics in logistic regressions using generalized linear models (GLMs) with a logit link function. Minimum residence time in cultivation, calculated as years since introduction to Great Britain for cultivation (relative to 2021), was included as a covariate in all GLMs to account for its effect. We also fit GLMs where invasiveness was the response variable; because invasiveness was a rare event with few observations, we fit invasiveness models with Firth's penalized likelihood method (Firth, 1993) using the 'logistf' R package (Heinze et al., 2020). For models of invasiveness, native region and aquatic habit were not included as covariates and cultivated habitat was categorized as outdoor versus indoor to reduce bias from perfect separation. Height, native range size, and minimum residence time were natural log-transformed to improve model fit and linearity. We centred continuous covariates and standardized them by dividing by two standard deviations to aid in comparison of coefficients between binary and continuous covariates (Gelman, 2008). We assessed model fit using the Akaike information criterion (AIC), and models were considered to have significantly better fit if $\Delta\text{AIC} \geq 10$ relative to a model not including the variable(s) of interest. We used Nagelkerke's pseudo- R^2 to assess the explanatory power of GLMs (Nagelkerke, 1991). We tested whether models including an interaction term with log minimum residence time (LMRT) had a significantly better fit than first-order models. Two additional models of naturalization and invasiveness were fit: (a) as a function of LMRT, flowering duration, cultivated habitat, and the interaction between flowering duration and cultivated habitat, and (b) as a function of LMRT, log height, woodiness (woody versus herbaceous growth forms), and the interaction between log height and woodiness. For the latter, log height was centred and standardized within woody and within herbaceous groups. To measure interrelationships among covariates, we fit GLMs in which cultivation variables were response variables modelled as a function of species characteristics, and we fit linear models in which LMRT was the response variable modelled as a function of each of the other covariates.

Second, we fit multiple GLMs of naturalization as a function of explanatory variables to estimate the effect of each covariate controlling for the others, that is, assuming all other covariates are at their mean (continuous covariates) or baseline values (categorical and binary covariates). Four GLMs were compared: (a) LMRT only, (b) LMRT and all species characteristics, (c) LMRT and all cultivation variables, and (d) all variables (LMRT, species characteristics, and

cultivation variables). Multiple GLMs with invasiveness as the response variable were also fit. No interaction terms were included in multiple GLMs. The process was repeated separately for the covariate set including first flowering month and flowering duration, because 2,146 taxa were missing flowering phenology data. Covariates included in multiple regressions were not collinear (all variance inflation factors < 5, Supporting Information Table S3.4). Models were ranked using AIC and Akaike weights.

Third, we conducted mediation analysis to quantify the indirect effect of cultivation variables on the relationship between species characteristics and naturalization. Evidence for two paths resulting in naturalization were compared: the direct path in which naturalization occurred as a result of species characteristics, and the indirect path in which naturalization occurred as a result of the mediating influence of cultivation variables (Baron & Kenny, 1986; Pearl, 2010). We estimated direct and indirect effects by comparing the estimate of the effect of the explanatory variable, a species characteristic of interest (set at two thresholds or levels for comparison), on the response, naturalization, and on the mediating variable, the cultivation variable of interest (Imai, Keele, & Tingley, 2010; Imai, Keele, & Yamamoto, 2010, see Supporting Information Appendix S2 for details). Mediation models with invasiveness as the response variable were also fit. We included LMRT and additional species characteristics in mediation models as confounding variables to isolate the effect of the characteristic of interest. Indirect and direct effects were estimated only if the effect of the species characteristic on the response, the effect of the characteristic on the mediating variable, and the effect of the mediating variable on the response all differed from zero [i.e., the 95% confidence intervals (CIs) of the coefficients did not overlap zero]. We estimated average direct and indirect effects using a nonparametric bootstrap with 1,000 iterations. We evaluated the sensitivity of estimates of indirect and direct effects to different thresholds (for continuous covariates, e.g., the 10th and 90th percentiles) or levels (for categorical covariates) used for comparison. We conducted mediation analysis using the 'mediation' R package (Tingley et al., 2014).

Because traits that facilitate introduction and naturalization may be reflected in phylogenetic relationships among taxa, we estimated the degree to which phylogenetic correlation structured GLM residuals by fitting phylogenetic logistic regressions (PGLMs, Ives & Garland, 2010). We pruned Smith and Brown's (2018) megaphylogeny of spermatophytes to construct the expected phylogenetic correlation matrix, which we then used to estimate a phylogenetic signal parameter using the 'phylolm' function ('phylolm' function for models with a non-binary response variable) in the 'phylolm' R package (Ho & Ané, 2014). We fit models by maximizing penalized likelihood ('logistic_MPLE' method), and we bootstrapped 1,000 iterations to generate distributions for all estimated parameters. Because all of the models fit in this study had no significant phylogenetic signal (i.e., the phylogenetic correlation parameter indicated no phylogenetic signal and PGLM coefficient estimates were similar to GLM coefficient estimates), we present the results from PGLMs only in Supporting Information Table S3.2.

3 | RESULTS

Of the 17,396 taxa (species and infraspecific taxa) introduced to Great Britain before 1850, 838 have naturalized by the present day (4.8%), and 31 have become invasive (0.2%).

3.1 | Minimum residence time in cultivation

Taxa were introduced from c. 1000 up to just prior to the publication of *Hortus Britannicus* (1846). Taxa that naturalized or became invasive tended to have longer residence times (Figure 1a,b). All variables of interest were associated with LMRT except for being a climber: cultivation in historical botanic gardens, availability in historical or

modern nursery catalogues, taller height, larger native range, earlier first flowering month, moderate flowering duration, short-lived herbaceous growth form, native range of Africa/Eurasia, and cultivation outdoors were all associated with relatively longer residence times (Figure 1c–n).

