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Special Feature: Management of Biological Invasions in China

Cultivated alien plants with high invasion potential are more likely to be traded online in China

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Abstract

Biological invasions have become a worldwide problem, and measures to efficiently prevent and control invasions are still in development. Like many other parts of the world, China is undergoing a dramatic increase in plant invasions. Most of the currently 933 established (i.e., naturalized) plant species, of which 214 are categorized as invasive, have been introduced into China for cultivation. It is likely that many of those species are still being traded, particularly online, by plant nurseries. However, studies assessing whether naturalized and invasive species are currently being traded more or less than nonnaturalized aliens are rare. We extracted online-trade information for 13,718 cultivated alien plant taxa on 1688.com, the largest website for domestic B2B in China. We analyzed how the presence in online-nursery catalogs, the number of online nurseries that offerred the species for sale, and the product type (i.e., seeds, live plants and vegetative organs) differed among nonnaturalized, naturalized noninvasive, and invasive species. Compared to nonnaturalized taxa, naturalized noninvasive and invasive taxa were 3.7–5.2 times more likely to be available for purchase. Naturalized noninvasive and invasive taxa were more frequently offered as seeds by online nurseries, whereas nonnaturalized taxa were more frequently offered as live plants. Based on these findings, we propose that, to reduce the further spread of invasive and potentially invasive plants, implementation of plant-trade regulations and a monitoring system of the online horticultural supply chain will be essential.

KEYWORDS
Alibaba platform, e-commerce, horticultural supply chain, invasive plants, naturalized plants, online nurseries, plant invasions

INTRODUCTION

Biological invasions cause major ecological problems around the world (Pyšek et al., 2020; Vilà & Hulme, 2017). Globally, over 13,900 vascular plant species have become naturalized (i.e., have established self-sustaining populations) outside their native ranges (van Kleunen et al., 2019) and over 2500 are considered invasive (i.e., have negative ecological impacts) in at least one region (Pagad et al., 2015). Cultivated alien plants are considered to be the

major source pool of naturalized and invasive plants worldwide (Hulme et al., 2008; van Kleunen et al., 2018; Wilson et al., 2012). Naturalization success and invasiveness of cultivated alien plants can be attributed not only to their traits, such as fast and easy propagation, but also to human factors such as globalization of horticultural industries and advancement of breeding techniques (Azadi et al., 2016; Dehnen-Schmutz et al., 2010; Roberto & Colombo, 2020). Therefore, studying the factors that drive invasions of cultivated alien plants is essential for understanding current invasions, predicting potential future invasions, and ultimately controlling current invasions and preventing new ones.

The number of alien plants that have been introduced into public and private gardens for cultivation purposes and are traded through wholesalers and retailers is enormous (Dehnen-Schmutz et al., 2007a; Hulme, 2015; Hulme et al., 2018; van Kleunen et al., 2018). The horticultural supply chain of wholesalers and retailers has been growing rapidly in recent decades due to the liberalization of international trade and is a critical pathway for the introduction of alien plants (Hulme et al., 2008; Pergl et al., 2017; Pyšek et al., 2011; Reichard & White, 2001). The availability in the horticultural supply chain thus determines the propagule pressure and the invasion potential of cultivated alien plants (i.e., whether they can escape from public gardens, green spaces, and domestic gardens) (Dehnen-Schmutz et al., 2007a; Hulme et al., 2008; Reichard & White, 2001).

With the general increase in e-commerce in recent decades, a rapidly growing branch of the horticultural supply chain is the online-nursery trade. As online trade can easily bypass border control and existing plant-trade regulations, it could accelerate the between- and within-country exchange of live plants and propagules of species with invasion potential (Giltrap et al., 2009; Hulme, 2021; Olden et al., 2021). Indeed, Humair et al. (2015) found that at least 510 plant species (~40%) of a global invasive species list were offered for sale on eBay.com, one of the world's largest online marketplaces. These invasive species were significantly overrepresented in the plant trade on eBay.com compared to the rest of the global flora (Humair et al., 2015). With increased internet access and the availability of express delivery, the online-nursery trade has thus created a fundamentally novel pathway for plant invasions (Humair et al., 2015; Lenda et al., 2014; Pergl et al., 2016; van Kleunen et al., 2018). To develop effective strategies on the management and prevention of plant invasions, we need to know which species are being traded online and whether they are already naturalized or invasive.

