Received: 10 October 2022 | Revised: 26 September 2023 | Accepted: 9 October 2023

DOI: 10.1111/ddi.13788

RESEARCH ARTICLE

Diversity and Distributions WILEY

Naturalization of introduced plants is driven by life-form-dependent cultivation biases

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Funding information
National Natural Science Foundation of China, Grant/Award Number: 31500331 and 32071527; The Chinese Scholarship Council, Grant/Award Number: 201906515001; The Third Xinjiang Scientific Expedition Program, Grant/Award Number: 2021xjkk0601; Deutsche Forschungsgemeinschaft, Grant/Award Number: 432253815

Editor: Severin D. H. Irl

Abstract

Aims: Most naturalized plants are escapees from cultivation. Inventories of cultivated introduced species thus offer unique, still underutilized, opportunities to assess naturalization drivers of introduced plants. We used a comprehensive inventory of 13,718 introduced species cultivated in China's botanical gardens to test which species characteristics distinguish the 739 species that have naturalized.

Locations: China.

Methods: We used generalized linear models to test whether the naturalization of cultivated introduced plants in China is associated with functional traits, propagule pressure, environmental niche and introduction history. To test direct and indirect effects of those variables and their relative importance in driving naturalization, we used structural equation models.

Results: We showed that species were more likely to naturalize when they originate from the Americas, are more widely cultivated, and have a longer residence time. Moreover, species were more likely to naturalize if they have a good environmental match, are short-lived herbs, are predominantly propagated from seeds, and, in the case of herbs, are relatively tall compared to other herbs. Part of the latter effects are mediated by how these variables relate to propagule pressure proxies, and this varies among short-lived herbs, long-lived herbs and woody plants.

Main Conclusions: Naturalization is partly driven by life-form-dependent cultivation biases.

KEYWORDS
Alien plants, climatic niches, economic use, exotic plants, introduction history, life-history traits, ornamental plants, planting frequency

1 | INTRODUCTION

Biological invasions are one of the major threats to native biodiversity and ecosystem services (Gioria et al., 2023; Pyšek et al., 2020; Vilà & Hulme, 2017). Globally, over 13,000 vascular plant species introduced by humans have established self-sustaining populations without further human intervention outside their native ranges (i.e. have become naturalized) (van Kleunen, Dawson, Essl, et al., 2015). To understand what drives naturalization, we need data on naturalized species, but also on introduced species that have failed to naturalize (van Kleunen, Dawson, et al., 2010). As most naturalized plants have been introduced intentionally, particularly for cultivation in gardens (Ni & Hulme, 2021; van Kleunen et al., 2018), inventories of cultivated introduced plants offer unique, though still underutilized, opportunities for studying drivers of naturalization.

One group of potential drivers of naturalization are species traits that determine the ability of organisms to survive, grow and reproduce (Gioria et al., 2023; Pyšek & Richardson, 2007; van Kleunen, Dawson, & Maurel, 2015; Wang et al., 2017, 2022), which are usually referred to as functional traits (Violle et al., 2007). Indeed, traits such as those related to resource capture and competition (e.g. plant height), longevity (e.g. life form) and offspring recruitment (e.g. number and size of seeds or vegetative propagules) have frequently been reported to be associated with naturalized or invasive plants (Daehler, 2003; Pyšek & Richardson, 2007; van Kleunen, Weber, et al., 2010). However, most of these studies were restricted to few species, and many did not compare introduced plants that successfully naturalized with those that failed.

Botanical gardens have historically played paramount roles in introducing, cultivating and distributing plants native to other parts of the world (Hulme, 2011; Ni & Hulme, 2021; Pyšek et al., 2011; van Kleunen et al., 2018). Therefore, cultivation in botanical gardens may result in a larger opportunity for introduced plants to escape and naturalize (Hanspach et al., 2008). Indeed, at least 93% of the naturalized plants worldwide are known to be grown in botanical gardens (van Kleunen et al., 2018). Importantly, the selection of plants introduced for cultivation is not random, as species with certain traits (e.g. fast growth and cold hardiness) and with economic uses (e.g. as human food, animal fodder and medicines) are preferred for cultivation (van Kleunen et al., 2018, 2020). Therefore, species traits might affect naturalization not only directly but also indirectly by influencing planting frequency, a proxy for propagule pressure (Lockwood et al., 2005; Maurel et al., 2016; Simberloff, 2009).

The geographical origin and introduction history of introduced plants may also influence their naturalization. Globally, species from the Northern Hemisphere are overrepresented among naturalized species (Fristoe et al., 2023; van Kleunen, Dawson, Essl, et al., 2015). It is possible that Northern Hemisphere species have become naturalized in many regions of the world due to their innate invasiveness linked with their functional traits (di Castri, 1989; van Kleunen, Dawson, Essl, et al., 2015). It is also likely that the history of human movements, such as European exploration and subsequent massive migration, have resulted in the introduction of Northern Hemisphere species to areas beyond their native ranges (Lenzner et al., 2022). In addition, the Northern Hemisphere continents are overrepresented as donors of species with economic uses, many of which are being cultivated (Fristoe et al., 2023; van Kleunen et al., 2020). Indeed, in some regions, the overrepresentation of naturalized species from certain continents is predominantly driven by their higher likelihood of introduction for cultivation (Omer et al., 2021). Furthermore, as there are time lags before a species establishes in the wild, the year of introduction may be important for naturalization (Duncan, 2021; Kowarik, 1995). Although the year of first introduction is rarely available (but see Kinlock et al., 2022), the first record of a species in the wild provides an estimate of the residence time, and this is frequently strongly correlated with naturalization (Pyšek et al., 2003; Rejmánek, 2000). So, studies on naturalization should ideally consider the origin and residence time of the introduced species.

A likely reason for naturalization failure is that the environment, and particularly the climate, in the introduced range is not suitable (Haeuser et al., 2018; Liu et al., 2020). Therefore, introduced species with high climatic suitability, which can be estimated, for example, from species distribution models (Thuiller et al., 2009), and those with large geographical native ranges, indicative of wide habitat breadth (Fristoe et al., 2021), should have the highest naturalization likelihood (Theoharides & Dukes, 2007). Moreover, a species might also fail to naturalize, even if the environment is suitable, if its propagule pressure (i.e. the number of introduction events and the number of individuals per introduction) is too low (Lockwood et al., 2005; Simberloff, 2009). Therefore, studies on success and failure of naturalization should consider environmental suitability and estimates of propagule pressure, such as planting frequencies.

Like many other parts of the world, China has seen a steady increase in plant invasions (Hao & Ma, 2023; Lin et al., 2022). To increase our knowledge about drivers of naturalization, we used the most comprehensive dataset of plant species introduced to China for cultivation (Lin, 2018), and combined it with information

on naturalization and species characteristics. We used generalized linear models to test whether naturalization is associated with functional traits (i.e. life form, propagation mode and maximum height), propagule pressure (i.e. number of botanical gardens, number of provinces where planted, availability in online nursery catalogue and economic use), environmental niche (i.e. continent of origin, number of regions the species is native to and climatic suitability) and introduction history (i.e. residence time). We used structural equation models to test direct and indirect effects of those variables and their relative importance in driving naturalization.