3.2 | Associations among species characteristics, cultivation variables, naturalization, and invasiveness

Accounting for LMRT, most species characteristics had significant relationships with naturalization (Supporting Information Tables S3.1–2). Taxa cultivated outdoors, native to Eurasia or the Arctic, non-climbers, aquatic species, long-lived herbs, and taxa

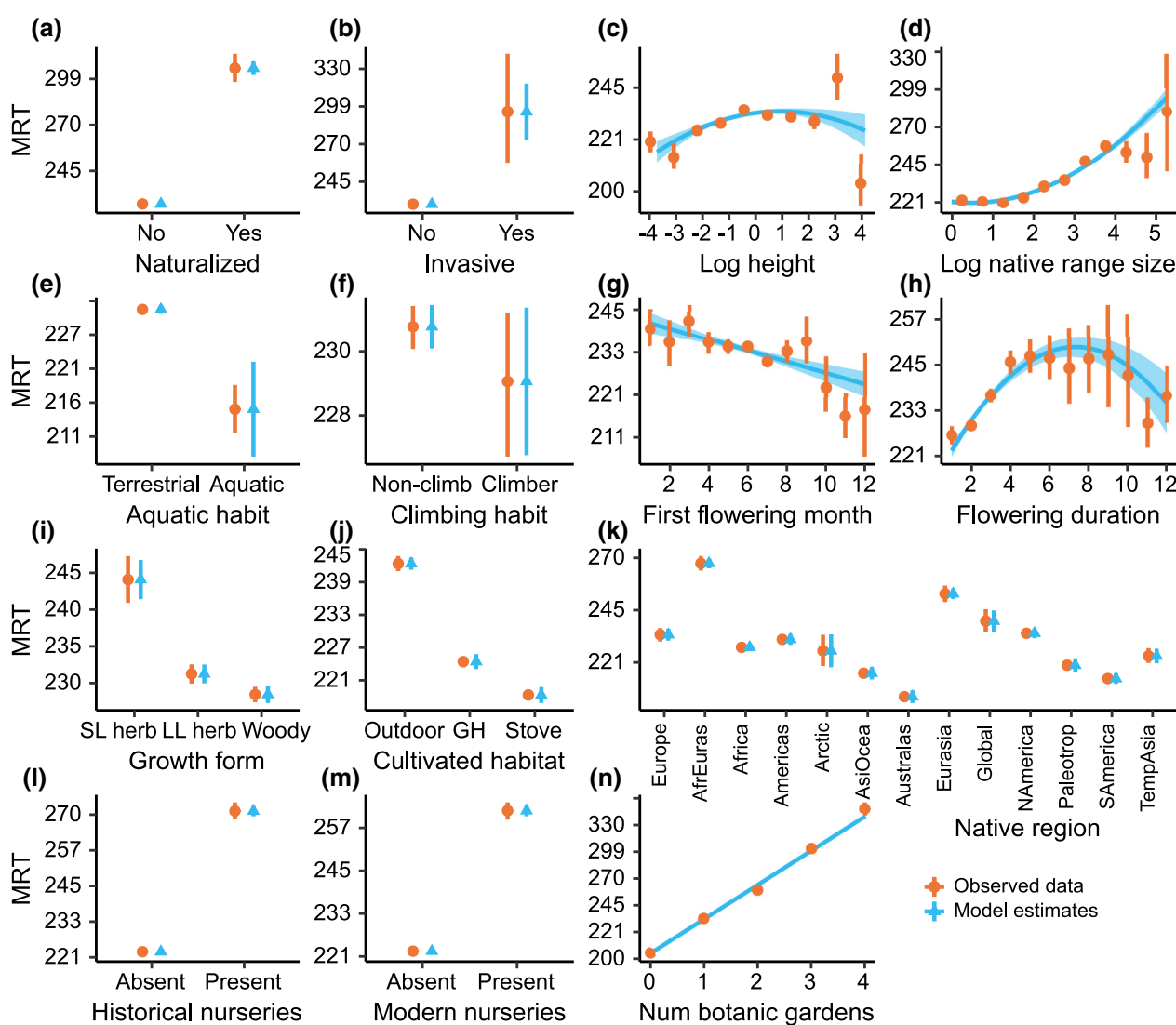


FIGURE 1 Minimum residence time (MRT) in cultivation as a function of (a) naturalization, (b) invasiveness, (c–k) species characteristics, and (l–n) cultivation variables. Observed means and bootstrapped 95% confidence intervals (CIs) are shown in orange (continuous variables were binned). MRT was log-transformed for analysis, and back-transformed means and 95% CIs from LMs are shown in blue. The models for log native range size, flowering duration, and log height included a quadratic term. GH, greenhouse; SL, short-lived; LL, long-lived; AfrEuras, Africa Eurasia; AsiOcea, Asia Oceania; Paleotrop, Paleotropics; TempAsia, Temperate Asia

with larger native ranges or that flowered earlier in the year had relatively higher naturalization probabilities (Figure 2, Supporting Information Table S3.1). Height had a positive association with naturalization among woody taxa, and flowering duration had a positive

association with naturalization among taxa cultivated outdoors (Figure 2b,d, Supporting Information Table S3.1). Some species characteristics also had significant relationships with invasiveness; taxa cultivated outdoors and taxa with earlier first flowering months