A plant's propagation mode is likely to affect its invasion potential (Daehler, 2003; Pyšek & Richardson, 2007; van Kleunen et al., 2010). Cultivated alien plants that are primarily propagated from seeds are likely to be short-lived species that produce seeds in copious amounts, and this characteristic is also likely to facilitate their escape from gardens and their spread in the landscape (van Kleunen et al., 2018). Cultivated alien species, and particularly their cultivars, also tend to have high germination rates (Chrobock et al., 2011), which could further promote invasiveness. Cultivated alien species that are primarily propagated from vegetative organs are usually long-lived clonal plant species, which can rapidly form dense stands. Consequently, some clonal plants also have become extremely invasive (Liu et al., 2006; Pyšek, 1997), particularly when they also produce lots of seeds (Groeneveld et al., 2014; Liu et al., 2020). Nurseries, however, do not only sell seeds or vegetative organs but also sell live plants (i.e., "plants for planting"). For customers, those live plants have the advantage of being ready to plant or ready for use. Some of the species traded as live plants can also easily be propagated from seeds (e.g., *Quercus rubra* L. and *Trachycarpus fortunei* [Hook.] H. Wendl.; Fehr & Burga, 2016; Nicolescu et al., 2020) and/or vegetative propagules (e.g., *Carpobrotus* sp.; Campoy et al., 2018). However, it is also likely that many species sold as live plants are difficult to propagate from seeds or vegetative organs without specific pretreatments, and those species are likely to have a low invasion potential (e.g., *Phalaenopsis aphrodite* Rchb. f.; Hsiang et al., 2011). Nevertheless, although there will be exceptions, given that most naturalized and invasive species can easily be propagated from seeds, we expect that these plants are traded online more often as seeds than as live plants or vegetative organs.

China has one of the largest e-commerce markets worldwide (Statista, https://www.statista.com/study/42335/ecommerce-report/2021). Over the past decade, China's e-commerce market has been gradually replacing the role of the traditional offline marketplace (Li et al., 2020; Zhang & Chen, 2019). As online trade is more difficult to control and offers customers a larger assortment of plant species, the transition from offline to online trade may strongly influence the invasion risk of many cultivated alien plants in China. Currently, already 933 alien plant taxa are naturalized in China, and 214 of those are classified as invasive (Yan et al., 2019). Therefore, by analyzing the e-commerce of cultivated alien plants in the domestic business-to-business (B2B) markets in China, we addressed the following questions: (1) Are plant species that are already naturalized (but noninvasive) or invasive plants currently traded online more frequently than nonnaturalized alien plants? (2) Are naturalized and invasive plants preferentially traded as seeds rather than as vegetative organs or live plants compared to nonnaturalized plants? Based on our findings,

we propose potential management strategies for the online trade of cultivated alien plants in China.

METHODS

Data compilation

We extracted the checklist of alien plant taxa that are cultivated for ornamental purposes in China from the *Catalogue of Cultivated Plants in China* (Lin, 2018). Latin names of all cultivated alien plant taxa were standardized according to The Plant List (TPL, version 1.1; http://www.theplantlist.org) using the R package Taxonstand (Cayuela et al., 2021). Each alien plant taxon was classified according to its invasion status in China as nonnaturalized (i.e., taxa that do not form self-sustaining populations outside of cultivation), naturalized but noninvasive (i.e., taxa that form self-sustaining populations outside of cultivation but not yet widespread), and invasive (i.e., taxa that have spread rapidly and widely and cause adverse effects to biodiversity) following the definitions of Richardson et al. (2000) and the International Union for Conservation of Nature (1999). Information on the status of alien plant taxa was taken from Lin (2018), Ma and Li (2018), and Yan et al. (2019). This resulted in 13,718 alien seed-plant taxa with recognized names (accepted or unresolved), of which 12,979 alien taxa are not yet naturalized in China, 528 are naturalized but noninvasive, and 211 are invasive (Ma & Li, 2018; Yan et al., 2019).

The B2B e-commerce market in China is now led by the Alibaba group (Anwar, 2017; Yun et al., 2020), with its domestic marketplace 1688.com and international wholesale platform Alibaba.com (Statista, https://www.statista.com/study/44442/in-depth-report-b2b-e-commerce/). Although 1688.com mainly serves Chinese B2B, it is designed to allow people in China (including all individual buyers) to order goods and products from suppliers in China. For this study, online-trade information for each cultivated alien plant taxon was extracted from 1688.com. For each plant taxon for sale on 1688.com, the e-commerce platform provides information about the plant product (seeds, live plants, or vegetative organs, the latter including, e.g., bulbs, rhizomes, tubers, and succulent plant cuttings), the names of the online nurseries that sell it, and the provinces and cities where these online nurseries are located. A city here refers to the administrative area of a municipality or a prefecture-level city that contains the city proper and rural counties associated with the city. Using Chinese names of the alien plant taxa as keywords, we searched the online-trade information on 1688.com (accessed 29 July–15 August 2019) for each of the 13,718 cultivated alien plant taxa listed in Lin (2018). To reduce potential mismatches between Chinese and Latin names, we filtered out inaccurate online-trade information of searched alien plant taxa by manually comparing information from the photos and species descriptions provided on 1688.com to information from the Plant Science Data Center of China (https://www.plantplus.cn/). The latter is a searchable website that provides an open-access comprehensive catalog of alien and native vascular plants in China. It features full descriptions of about 40,000 plant species and over eight million plant photos verified by experts. In the end, we obtained 13,468 online-trade information lines for 987 cultivated alien plant taxa, of which 779 taxa are not naturalized in China yet, 162 are naturalized but noninvasive, and 46 are invasive.