2 | METHODS

2.1 | Data compilation

As the basis for our analyses, we used the list of plants introduced in China for cultivation from the *Catalogue of cultivated plants in China* (Lin, 2018). This catalogue includes a total of 29,631 cultivated plant taxa of which 14,565 are not native to China. The number of botanical gardens ($n=29$) and provinces ($n=33$, also including autonomous regions and other administrative regions such as Taiwan, whereby Macao was merged with Guangdong) of China in which each taxon is cultivated is listed in the catalogue. The botanical gardens are public institutions, affiliated with the Chinese Academy of Sciences (CAS) and/or the State Construction Ministry, and are members of the Chinese Union of Botanic Gardens (CUBG; https://www.cubg.cn/member/). The spatial distribution and founding years of the botanical gardens are provided in Figure S1 of Appendix S1.

To harmonize taxon names in the cultivated flora of China with other datasets (see below), we standardized them according to The Plant List (TPL, version 1.1; http://www.theplantlist.org) using the R package 'Taxonstand' (Cayuela et al., 2021). Our final dataset included 13,718 introduced seed-plant taxa that are recognized by TPL as accepted or unresolved (i.e. potentially accepted). According to *The checklist of naturalized plants in China* (Yan et al., 2019), which defines naturalized species as introduced species that reproduce (i.e. maintain populations) without human intervention, 739 (5.4%) of the cultivated species are currently naturalized in China. The highest numbers of cultivated and naturalized species are found in the coastal provinces (Figure S2).

To assess the effects of geographic origin and native range size on naturalization, we used data on native occurrences in the Taxonomic Databases Working Group (TDWG) level-1 and level-3 regions (Brummitt, 2001), respectively. The TDWG level-1 regions ($n=9$) largely correspond to continents, with the exception that Asia is split into Temperate and Tropical Asia and the Pacific Islands form a separate 'continent'. The TDWG level-3 regions ($n=369$) largely correspond to countries or, for large countries such as the USA and Brazil, to states or provinces. Data on the native TDWG level-3 regions of the introduced species were obtained from Plants of the World Online (POWO; http://www.plantsoftheworldonline.org, last accessed on 6 October 2021) (Govaerts et al., 2021), the Germplasm Resources Information Network (GRIN; https://ars-grin.gov, accessed on 6 November 2021), the Global Compositae Database (GCD, 2021; https://www.compositae.org, accessed on 10 September 2021) and the IUCN Red List (IUCN, https://www.iucnredlist.org, accessed on 30 July 2021). We quantified native range size as the number of TDWG level-3 regions to which a species is native. These data were available for 12,754 of the 13,718 introduced species.

To test the effects of functional traits on naturalization, we compiled data on life form (short-lived herb, long-lived herb and woody), maximum growth height and propagation mode (seeds, vegetative and both) of the cultivated plants. Life form, which is associated with stress resistance and intrinsic growth rate (Guo et al., 2018), was extracted from multiple sources (for details, see Omer et al., 2021), and was available for 10,967 of the 13,718 introduced species. Maximum growth height, which is relevant for competitive ability and seed dispersal distance (Canavan et al., 2019; Thomson et al., 2011), was extracted from multiple sources, including Dave's Garden (one of the largest online encyclopaedias on gardening plants; https://davesgarden.com), the *European Garden Flora* (Cullen et al., 2012), *PLANTATT* (Hill et al., 2004), the *Flora of the USSR* (Cherepanov, 2007) and the *Enzyklopädie der Gartengehölze* (Bärtels & Schmidt, 2014), and was available for 9174 of the 13,718 introduced species. However, as we only used growth height (from here on referred to as just 'height') for species with known life form (see below), the number of species with height data used in the analyses was 7806. Propagation mode (seeds, vegetative and both) refers to the main mode of propagation in cultivation and is indicative of a species' reproductive potential. It was extracted from the European Garden Flora and Dave's Garden for 8094 of the 13,718 introduced species.

To assess the effect of planting frequency, we extracted from Lin (2018) the numbers of botanical gardens and provinces of China in which each species is being cultivated. In addition, because species with economic are more likely to be cultivated than species without economic uses, we extracted economic use information for all species from the *World Checklist of Useful Plant Species* (WCUPS) (Diazgranados et al., 2020). Furthermore, as species that are traded online by plant nurseries (hereafter named 'online-nursery availability') are more likely to be also cultivated outside of botanical gardens, we checked whether or not species were traded as, for example, seeds, live plants or vegetative organs on the Alibaba website (https://www.1688.com/; accessed 29 July–15 August 2019), which is the largest online business-to-business e-commerce platform in China (Yun et al., 2020).

To estimate the potential effect of residence time, we extracted the year of first record in the wild for the species with specimens in the Chinese Virtual Herbarium (http://www.cvh.ac.cn/; accessed 9 June–2 September 2019) as the minimum residence time (i.e. the minimum duration that a non-native species has been present in the introduced range; Rejmánek, 2000). By September 2019, the Chinese Virtual Herbarium contains >7.9 million digitized specimen records from 106 provincial herbariums and provides the collection year for most of the specimens. Such data were available for 620 of

the 739 naturalized species and 2052 of the 12,979 non-naturalized species.

2.2 | Climatic suitability

To quantify climatic suitability of the cultivated introduced species in China, we extracted data on occurrences outside of China from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/; accessed 24 June–12 August 2019), using the R package 'rgbif' (Chamberlain & Boettiger, 2017). We removed obviously erroneous records (e.g. zero coordinates, coordinates in the sea, coordinates with country mismatches, coordinates assigned to country centroids and capitals and coordinates assigned to biodiversity institutions), using the R package 'CoordinateCleaner' (Zizka et al., 2019). When there were multiple occurrences of a species within a 10′ × 10′ grid cell (18.5 km × 18.5 km at the equator, between 17.5 km × 17.5 km and 11.0 km × 11.0 km in China), we kept only one, using the R package 'biogeo' (Robertson et al., 2016). To allow a precise estimation of climatic suitabilities, we only kept species that had at least 40 occurrence records. We found such data for 6094 of the 13,718 introduced species.

To characterize recent climatic conditions, we used climate data averaged from 1970–2000 from the WorldClim database (version 2.1; https://worldclim.org) at a 10′ × 10′ resolution. We selected five of the 19 bioclimatic variables provided by WorldClim: (1) temperature seasonality, (2) minimum temperature of coldest month, (3) precipitation seasonality, (4) precipitation of wettest quarter and (5) precipitation of driest quarter. These climatic variables were chosen as they are known to have the largest influence on plant species distributions (Root et al., 2003). Pearson's correlations among these variables were <0.75 throughout, and the impact of multi-collinearity on model projections should therefore be negligible (Dormann et al., 2013; Dullinger et al., 2017).