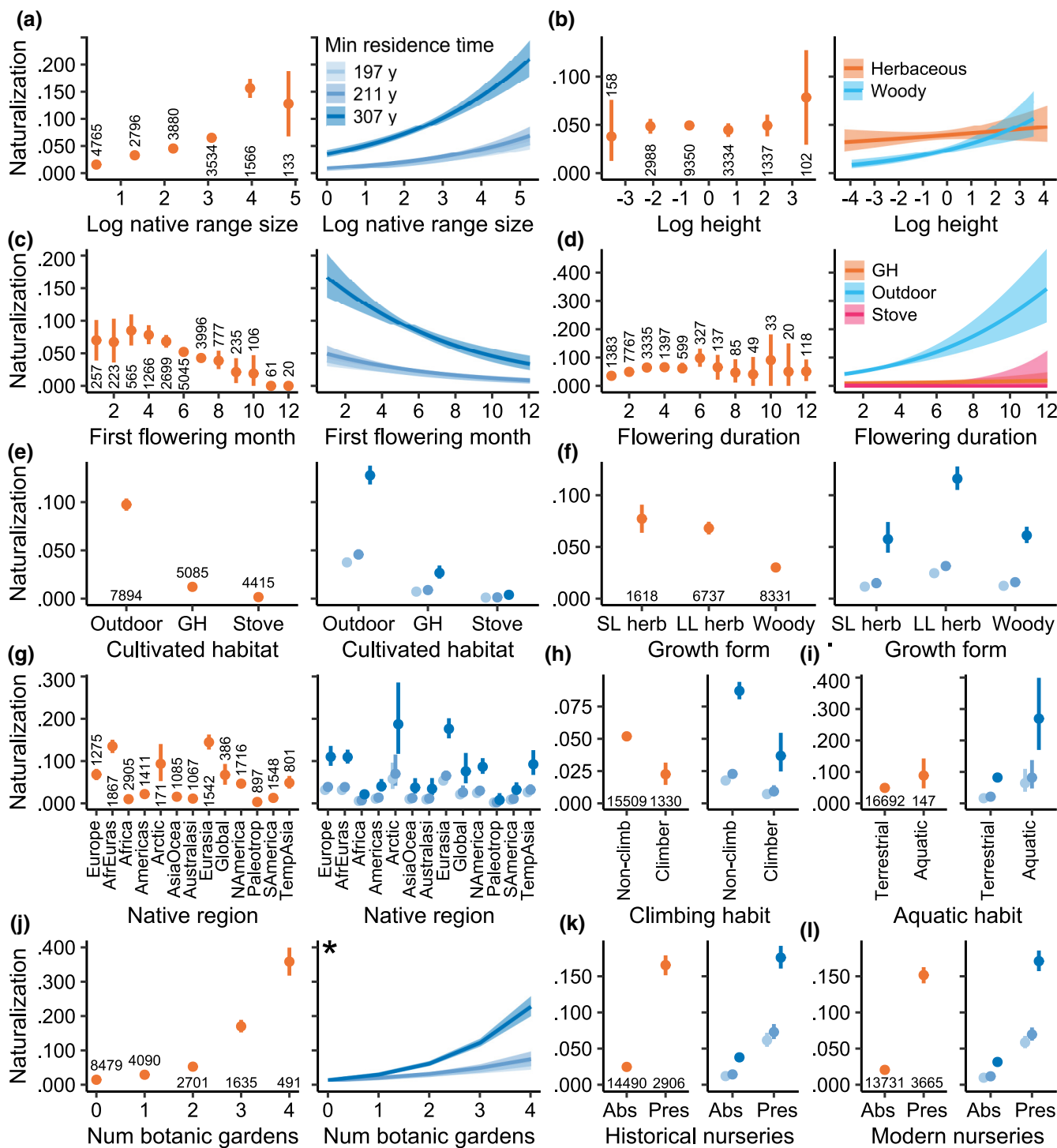


FIGURE 2 Probability of naturalization as a function of (a–i) species characteristics and (j–l) cultivation variables. Observed means and bootstrapped 95% confidence intervals (CIs) are shown in orange, means and 95% profile likelihood CIs from generalized linear models (GLMs) with the covariate of interest and log minimum residence time (LMRT) are shown in shades of blue for three different LMRTs (10th, 50th, and 90th percentiles, the legend shows back-transformed values). The model marked with an asterisk included an interaction term between botanic garden availability and LMRT, because its inclusion significantly improved model fit. The number of taxa in each category is shown above the x axis. AsiaOcea, Asia Oceania; Abs, absent; Pres, present

had relatively higher probabilities of invasiveness (Figure 3d,e, Supporting Information Tables S3.1–2). Height had a positive association with invasiveness among woody taxa and a negative association among herbaceous taxa (Figure 3c, Supporting Information Table S3.1).

Cultivation variables had significant relationships with naturalization (Supporting Information Tables S3.1–2). The number of historical botanic gardens in which taxa were cultivated was positively associated with naturalization (Figure 2j, Supporting Information Table S3.2). Species available in historical and/or modern nurseries had higher naturalization probabilities (Figure 2k,l, Supporting Information Table S3.1). Availability in historical and modern nurseries was also significantly associated with invasiveness (Figure 3a,b), though cultivation in botanic gardens was not (Supporting Information Table S3.2). Models incorporating the number of historical and modern nursery catalogues in which species were available had worse fit than models with presence/absence only (Supporting Information Figure S3.1).

Species characteristics were themselves associated with cultivation variables, especially availability in historical and modern nursery catalogues, and the associations generally matched the relationships between species characteristics and naturalization (Supporting Information Figure S3.2, Tables S3.1–2). The results were overall very similar when the analysis was conducted with

only neophytes, though naturalization rates were slightly lower (Supporting Information Table S3.3).

3.3 | Multivariate models of naturalization and invasiveness

The full model including all species characteristics, all cultivation variables, and LMRT had the best fit and highest explanatory power for naturalization (Nagelkerke's pseudo- $R^2 = .36$, Table 1). Models including only LMRT, LMRT and species characteristics, or LMRT and cultivation variables had lower explanatory power (Nagelkerke's pseudo- $R^2 = .15$, .26, and .28, respectively) and had almost no support relative to the full model (Akaike weight ≈ 0 , Table 1). In the full model, the largest negative coefficients were stove or greenhouse cultivation and North American or Palaetropical native range, and the largest positive coefficients were native range size, presence in modern nurseries, and aquatic habit (Figure 4a, Supporting Information Table S3.4).

For invasiveness, the full model had the best fit and the highest explanatory power (Nagelkerke's pseudo- $R^2 = .21$, Table 1); however, the model with LMRT and cultivation variables had similarly good fit ($\Delta AIC = 5.9$, Table 1). Availability in historical nurseries, availability in modern nurseries, and month of first flowering were the only

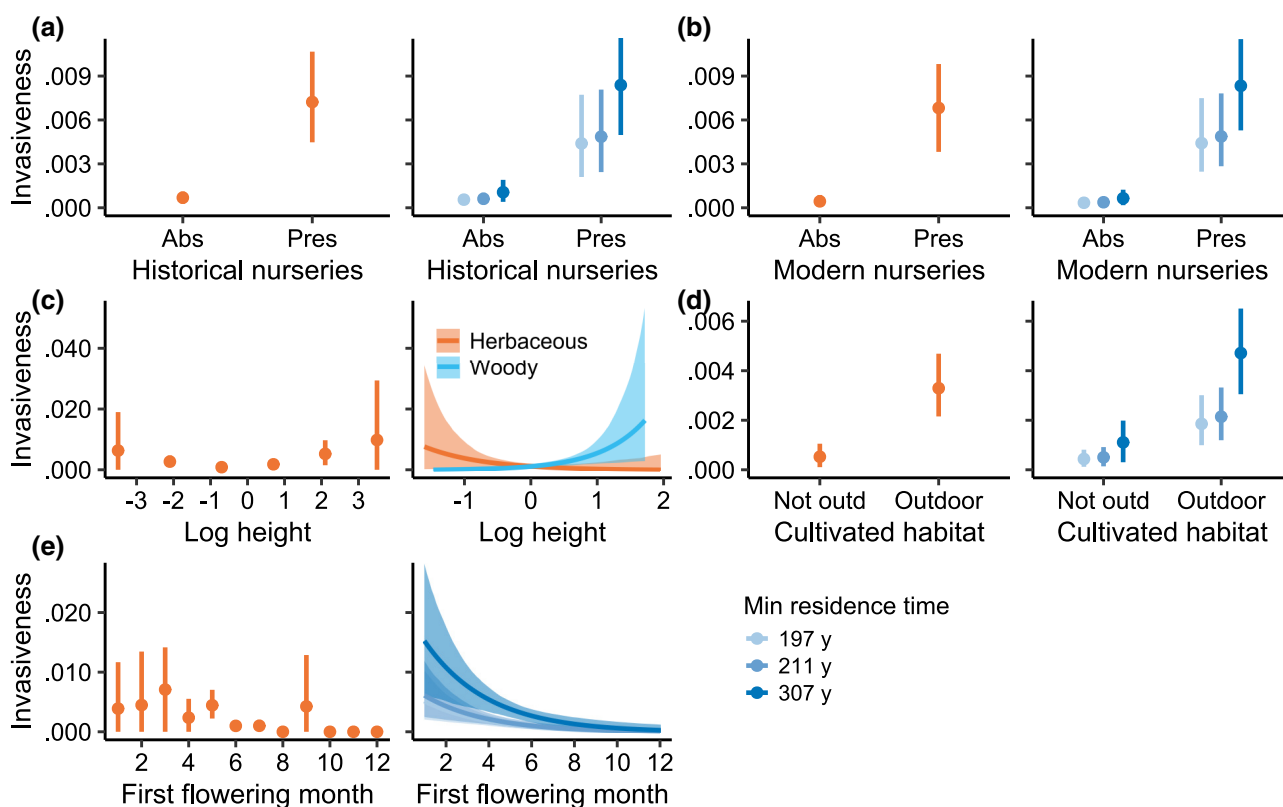


FIGURE 3 Probability of invasiveness as a function of (a, b) cultivation variables and (c–e) species characteristics. Observed means and bootstrapped 95% confidence intervals (CIs) are shown in orange, means and 95% bootstrapped CIs from generalized linear models (GLMs) with the covariate of interest and log minimum residence time (LMRT) are shown in shades of blue for the 10th, 50th, and 90th percentiles of LMRT (the legend shows back-transformed values)

TABLE 1 Fit and explanatory power of multiple generalized linear models (GLMs) of naturalization or invasiveness

Response	Model	n	k	LL	AIC	ΔAIC	Akaike weight	p-R ²
Naturalization	LMRT	15,194	2	-2,427	4,858.3	948.4	1.14×10^{-206}	.16
Naturalization	LMRT, Cultivation variables	15,194	5	-2,148	4,307.0	397.1	5.90×10^{-87}	.27
Naturalization	LMRT, Species characteristics	15,194	22	-2,091	4,226.0	316.1	2.29×10^{-69}	.29
Naturalization	All variables	15,194	25	-1,930	3,909.9	0.0	1.00	.36
Naturalization	LMRT	13,361	2	-2,363	4,729.7	884.7	7.76×10^{-193}	.15
Naturalization	LMRT, Cultivation variables	13,361	5	-2,107	4,223.3	378.3	7.13×10^{-83}	.26
Naturalization	LMRT, Species chars incl. flowering	13,361	24	-2,032	4,112.3	267.3	9.05×10^{-59}	.29
Naturalization	All variables incl. flowering	13,361	27	-1,895	3,845.0	0.0	1.00	.35
Invasiveness	LMRT	15,194	2	-202	408.9	48.0	3.59×10^{-11}	.06
Invasiveness	LMRT, Cultivation variables	15,194	5	-178	366.8	5.9	4.97×10^{-2}	.17
Invasiveness	LMRT, Species characteristics	15,194	8	-187	389.6	28.7	5.57×10^{-7}	.13
Invasiveness	All variables	15,194	11	-169	360.9	0.0	0.950	.21
Invasiveness	LMRT	13,361	2	-200	403.7	53.6	2.29×10^{-12}	.05
Invasiveness	LMRT, Cultivation variables	13,361	5	-177	364.1	14.0	9.11×10^{-4}	.16
Invasiveness	LMRT, Species chars incl. flowering	13,361	10	-177	373.6	23.5	7.88×10^{-6}	.17
Invasiveness	All variables incl. flowering	13,361	13	-162	350.1	0.0	0.999	.24