We used the BIOMOD framework to parameterize the species distribution models (SDMs) by relating occurrence data from GBIF to the five bioclimatic variables, using the R package 'biomod2' (Thuiller, 2003; Thuiller et al., 2009). Following the approach of Dullinger et al. (2017), four modelling algorithms were used in the SDMs, including generalized linear model (GLM), generalized additive model (GAM), boosted regression tree (BRT) and random forest (RF). Because these algorithms require presence–absence data, whereas GBIF only provides presence data, we generated pseudo-absences. In line with the best-practice recommendations of Barbet-Massin et al. (2012), we used different approaches for the different modelling algorithms: (1) for GLM and GAM, 10,000 randomly distributed pseudo-absences were generated; (2) for BRT and RF, the number of pseudo-absences was set equal to the number of cleaned presences in GBIF. For BRT and RF, the pseudo-absences were selected outside a radius of 200 km around the presences; the generation of pseudo-absences and hence model calibration were repeated 10 times per species to ensure that selected pseudo-absences did not bias the final predictions (Dullinger et al., 2017). For all models, the sum of presences was weighted equally to the sum of pseudo-absences. The predictive performance of the models was evaluated by the true skill statistic (TSS) and the area under the curve (AUC) (Allouche et al., 2006), based on a three-times repeated split-sampling approach in which models were calibrated with 80% of the data and evaluated on the remaining 20%.

The calibrated models were then used to estimate the climatic suitability for each of the 6094 species with sufficient presence records in each of the 34,622 10′ × 10′ grid cells within China under recent climatic conditions through an ensemble forecast approach (Araújo & New, 2007; Thuiller et al., 2009). Because only TSS may be not sufficient to ensure the robustness of the ensemble projection (Leroy et al., 2018; Li & Guo, 2013), we kept models with a TSS score above 0.6 and an AUC above 0.8 (e.g. Bellard et al., 2013). Only the models that met these criteria, were then used to build the ensemble projections. All these models performed very well with an average TSS value of 0.926 ± 0.0005 and an average AUC value of 0.984 ± 0.0002. Furthermore, for each species, we weighted the contribution of each model to the ensemble projection based on its TSS score. The final ensemble projections were thus obtained by calculating the weighted mean of each model. For further analysis, we calculated the mean values across all grid cells in China, as well as across all grid cells per province.

2.3 | Data analysis

First, to test whether introduced species from certain continents (i.e. the nine TDWG level-1 regions) were more likely to naturalize in China than expected by chance, we used a randomization test (see Omer et al., 2021). We randomly shuffled the naturalization status of the introduced plants for which we had information on their continents of origin ($n = 12{,}754$), and repeated this process 9999 times. We then compared the observed number of naturalized species from each donor continent to the numbers expected based on the 9999 randomizations. If the observed value was below the 2.5th percentile or above the 97.5th percentile of the resampled values, we considered it to be significantly lower or higher than expected, respectively. To account for the fact that some species are native to multiple continents, we also conducted an additional randomization test using the subset of taxa native to only a single continent (naturalized: $n = 247$, introduced: $n = 10{,}175$).

Second, to test how naturalization in China (binary data) is related to the other species characteristics, we fitted binomial generalized linear models (GLMs). We used a complementary log–log (cloglog) link function, because the binomial response variable naturalization had many more zeros than ones (Zuur et al., 2009). As the completeness of the data varied among species characteristics, we first analysed each species characteristic separately. The species characteristics included functional traits (life form [categorical; $n = 10{,}967$], propagation mode [categorical; $n = 8094$] and maximum height [continuous; $n = 7806$]), and variables related to propagule pressure (number of botanical gardens [integer; $n = 13{,}718$], number

of provinces [integer; $n = 13{,}718$], availability in online plant nurseries [binary; $n = 13{,}718$] and economic use [binary; $n = 13{,}718$]), the environmental niche (native range size [integer; $n = 12{,}754$], and climatic suitability [continuous; $n = 6094$]), and introduction history (minimum residence time [continuous; $n = 2672$]). As the species are phylogenetically non-independent, we also fitted phylogenetic logistic regressions using the R package "phylolm" (Tung Ho & Ané, 2014; Ives & Garland, 2010). The phylogenetic tree in the analysis (see details in van Kleunen et al., 2020) was modified from the phylogenetic tree of Smith and Brown (2018). As the cloglog link is not available in 'phylolm', we used the default logit link ('logistic_MPLE'). However, as the results were similar to those of the non-phylogenetic GLM (Table 1, Tables S1–S3), we only present the results of the latter in the main text. To facilitate comparisons of the effects of the different explanatory variables, we scaled all continuous variables to have a mean of zero and a standard deviation of one. Moreover, prior to scaling, we natural-log($x+1$)-transformed the number of botanical gardens and the number of provinces, natural-log($x+0.001$)-transformed climatic suitability, and natural-log-transformed native range size, maximum height and residence time to achieve more regular distributions of these variables. As maximum height is associated with life form (i.e. woody plants are usually taller than herbs), we scaled maximum height separately within each life-form category, and then analysed maximum height, life form and their interaction in a single GLM. As an indicator of the explanatory power of each species characteristic, we calculated the pseudo-R^2 of each model (Nagelkerke, 1991).

Third, as some of the explanatory variables in the GLMs might both directly and indirectly affect naturalization, we also analysed the data with structural equation models (SEMs). In the SEMs, we assumed that naturalization of cultivated introduced plants in China could first depend on functional traits, propagule pressure and environmental niche variables. However, as propagule pressure could also depend on plant functional traits and environmental niche variables, we also included paths from functional traits and environmental niche variables to the propagule pressure proxies. Furthermore, as there might be non-unidirectional correlations between three propagule pressure proxies (i.e. number of botanical gardens, number of provinces where planted, and availability in online nursery catalogue), we included correlated errors between the three variables (Figure S3). Given that the effect of maximum height depended on life form, and that the correlations between continuous variables used in the SEMs strongly depended on life form (Figure S4), SEMs were fitted separately for each life form. As residence time was only available for a small proportion of the species, we did not include it in the SEMs. Species with incomplete data were also removed from the SEMs. Because the assumption of multivariate normality was violated, we used piecewise SEMs, which allow for the independent estimation of regression coefficients for each set of variables, as an alternative approach to the traditional variance–covariance based SEMs (Shipley, 2009). To assess model fit, we used the p-value of the global goodness-of-fit test (Fisher's C statistic), the Akaike's information criterion (AIC) and pseudo-R^2 of each component model. The whole-model fit is considered to be good when the p-value (Fisher's C statistic) > .05 (Lefcheck, 2016). We manually compared various combinations of paths within the SEMs by strategically adding or removing paths to optimize the overall model fit and lower the global AIC. Piecewise structural equation modelling was done using the R package 'piecewiseSEM' (Lefcheck, 2016).

TABLE 1 Results of univariate generalized linear models testing the effects of individual species characteristics on naturalization of cultivated species in China.