Note: n = number of data points; k = number of parameters; LL, log likelihood; AIC, Akaike information criterion; p-R², Nagelkerke's pseudo-R²; LMRT, log minimum residence time. Separate models were fit with the subset of taxa that had flowering phenology data available.

coefficients with 95% confidence intervals that did not overlap zero (Figure 4b, Supporting Information Table S3.4).

3.4 | Direct effects of species characteristics and indirect effects of cultivation variables on naturalization and invasiveness

The indirect effect of botanic garden and nursery availability on the relationship between species characteristics and naturalization differed substantially among characteristics (Supporting Information Figures S3.3–5, Table S3.6). For example, while long-lived herbaceous species had higher rates of naturalization than short-lived herbaceous species (after accounting for LMRT), this was attributable to the indirect effect of their broader availability in modern nurseries (average indirect effect > average direct effect, Figure 5b, Supporting Information Table S3.6). Over-representation in modern nurseries also mediated a proportion of the positive effect of aquatic habit on naturalization (Figure 5c, Supporting Information Table S3.6), and presence in modern nurseries tended to have a stronger indirect effect relative to historic nurseries. The positive effect of height, earlier month of first flowering, and outdoor cultivated habitat were partly mediated by over-representation in historical and modern nurseries (Figure 5a,d,f, Supporting Information Table S3.6). In contrast, non-climbing species had higher naturalization rates than climbers despite the latter being over-represented in historical nursery catalogues (i.e., the indirect effect was negative, Figure 5g, Supporting Information Table S3.6).

The indirect effect of cultivation on the relationship between native region and naturalization depended on which two regions were contrasted. For example, presence in modern nurseries mediated the effect of Eurasian origin (relatively high naturalization probability) relative to Palaeotropical origin (relatively low naturalization probability, Supporting Information Table S3.6). However, the indirect effect of botanic garden and nursery availability on the effect of European origin (relatively high naturalization probability) relative to North American or temperate Asian origin (both with relatively low naturalization probability) was negative (Supporting Information Table S3.6), as species from these regions were actually somewhat over-represented in botanic gardens and nurseries when accounting for other factors.

Among species characteristics, only first flowering month and cultivation habitat had a relationship with invasiveness (Supporting Information Table S3.5), and the positive effects of earlier first flowering month or outdoor cultivated habitat on invasiveness were partly mediated by availability in historical and modern nurseries (Supporting Information Figures S3.4–5, Table S3.6).

4 | DISCUSSION

We used a large and comprehensive dataset of seed plants introduced to Great Britain before 1850, including both naturalized species and species that failed to naturalize, to determine the extent to which the effect of species characteristics on the invasion process can be attributed to ecology and human cultivation.

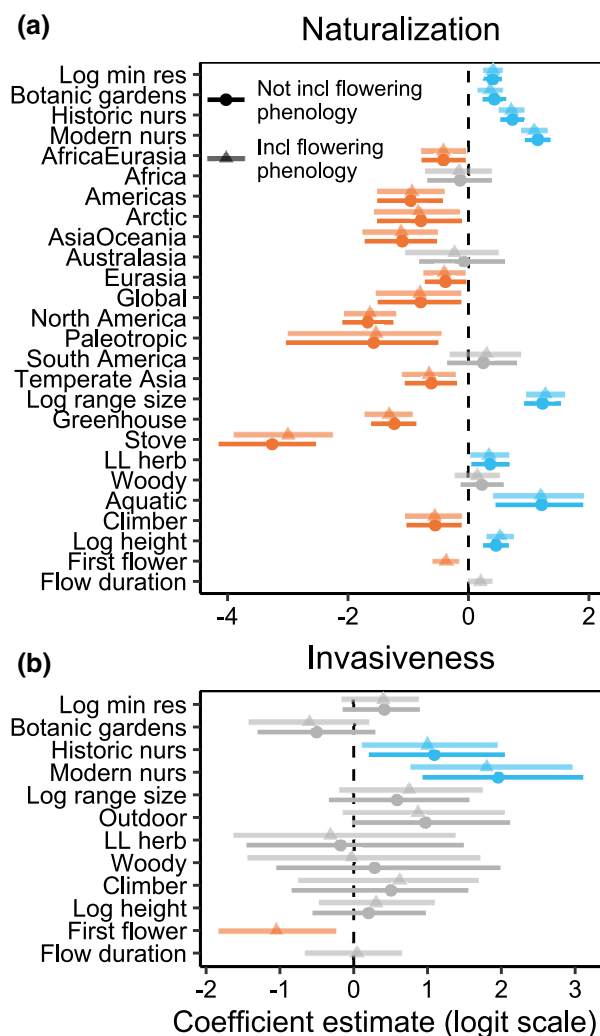


FIGURE 4 Partial regression coefficients estimated in multiple generalized linear models (GLMs) of (a) naturalization and (b) invasiveness as a function of log minimum residence time (LMRT), species characteristics, and cultivation variables. Points are means and error bars are 95% confidence intervals (CIs). Intercepts were fitted but are not shown. Estimates in blue have positive associations and estimates in orange have negative associations with the response. Grey points and error bars have CIs that overlap zero. Baselines for continuous covariates were means; baselines for binary covariates were absences (e.g., not available in historical nursery catalogues, not climbers); and baselines for categorical covariates were Europe for native region, outdoor for cultivated habitat, and short-lived herb for growth form. Log min res, log minimum residence time; nurs, nursery; Flow duration, flowering duration