Response variable	n	Estimate	SE	z-Value	p-Value	R^2
No. botanical gardens[a]	13,718	**0.710**	**0.029**	**24.217**	**<.001**	.104
No. provinces[a]	13,718	**0.736**	**0.030**	**24.316**	**<.001**	.108
Online-nursery availability	13,718	**1.715**	**0.082**	**20.927**	**<.001**	.068
Economic use	13,718	**2.182**	**0.108**	**20.285**	**<.001**	.132
Climatic suitability[b]	6094	**0.703**	**0.036**	**19.541**	**<.001**	.122
Native range size[c]	12,754	**1.343**	**0.042**	**31.729**	**<.001**	.275
Min. residence time[c]	2672	**0.291**	**0.048**	**6.014**	**<.001**	.023
Life form[d]	10,967					.066
Short-lived herb		**1.978**	**0.106**	**18.686**	**<.001**	
Long-lived herb		**0.235**	**0.087**	**2.696**	**.007**	
Propagation mode[e]	8094					.030
Vegetative		**−1.088**	**0.155**	**−6.999**	**<.001**	
Both		**−0.908**	**0.096**	**−9.427**	**<.001**	
Maximum height[c]	7806	**0.325**	**0.043**	**7.635**	**<.001**	.019

Note: Significant estimates ($p < .05$) are highlighted in bold. Nagelkerke R^2 for each model is given.
[a]These variables were natural-log($x+1$) transformed.
[b]This variables was natural-log($x+0.001$) transformed.
[c]These variables were natural-log transformed.
[d]For life form, woody was the baseline.
[e]For propagation mode, seed was the baseline.

3 | RESULTS

China's botanical gardens cultivated 13,718 introduced plant species, and of the 933 naturalized plant species in China, 739 (79.2%) are cultivated.

3.1 | Continents of origin

The continent (i.e. TDWG level-1 region; Figure 1a) that has donated the largest number of naturalized species introduced to China for cultivation is Southern America ($n=369$; 25.7%), followed by Northern America ($n=358$; 24.9%). All continents except Africa, Australasia and the Pacific Islands have donated more naturalized species than expected from randomization tests (Figure 1b). However, among the subset of 10,175 cultivated species native to only a single continent, the number of naturalized species was higher than expected only for Southern America and Northern America, and lower than expected for Africa, Australasia and the Pacific Islands (Figure 1c).

3.2 | Effects of species characteristics on naturalization in China

3.2.1 | Univariate analyses

Univariate analyses showed that naturalization probability increased significantly with the numbers of botanical gardens and provinces where the species is cultivated, and with residence time (Table 1, Figure 2). Naturalization probability also increased significantly with native range size and climatic suitability (Table 1, Figure 2). Furthermore, naturalization probability was 10 times higher when the species has a known economic use, and five times higher when it was available from online plant nurseries (Table 1, Figure 2c,d).

The naturalization probability of a species was 2.4–3 times larger when propagated from seeds (0.12) than when propagated vegetatively (0.04) or by both propagation modes (0.05; Table 1, Figure 2i). Furthermore, naturalization probability was 4.7–5.6 times larger for short-lived herbs (0.28) than for long-lived herbs (0.06) or woody plants (0.05; Table 1, Figure 2h). Tall species were more likely to have naturalized, but while this effect was strong in herbs, it was absent among woody plants (Table 1, Table S2, Figure 2j).

3.2.2 | Structural equation models

Joint analysis of species characteristics in SEMs showed that their direct and indirect effects on naturalization partly varied among the three life forms (Figure 3, Tables S5–S7). For all three life forms, the propagule pressure proxies (number of botanical gardens, number of provinces and online-nursery availability) were positively correlated with each other, and were positively related to economic use (Figure 3). For short-lived herbs, none of the propagule pressure proxies had significant effects on naturalization (Figure 3a). For long-lived herbs and woody plants, the number of botanical gardens and online-nursery availability had significantly positive direct effects on naturalization, and for woody plants, the positive direct effects of economic use was also significant (Figure 3b,c).

The environmental niche variables, climatic suitability and native range size, had strong positive direct effects on naturalization, for all three life forms (Figure 3). For long-lived herbs and woody plants, climatic suitability had additionally positive indirect effects, via the propagule pressure variables, on naturalization (Figure 3b,c), and these were, respectively, 52.1% (long-lived herbs) and 194.9% (woody plants) of the magnitudes of the direct effects. For woody plants, native range size had a weak negative indirect effect on naturalization through online-nursery availability (Figure 3c), which was only 14.7% of the magnitude of the positive direct effect.

Of the two functional traits included in the SEMs, propagation mode had a significant direct effect on naturalization of long-lived herbs and woody plants. Species with both vegetative and seed propagation, or in the case of woody plants also vegetative propagation only, were less likely to naturalize than those with seed propagation only (Figure 3b,c). In addition, for long-lived herbs, species with vegetative propagation had small positive indirect effects through the number of botanical gardens (Figure 3b). For woody plants, species with vegetative propagation or both vegetative and seed propagation had positive indirect effects through the propagule pressure variables, and their magnitudes were, respectively, 127.8% and 186.5% of the magnitudes of the negative direct effects (Figure 3c). Maximum height had a significantly positive direct effect on naturalization for long-lived herbaceous species, but a significantly negative one for woody species (Figure 3b,c). Maximum height had positive indirect effects on naturalization of both life forms through the numbers of botanical gardens and provinces, or, for woody plants, through online-nursery availability (Figure 3b,c). For long-lived herbs, the positive indirect effect of maximum height was similar (99.6%) to the positive direct effect, and, for woody species, it was smaller (72.3%) than the magnitude of the negative direct effect (Figure 3).

4 | DISCUSSION

Data on plants introduced for cultivation provide unique opportunities to uncover why some introduced species have naturalized whereas others failed. Among the 13,718 introduced species cultivated in China, 739 (5.4%) have naturalized. A species was more likely to naturalize when it is from the Americas, widely planted, a short-lived herb, relatively tall and predominantly propagated from seed, and has a good climatic match and a longer residence time. However, SEMs for each life-form category showed that part of the effects of functional traits and environmental niche variables on naturalization are mediated by how they relate to the propagule pressure proxies. Nevertheless, their direct effects on naturalization

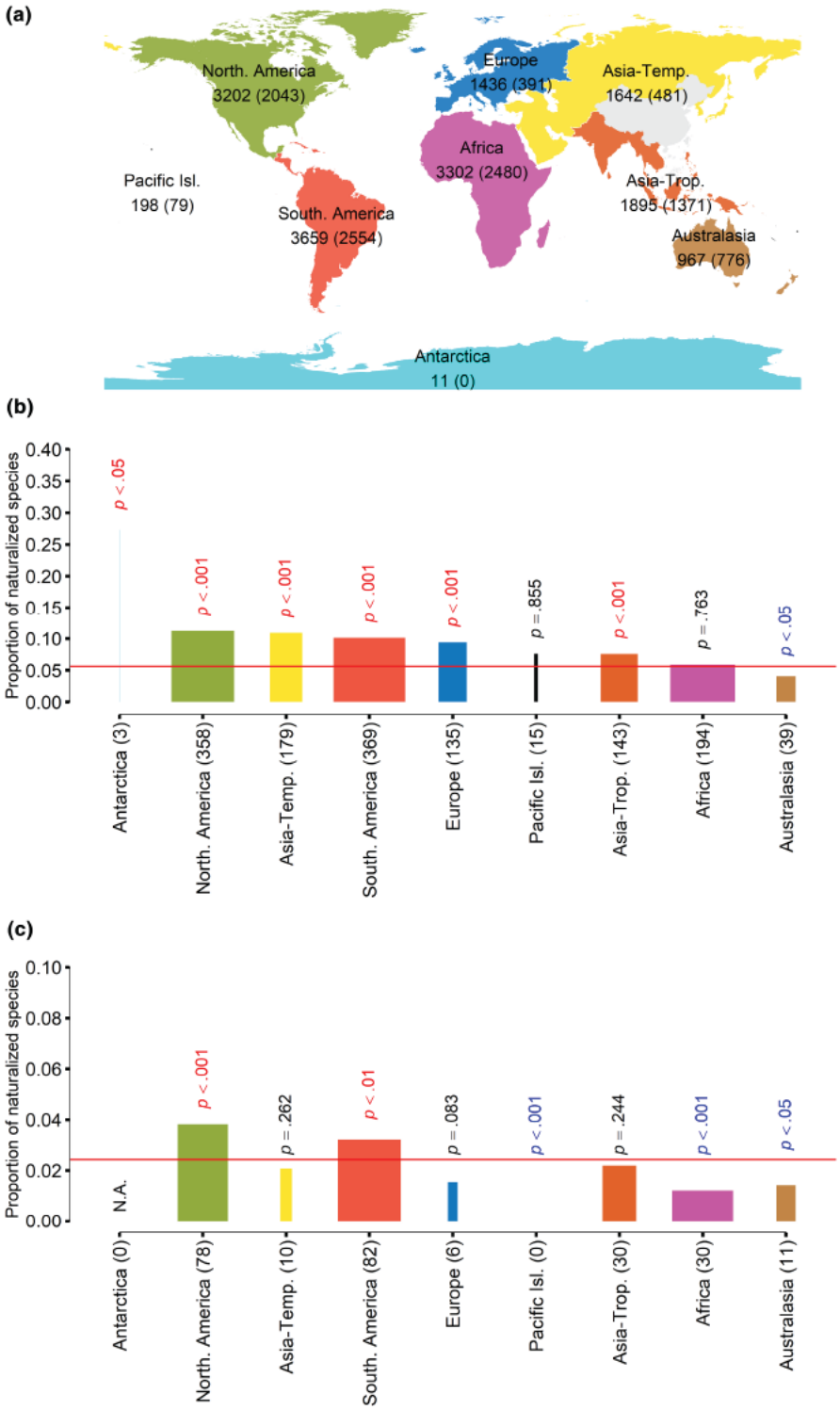

FIGURE 1 Proportions of naturalized species among cultivated species in China donated by each TDWG continent. (a) Map showing the nine TDWG continents with numbers of cultivated species that they donated to China. In brackets are the numbers of species that are only native to the respective continent. (b) Spine plot for the proportion of naturalized cultivated species in China donated by each TDWG continent. (c) Spine plots for the proportion of naturalized cultivated species in China donated by each TDWG continent for the subset of 10,175 species native to only a single continent. The width of each bar is proportional to the number of cultivated species donated by each continent. The red horizontal line indicates the overall proportion of cultivated alien species that has become naturalized in China. The *p* values, which are from two-sided resampling tests, indicate whether the proportion of naturalized cultivated alien species is significantly higher (red) or lower (blue) than expected or does not deviate from expectation (black). The number of naturalized plants donated by each continent is indicated in brackets along the *x*-axis. Note that in b the cumulative number (1435) is larger than the total number of naturalized species (739), because many species are native to multiple continents. Antarctica was excluded from the randomization analysis in c since no cultivated alien plants are only native to Antarctica, but the Pacific Islands were included in the analysis with zero records of naturalized plants and 79 records of alien plants only native to this TDWG continent.

exceeded their indirect effects. Importantly, we found that some of the direct and indirect effects depended on life form. For example, naturalization increased with height for herbs, but not for woody plants. Furthermore, planting frequency variables were least important for short-lived herbs and most important for woody plants, indicating that drivers of naturalization are life-form dependent.

The origins of the cultivated plant species had a significant effect on their naturalization. Almost all TDWG continents had donated more naturalized species than expected. This seemingly surprising result reflects that species with large native ranges, covering multiple continents, were more likely to naturalize. When we restricted the analyses to those species that are native to a single continent, only the ones from Northern and Southern America naturalized more often than expected. This is in line with previous reports that the Americas are also the major donors of invasive species in China (Hao & Ma, 2023; Liu et al., 2006; Weber