Previous work has emphasized the importance of introduction history in understanding invasion, because species introductions are not random and are biased in their geographic origins and in their taxonomic and trait composition (Blackburn et al., 2020; Diez et al., 2009; Maurel et al., 2016; Omer et al., 2021; van Kleunen et al., 2020). Previous work has also demonstrated the importance of cultivation in understanding invasion, because cultivation

increases survival, population persistence, propagule pressure, and involves selection for traits desirable and/or advantageous in horticulture (Dehnen-Schmutz et al., 2007a; Guo et al., 2019; Minton & Mack, 2010; Pyšek et al., 2015). We incorporated both introduction history and cultivation in our analysis, first by determining which set of variables had the strongest effects and the highest explanatory power for invasion, and second by estimating the indirect effects of cultivation, measured as availability in botanic gardens and nurseries, in mediating the effects of species characteristics on invasion. We contrasted the relative influences of species characteristics and patterns of historical and modern cultivation for two stages of the invasion process, naturalization and invasiveness.

The link between the length of time since alien taxa were introduced and their subsequent naturalization has been well established (Caley et al., 2007; Kowarik, 1995; Phillips et al., 2010; Pyšek & Jarošík, 2005), and may in some cases have a stronger influence on naturalization than traits (as in Pyšek et al., 2015). In this study, though minimum residence time in cultivation explained naturalization to some extent, the standardized effect size of minimum residence time on naturalization was small relative to the effect sizes of species characteristics and cultivation variables, and the relative effect of minimum residence time on invasion was even further reduced. This is likely because all taxa were introduced before 1850, and thus more recently introduced taxa for which residence time may be particularly relevant have been left out. Importantly, however, minimum residence time was significantly associated with almost all variables in the study, meaning that the trends of which taxa were planted in botanic gardens or were sold in nurseries varied over time, and that the life-history traits, flowering phenology, and origin of taxa introduced over time likewise varied. Thus, failure to account for minimum residence time could lead to inflated estimates of the effects of other variables of interest or even spurious effects (Pyšek & Jarošík, 2005).

Cultivation had high explanatory power and had significant effects on naturalization. For most species characteristics, naturalization was at least in part indirectly mediated by cultivation (Maurel et al., 2016), though direct effects of species characteristics tended to be stronger than indirect effects. Unlike in previous studies (Bucharova & van Kleunen, 2009; Feng et al., 2016; Hanspach et al., 2008; Pemberton & Liu, 2009; Pyšek et al., 2009), cultivation variables did not have the strongest effect size or the highest explanatory power for naturalization relative to species characteristics. This could be explained by the large number of taxa included in this dataset, which contained considerable variation in traits and disparate origins. The difference may also be partially context-specific, as beginning in the late 17th century many British nursery owners specialized in rare and/or exotic plants (Alcorn, 2020), and interest in unusual plants was a feature of Victorian British culture (Valen, 2016). However, cultivation variables, in particular availability in nurseries, had larger effect sizes and better explained invasiveness relative to species characteristics. Among the small set of taxa invasive in Great Britain, there were few distinguishing

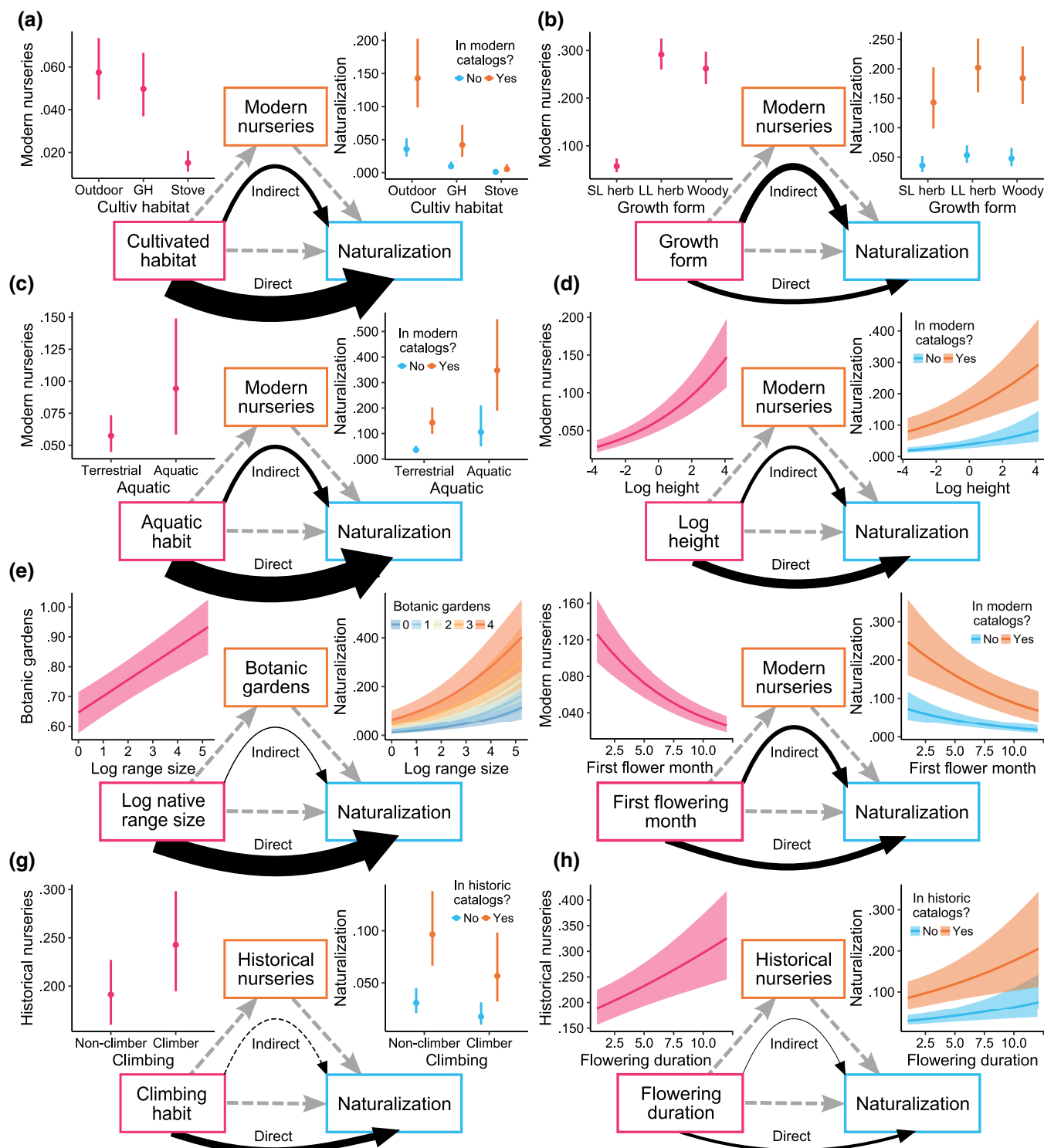


FIGURE 5 A selection of mediation analyses of the direct and indirect effects of species characteristics on naturalization, mediated by cultivation variables. Path diagrams are shown with grey arrows and estimated average direct and indirect effects are shown as black arrows (arrow width is the effect size on the probability scale multiplied by 150). Effects were estimated by comparing the 10th and 90th percentiles for continuous variables, short-lived versus long-lived herbs for growth form, and outdoor versus stove for cultivated habitat. Partial regression estimates, assuming all other variables are at their baseline, are shown on either side of the path diagrams: to the left is the effect of the species characteristic on the cultivation variable, and to the right is the effect of the species characteristic on naturalization (grouped by the cultivation variable). The black dashed arrow represents a negative indirect effect. Cultiv, cultivated

characteristics, but the majority (81%) were available in nurseries. This is in contrast to previous studies, in which species characteristics have been found to be increasingly influential at later invasion stages (Hanspach et al., 2008; Pyšek et al., 2009; but see Pemberton & Liu, 2009). In this study, availability in modern nurseries (2021) was the best predictor of being invasive, and many of the invasive taxa in this dataset are popular ornamentals with many available cultivars (e.g., *Berberis aquifolium*, *Prunus laurocerasus*, *Robinia pseudoacacia*). Only one invasive taxon in this dataset was banned from sale at the time of this study (*Hydrocotyle ranunculoides*), and while six are listed under Schedule 9 of the Wildlife and Countryside Act (1981) for the United Kingdom, meaning it is illegal to allow these taxa to grow in the wild, this does not preclude their sale by nurseries. The relative importance of availability in modern nurseries, which had stronger effects than historical nursery availability on both naturalization and invasiveness, may reflect differences in data availability (19 historical nurseries versus 530 modern nurseries), but nevertheless demonstrates that modern gardening trends are associated with invasion for species introduced centuries ago.

Most of the relationships between species characteristics and naturalization or invasiveness were mirrored in the relationships between species characteristics and cultivation variables, and thus we accounted for the indirect pathway of naturalization or invasiveness via cultivation to derive ecologically meaningful interpretations of the effects of life-history traits and native provenance on the invasion process. We found, for example, that differences in naturalization among growth forms were attributable more to differential presence in modern nursery catalogues rather than to any inherent biological differences (e.g., annual herbs having a reproductive advantage over other growth forms because of shorter generation time, Sutherland, 2004). This adds to the findings of other studies that have incorporated introduction history of plants; for example, Maurel et al. (2016) found that higher naturalization of woody relative to herbaceous ornamental alien plants in Germany could be explained by planting frequency. In sum, cultivation biases can be reflective of effective ecological strategies but should still be accounted for, as demonstrated by studies showing that species with competitive and ruderal functional types were more likely to naturalize (Guo et al., 2018) but were at the same time disproportionately represented in cultivation (Guo et al., 2019).

Among species characteristics, cultivation outdoors (as indicated by Loudon, 1850) had the strongest effects on naturalization and was similarly associated with invasiveness. A portion of this effect was attributable to the over-representation of species cultivated outdoors in botanic gardens and nurseries, but a large portion of the effect was direct. That species cultivated outdoors had higher invasion rates likely reflects suitability to Great Britain's climate and thus winter hardiness. Indeed, winter hardiness has been found to be a strong predictor of naturalization and invasiveness for plants introduced in Great Britain (Dehnen-Schmutz et al., 2007a), Germany (Hanspach et al., 2008; Maurel et al., 2016), and Quebec (Lavoie et al., 2016). The effectiveness of using hardiness as a metric of invasion risk may be limited, however; while alien species are certainly

limited by their physiological tolerances, they are capable of rapid evolution following introduction (Colautti & Lau, 2015), particularly when aided by human selection and hybridization (e.g., in Great Britain, the now highly invasive *Rhododendron ponticum* became hardy through human selection and hybridization, Dehnen-Schmutz & Williamson, 2006; see also Hovick & Whitney, 2014). Further, rising minimum winter temperatures because of climate change may facilitate the naturalization of plants that are currently limited by cold tolerance (Kreyling, 2010).