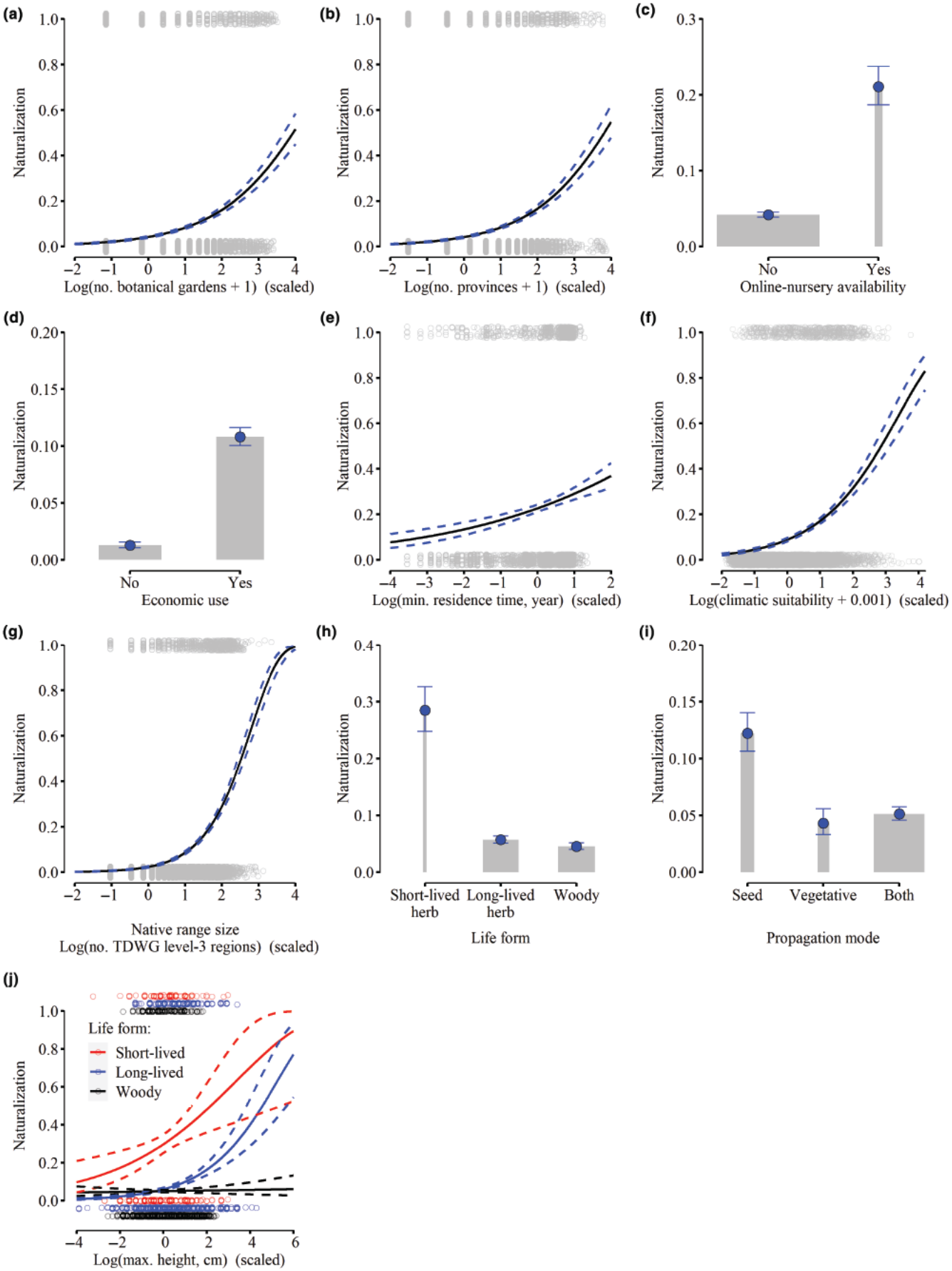
(a)
Naturalization
Log(no. botanical gardens + 1) (scaled)
(b)
Naturalization
Log(no. provinces + 1) (scaled)
(c)
Naturalization
No
Yes
Online-nursery availability
(d)
Naturalization
No
Yes
Economic use
(e)
Naturalization
Log(min. residence time, year) (scaled)
(f)
Naturalization
Log(climatic suitability + 0.001) (scaled)
(g)
Naturalization
Native range size
Log(no. TDWG level-3 regions) (scaled)
(h)
Naturalization
Short-lived herb
Long-lived herb
Woody
Life form
(i)
Naturalization
Seed
Vegetative
Both
Propagation mode
(j)
Naturalization
Life form:
Short-lived
Long-lived
Woody
Log(max. height, cm) (scaled)

FIGURE 2 Naturalization success of cultivated alien plants in China in relation to (a) number of botanical gardens where cultivated, (b) number of provinces where cultivated, (c) online-nursery availability, (d) economic use, (e) minimum residence time (i.e. number of years since first herbarium record), (f) climatic suitability, (g) native range size (number of TWDG level-3 regions), (h) life form, (i) propagation mode and (j) maximum height. For continuous variables, individual data points (jittered to increase visibility), and the fitted lines with 95% confidence intervals from the univariate GLMs are shown. As the effect of maximum height depended on life form, the fitted lines from a GLM including both maximum height and life form are shown. For non-continuous variables, the means (±95% CIs) are shown, and the width of each bar is proportional to the number of species.

et al., 2008). Most likely, this reflects that on average American species are planted in more provinces, are more likely to have economic uses and be available from online nurseries, and that many of them are short-lived herbs propagated from seed (Tables S8 and S9). In addition, the species from North America, but not those from South America, have on average high climatic suitabilities in China (Tables S8 and S9). Furthermore, the extensive trade and travel between the Americas and China over the past half-century have significantly increased the likelihood of native species from the Americas being introduced into China either for cultivation or accidentally (e.g. the trade between the USA and China in Jenkins & Mooney, 2006; Normile, 2004). With the recently established intra-BRICS trade and investment between Brazil and China (Gusarova, 2019), and given the hotspots of biodiversity in Brazil (Myers et al., 2000), the introduction of species from the Americas to China might further increase. Also, the similarity of biomes and taxa between the Americas and China may make it easier to cultivate the American species in China and may have facilitated the successful establishment of American species (Callaway et al., 2006; Guo, 1999). So, the higher naturalization of cultivated species from the Americas in China might largely be driven by differences in propagule pressure, functional traits environmental suitability and trade relationships.

Data on residence time in China was available for only a small proportion of the introduced species, which reflects that most have never been found in the wild yet. The average residence time was c. 70 years, which is relatively short compared to estimates for other regions (Pyšek et al., 2003; Rejmánek, 2000). Likely this can be attributed to the fact that China's economy opened relatively late to the rest of the world. Furthermore, botanical gardens, which have introduced many species into cultivation (van Kleunen et al., 2018), were founded in China mostly in the mid-20th century, later than in, for example, Europe (He, 2002; López-Pujol et al., 2006; Rakow & Lee, 2015). Despite the relatively short range of residence time, we found, like other studies (e.g. Pyšek et al., 2003; Rejmánek, 2000), that residence time was positively associated with naturalization. While residence time is frequently correlated with naturalization, one should keep in mind that successfully naturalized species are more likely to be recorded in the wild than non-naturalized species (Ni, 2023). Indeed, although we found first record data for 620 of the 739 naturalized species (83.9%), we found such data only for 2052 of the 12,979 non-naturalized species (15.9%). Ideally, one would have data on the year of introduction into cultivation, but for most regions such data are rare (Bucharova & van Kleunen, 2009; Feng et al., 2016; Kinlock et al., 2022; Maurel et al., 2016). Nevertheless, residence time is still a valuable estimator of introduction history for non-native flora, especially when historical records for introduced plants are extremely incomplete.

Propagule pressure is considered key to understanding why some introduced species naturalize and become invasive and others do not (Gioria et al., 2023; Lockwood et al., 2005; Simberloff, 2009). Although exact propagule pressures for the introduced species in China are unknown, we considered four proxies: the numbers of botanical gardens and provinces where planted, availability in online nurseries and economic use of the plants. Indeed, when considering all life forms together, all those proxies were positively associated with naturalization and interrelated, indicating the potential role of botanical gardens in the horticulture supply chain (Hulme et al., 2018), and the potential role of botanical gardens in plant invasions (Hulme, 2011; van Kleunen et al., 2018). Species with economic uses, such as for human and animal food, are more likely to be cultivated on agricultural fields and in plantations but also in domestic gardens. In line with the latter, we found that, at least for long-lived herbaceous and woody species, online-nursery availability was positively related to economic use. Previous studies have pointed out the importance of the offline plant-nursery-supply chain as the driver of plant naturalization and invasiveness (Beaury et al., 2021; Hulme et al., 2018; Pemberton & Liu, 2009), but the role of online plant nurseries has been rarely considered (Dong et al., 2023; Humair et al., 2015). Because the online trade in plants started only a few decades ago, it cannot be a cause of plant invasions that happened half a century ago. However, as many online nurseries started as offline nurseries, the current online availability of plants is likely to reflect their offline availability decades earlier (Beaury et al., 2021). More importantly, our finding that naturalized species are more likely to be available online than non-naturalized species shows that introduced species with proven naturalization potential in China continue to have high propagule pressures, and could therefore also spread to parts of China where they are not yet naturalized.