Native range size had a strong, mostly direct relationship to naturalization. A relationship between native range size and naturalization has been consistently reported in the literature (Dehnen-Schmutz et al., 2007b; Maurel et al., 2016; Omer et al., 2021; Razanajatovo et al., 2016). This relationship has been explained by differential introduction probability (species present in a larger extent are more likely to be introduced elsewhere, Goodwin et al., 1999), but because introduction bias was accounted for in this study, we conclude that this effect can be attributed to ecological or evolutionary factors. For example, species that occur over larger geographic extents may have wider niche breadths as they are exposed to more diverse abiotic and biotic conditions (Brown, 1984), and a recent study has identified positive associations between the range sizes of native and invasive European plants with both local abundance and habitat breadth (Fristoe et al., 2021). However, we did not find a corresponding relationship between native range size and invasiveness, as has been found previously (Rejmánek, 1996; Scott & Panetta, 1993).

We found a positive effect of height on naturalization and invasiveness, particularly among woody species, that was partly attributable to availability in nursery catalogues. Height can increase competitiveness for light (Menges & Waller, 1983; Mitchley, 1988), as well as seed dispersal distance (Moles & Leishman, 2008; Thomson et al., 2011). For these reasons, height has been previously associated with invasion in comparisons between the native and alien flora of Great Britain (Crawley et al., 1996; Williamson & Fitter, 1996), but not the flora of Australia (Hamilton et al., 2005) or of Mediterranean islands (Lloret et al., 2005); with establishment of ornamentals in Britain (Dehnen-Schmutz et al., 2007b); and with naturalization of North American woody species in Europe (Bucharova & van Kleunen, 2009), but not naturalization of woody species in New England (Herron et al., 2007). Considering the heterogeneity of the evidence, it seems likely that cultivation and context dependence are important influences moderating the relationship between height and invasion.

Aquatic plants had higher naturalization rates than terrestrial plants in our study, though this was partly mediated by their over-representation in modern nursery catalogues (only one invasive taxon was aquatic, thus aquatic habitat was not included in invasiveness models). The proportion of introduced aquatic plants that become invasive is high compared to terrestrial plants (Hussner, 2012). While this is partly attributable to ecological factors such as growth form plasticity (Hussner et al., 2021), spread via both seeds and vegetative propagules (Eckert et al., 2016), and clonal integration (You et al., 2016), the role of cultivation and human-assisted propagation

should not be discounted (see also Les & Mehrhoff, 1999; Maki & Galatowitsch, 2004).

We found that climbers had lower rates of naturalization despite being overrepresented in historic nursery catalogues. Climbers have been associated with disturbance (Schnitzer & Bongers, 2011) and likewise with invasiveness (Sutherland, 2004) and establishment success (Dehnen-Schmutz et al., 2007b), but the reverse relationship we observed can likely be explained by climbers being sensitive to freezing embolism (Jiménez-Castillo & Lusk, 2013) and limited by winter temperatures in Great Britain. In the warmer climate of southern Africa, climbers indeed tended to be slightly overrepresented among naturalized species (Omer et al., 2021).

Flowering phenology also plays a key role in alien plant naturalization and invasiveness. Alien species that flower earlier in the year may be more successful by preempting resources from co-occurring species (Wolkovich & Cleland, 2011), and comparisons between native species and alien or invasive species have lent support to this hypothesis (Crawley et al., 1996; Pearson et al., 2012; Pyšek et al., 2003; Wolkovich et al., 2013; Zettlemoyer et al., 2019). In this study, we found that species that flowered earlier in the year had higher naturalization rates, though part of the observed effect was explained by availability in historical and present-day nursery catalogues. Earlier flowering was also the trait that had the strongest association with invasiveness, though again, part of this effect was mediated by availability in nurseries. Alien species that flower for longer may be more successful by having access to more resources and thus broader niches than co-occurring species (Wolkovich & Cleland, 2011), a hypothesis that also has empirical support (Cadotte & Lovett-Doust, 2001; Gerlach & Rice, 2003; Goodwin et al., 1999; Lake & Leishman, 2004). We found an effect of longer flowering duration on naturalization among species cultivated outdoors, but the effect was partly mediated by the positive relationship between flowering duration and historical nursery availability. The confounding influence of introduction bias has been hypothesized in previous flowering phenology comparisons; Godoy et al. (2009) attributed differences in flowering phenology between invasive and native species to the composition of invasive species in different regions rather than to a shared invasive ecological strategy.

5 | CONCLUSION

Patterns in species characteristics for the naturalized flora of a given region are products of species' ecologies, but are influenced by their histories of introduction and cultivation. Plant collecting and exchange mediated by European empires, especially during the 19th century, generated a huge pool of cultivated non-native species in Great Britain and other European countries. This history is apparent in modern landscapes, as 59% of the taxa that are presently naturalized in Great Britain were included in the 1850 dataset used in this study (Loudon, 1850), and of these, 90% were available in 19th century botanic gardens and/or nurseries. This history likewise fostered a culture of gardening in which exotic

species were and are valued, and availability in present-day nurseries was the best predictor of invasiveness in this dataset. We found that species with larger native ranges, particular growth forms, and earlier flowering tended to have higher naturalization success, but at the same time, these species were more likely to be planted in historical botanic gardens or sold in historical and present-day nurseries. The indirect, mediating influence of cultivation on naturalization was nearly always measurable, but its magnitude varied among different characteristics. Cultivation also became an increasingly important influence relative to species traits at later stages of invasion. Cultivation was an important factor for plant naturalization and invasiveness in the past and will remain so in the future; therefore, its indirect effects should be incorporated to distinguish features of introduced plants that confer invasion success from human biases in species introduction and cultivation.

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DATA AVAILABILITY STATEMENT


The data and code in support of this study are publicly available on Dryad (<https://doi.org/10.5061/dryad.kwh70rz5g>).

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BIOSKETCH

Nicole Kinlock is a postdoctoral ecologist interested in plant invasions and the factors that influence invasion at different scales, from individual interactions to macroecological factors. She seeks to characterize large-scale ecological patterns in order to better quantify the variability and understand the context-dependence associated with them.

SUPPORTING INFORMATION

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