Introduced species with a high environmental suitability should be more likely to naturalize. As environmental suitability determines the native distributions of species (Hui et al., 2011), it has been suggested that species with large native ranges have high environmental tolerances (Dehnen-Schmutz et al., 2007; Hanspach et al., 2008). In line with this, we found that naturalization of cultivated plants in China was positively associated with native range size. It has also been suggested that species with large native distributions are more likely to be collected and introduced into cultivation (Gravuer et al., 2008; Pyšek et al., 2004; van Kleunen et al., 2007). If that is true, we would have expected a positive association between native

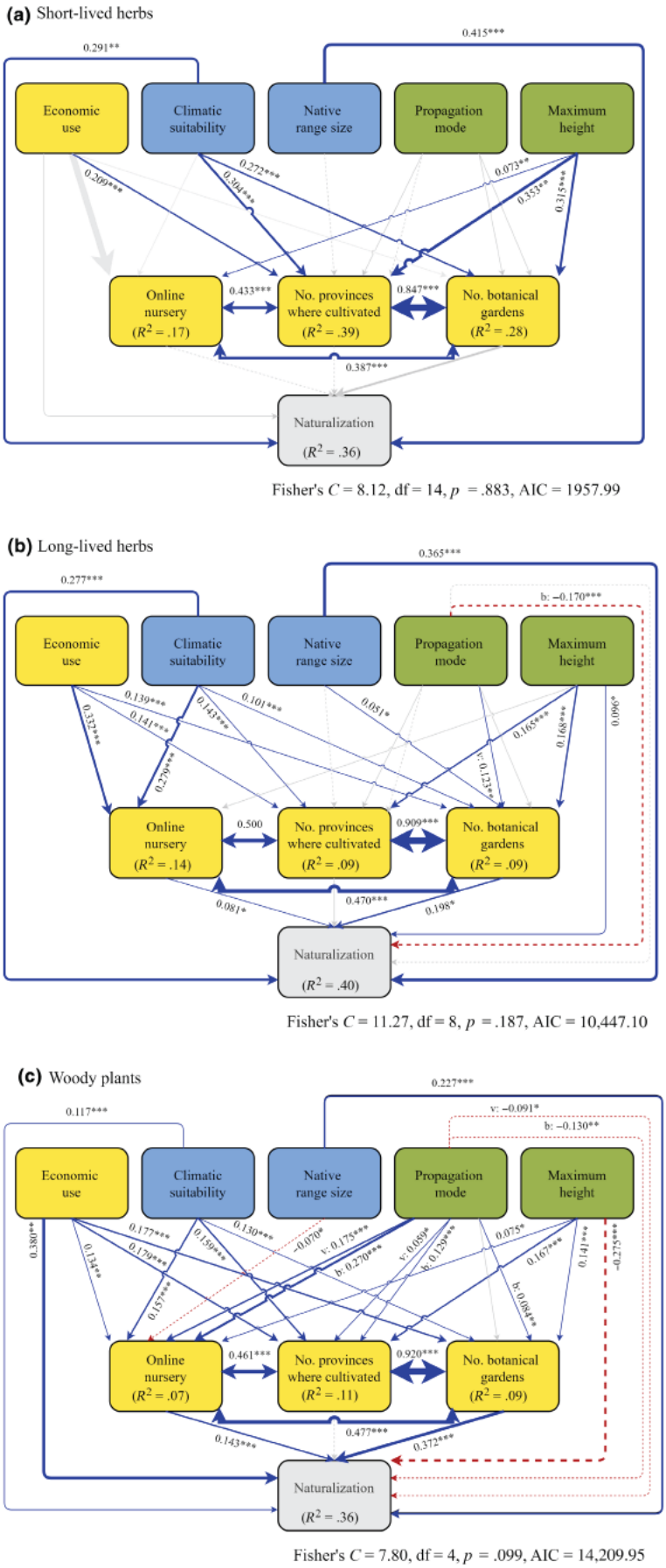

FIGURE 3 Results of piecewise structural equation models (SEMs) for direct and indirect effects of species characteristics on naturalization success of cultivated alien species in China. The SEMs were done for each of the three life forms separately: (a) short-lived herbs, (b) long-lived herbs and (c) woody plants. Species characteristics related to propagule pressure are in yellow, species characteristics related to the environmental suitability are in blue, and functional traits are in green. The full path conceptual diagram is shown in Figure S3, and the diagrams here only show the paths that were kept in the final model. Significantly positive and negative paths are displayed as solid blue and dashed red arrows respectively (*$p < .05$, **$p < .01$, ***$p < .001$), and non-significant paths that were retained in the final model are indicated in grey. Correlations between three of the propagule pressure proxies are shown as double-headed arrows. Path-coefficient estimates provide a measure of the importance of the relationship (the larger the coefficient, the stronger the relationship). The thickness of each line is proportional to the magnitudes of the coefficient. The number of observations for short-lived herbs, long-lived herbs and woody plants is 227, 1484 and 1910, respectively.

range size and our propagule pressure proxies. However, when there were any significant associations, they were actually slightly negative (Figure 3). Therefore, we conclude that the positive effect of native range size on naturalization most likely reflects the high environmental tolerance of species with large native ranges.

The importance of environmental suitability was also evident from the positive effects of climatic suitability on naturalization in China as a whole, as well as on naturalization in the provinces of China (Table S4, Figure S5). Climatic suitability of cultivated plants in China was 1.3 times greater for naturalized than non-naturalized species. Climatic suitability also had indirect positive effects on naturalization, as species with high climatic suitability were planted in more botanical gardens and provinces and were more likely to be available from online nurseries. This emphasizes that climatic suitability is an important criterion for deciding on which species to plant in a garden. Our findings are in line with those of other studies (Dullinger et al., 2017; Mayer et al., 2017; Pouteau et al., 2021) and show that although some introduced species might have shifted their climatic niches relative to those in their native ranges (Atwater et al., 2018; Guisan et al., 2014), climatic suitability based on occurrences outside the region of introduction is nevertheless a good predictor of naturalization potential. It is noteworthy, however, that at least 1980 species with climatic suitability values higher than the average value for the naturalized ones (i.e. climatic suitability >16%) have failed to naturalize yet. This might partly be due to a low planting frequency of these species. For example, *Silene behen*, which has 44.6% climatic suitability is planted in only one of the 29 botanical gardens considered in our dataset. This suggests that still many more of the cultivated plant species have potential to naturalize in China.

In China, 48.5% of the cultivated introduced plants are woody species, 46.9% are long-lived herbs, and the remaining 4.6% are short-lived herbs. However, the short-lived herbs had a five-fold higher proportion of naturalized species than the others. As short-lived species are predominantly propagated from seeds, this could also explain why species with seed propagation were more likely to naturalize than those that are propagated solely vegetatively or both vegetatively and from seed. As many short-lived plants have robust reproductive capacities (Fenesi & Botta-Dukát, 2010), for example, due to their ability of self-fertilization (Razanajatovo et al., 2016), this might allow them to build up large populations from a few initial individuals quickly. Due to their high reproductive capacity and short life cycles, many short-lived herbs are ruderal species that can easily establish in disturbed sites. As many ruderal species are weeds of agricultural fields, it could be that many of the short-lived species in our dataset have also been introduced accidentally as contaminants of imported grains, wool, fibres and other agricultural products (Yu et al., 2020), and therefore effectively had higher propagule pressures than species in the other life-form categories. Possibly, as a consequence of high propagule pressures due to accidental introductions, the effects of cultivation in botanical gardens and the online nursery trade – our proxies of propagule pressure – had no significant effects on naturalization of short-lived herbs, although they had strong effects on long-lived species.

In line with the idea that short-lived herbs might strongly rely on propagule pressure due to accidental introductions, we found that the naturalization of short-lived plants was more strongly correlated with their native range size than was the case for long-lived species (see Figure 3). A larger native range size should increase the likelihood that a species is accidentally picked up and introduced elsewhere, resulting in a high propagule pressure. In addition to the stronger effect of native range size, short-lived plants were also more likely to have overall larger native ranges, with an average of 21.7 ± 1.4 (mean ± SE) TDWG level-3 regions, compared to long-lived herbaceous species (17.3 ± 0.5) and woody species (12.7 ± 0.3; unpublished data). A large native geographical range is, in addition to the high chance of being introduced elsewhere, also likely to be associated with greater intraspecific trait variability and tolerance for a broad variety of environmental conditions. The generally large native ranges of short-lived species should thus confer these species with a greater likelihood of establishing successfully (Omer et al., 2021; Pyšek et al., 2009; Razanajatovo et al., 2016).

Tall plants often have a competitive advantage over short ones, and their propagules can be dispersed over longer distances (Canavan et al., 2019; Guo et al., 2018). Therefore, it is frequently thought that tall species should be better invaders. However, as most woody species are inherently taller than herbaceous species, and woody species have longer generation times, very tall species might actually be less likely to naturalize. Indeed, Omer et al. (2021) recently showed that in Southern Africa species with intermediate heights were most likely to naturalize. Here, we tested explicitly how the effect of height on naturalization varies among life forms. As expected, we found positive associations for the two groups of herbaceous species, whereas there was no such effect among woody species. Moreover, propagation mode, like propagule pressure, has direct effects on naturalization when considering all life forms, but not when considering only short-lived species. This shows that drivers of naturalization can differ among life forms.

Propagation mode and height also had indirect effects on naturalization that varied among the three life-form categories (Figure 3). For short-lived herbs, tall species were more likely to be widely planted and to be available from online nurseries, but without consequence for naturalization as the propagule pressure proxies had no significant effects. For long-lived herbaceous and woody species, tall species were more widely planted, resulting in positive indirect effects on naturalization, which for the woody plants partly counteracted the positive direct effect of height.

For short-lived herbs, propagation mode had no effects on the propagule pressure proxies, possibly reflecting that most are propagated from seed. For long-lived herbs, vegetatively propagated species were planted in more botanical gardens resulting in an indirect positive effect of vegetative propagation on naturalization. For woody plants, species with vegetative propagation or both propagation modes were more likely to be widely planted and to be available from online nurseries. This might reflect that propagation of woody species from seeds takes too long. However, for establishment in

nature, seed production is important as shown by the negative direct effects of vegetative propagation and propagation by both modes on naturalization. These negative direct effects were not yet fully compensated by the indirect positive effects.

Due to the still limited availability of functional traits for many species, we could examine for only a limited set of species traits their relationships with naturalization. This means that our analyses does not capture the full spectrum of traits that could contribute to naturalization. For instance, we did not evaluate traits associated with physiology (e.g. photosynthetic rate, nutrient-use efficiency and chlorophyll content), reproduction (e.g. self-compatibility, timing of flowering and breeding system) and responses to environmental stressors (e.g. tolerance to drought, low nutrients and fire), which may also play significant roles in naturalization (Pyšek & Richardson, 2007; van Kleunen, Weber, et al., 2010). Therefore, our results should be interpreted within the context of these limitations, and future research should strive to include a broader range of species traits to gain a more comprehensive understanding of plant naturalization.

5 | CONCLUSIONS

By combining a large inventory of the cultivated species introduced in China with data on propagule pressure proxies, environmental suitability and functional traits, we showed that all of these species characteristics were significantly associated with naturalization. However, environmental suitability and propagule pressure were more important than the functional traits for naturalization. Environmental suitability and functional traits were also associated with the propagule pressure proxies, and this varied among life forms, indicating that there are life-form dependent introduction or cultivation biases. Nevertheless, the consequences of these biases were smaller than the direct effects of environmental suitability and functional traits on naturalization success in China.

ACKNOWLEDGEMENTS

We thank Jan Hanspach, Holger Kreft, Ingolf Kühn, Noëlie Maurel and Marten Winter for sharing data on species characteristics, and Ji-Zhong Wan for providing suggestions regarding species distribution modelling. We thank the helpful comments by two anonymous reviewers, the handling editor and the editor-in-chief on previous versions of the manuscript. BCD thanks the Chinese Scholarship Council (grant 201906515001), the National Natural Science Foundation of China (grant 31500331, 32071527), and the Third Xinjiang Scientific Expedition Program (grant 2021xjkk0601), FHY thanks the National Natural Science Foundation of China (grant 32071527), MvK and NK thank the German Research Foundation DFG (grant 432253815) for funding.

CONFLICT OF INTEREST STATEMENT

None.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13788.

DATA AVAILABILITY STATEMENT

The data and code in support of this study are publicly available on Dryad (https://doi.org/10.5061/dryad.k6djh9wd3).

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BIOSKETCH

Bi-Cheng Dong is an ecologist who specializes in plant invasions and the ecological, environmental and socio-economic factors that influence invasions at the local, regional, and global scales. He seeks to systematically characterize large-scale invasion patterns, to better quantify the variability and understand the context-dependency associated with them, and also to better predict invasion risk under climate change.

Author contributions: BCD, FHY and MvK conceived and designed research. BCD performed research. BCD, QY, NR, RP, PP, PW, FHY and MvK contributed data. BCD analyzed data with the support of QY and MvK. BCD drafted the paper, and all authors have revised the subsequent drafts. All authors have contributed substantially to the interpretation and discussion of the results.

SUPPORTING INFORMATION

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

How to cite this article: Dong, B.-C., Yang, Q., Kinlock, N. L., Pouteau, R., Pyšek, P., Weigelt, P., Yu, F.-H., & van Kleunen, M. (2024). Naturalization of introduced plants is driven by life-form-dependent cultivation biases. *Diversity and Distributions*, *30*, 55–70. https://doi.org/10.1111/ddi.13788