To further explore the potential factors influencing the trade frequency and the types of plant products of the nonnaturalized, naturalized noninvasive, and invasive cultivated alien plant taxa, we compiled data on their life forms, minimum residence time, and climatic suitability in China. Life-form data were extracted from multiple sources (for details, see Omer et al., 2021) and categorized into short-lived herbs, long-lived herbs, and woody species. Life-form data were available for 869 of the 987 cultivated alien plant taxa for sale on 1688.com. The minimum residence time of an alien taxon was calculated as the time span between the year 2020 and the year of the collection of its first herbarium specimen in China. The latter data were extracted from the Chinese Virtual Herbarium (http://www.cvh.ac.cn/; accessed 9 June–2 September 2019) and were available for 540 of the 987 cultivated alien plant taxa.

The climatic suitability of each taxon was estimated by projecting its potential distribution in China under the current climatic scenario. In brief, we first used the BIOMOD framework to parameterize species distribution models (SDMs) by relating data on the global occurrence of each alien species, outside of China, from the Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/; accessed 24 June–12 August 2019) to five bioclimatic variables (temperature seasonality, minimum temperature of coldest month, precipitation seasonality, precipitation of wettest quarter, and precipitation of driest quarter) from the WorldClim database (version 2.1; https://worldclim.org) at a $10' \times 10'$ resolution, using the R package biomod2 (Thuiller, 2003). The calibrated models were then used to estimate the climatic suitability for each alien taxon with sufficient presence records (i.e., at least 40 records) under the current climate. Such data were available for 572 of the 987 cultivated alien plant taxa for sale on 1688.com. In Appendix S1, detailed information on data collection, analysis, and results are provided for life form, minimum residence time, and climatic suitability.

Data analysis

For each cultivated alien plant taxon, we calculated the number of online nurseries that offered it for sale, the number of provinces and the number of cities where these online nurseries were located, and the proportion of these online nurseries that sold the taxon as seeds, live plants, or vegetative organs.

We used three groups of generalized linear models (GLMs) to explore the relationships between online-trade variables and invasion status of the cultivated alien plant taxa (i.e., nonnaturalized, naturalized noninvasive, and invasive). We first tested whether the presence-absence on 1688.com of all 13,718 cultivated alien plant taxa on 1688.com is related to their invasion status, using a binomial GLM with a complementary log–log (cloglog) link function. The cloglog link function was used because the presence-absence of alien plant taxa on 1688.com was highly asymmetrical (i.e., the binomial response variable had many more zeros than ones) (Zuur et al., 2009). Second, for the subset of taxa present on 1688.com, we used other GLMs to test whether the number of online nurseries that sold a taxon and the number of provinces and the number of cities where these online nurseries were located depended on the invasion status of the taxon. As these numbers were always positive integers, we applied zero-truncated Poisson GLMs using the "vglm" function in the VGAM package (Yee, 2010). Third, we also tested the effects of invasion status on the proportions of online nurseries that sold a taxon as seeds, live plants, and vegetative organs. Since these binomial response variables were overdispersed, we used GLMs with the quasibinomial function. In the models described earlier, we specified two custom contrasts to separately compare the difference between nonnaturalized and naturalized taxa (including both naturalized noninvasive and invasive taxa) and the difference between naturalized noninvasive and invasive taxa (Schielzeth, 2010). We assessed the significance of the contrasts using likelihood-ratio tests (Zuur et al., 2009). All analyses were conducted using R version 4.1.1(R Core Team, 2021).

RESULTS

The proportion of naturalized plant taxa available from online nurseries in China was about four times higher than that of nonnaturalized taxa (Table 1 and Figure 1). However, compared to naturalized noninvasive taxa, the invasive ones had a significantly lower proportion that were available from online nurseries (31% vs. 22%; Table 1 and Figure 1).

The highest numbers of nurseries that offered alien plant taxa online are located in the coastal provinces and cities (Appendix S1: Figure S1). Accordingly, the highest numbers of nonnaturalized, naturalized noninvasive, and invasive taxa were also for sale from the online nurseries in these provinces and cities (Appendix S1: Figures S1–S3). For the subset of 987 taxa available from online nurseries, the number of online nurseries and the numbers of provinces and cities where these online nurseries were located were significantly higher for naturalized than for nonnaturalized taxa (Table 2 and Figure 2). However, compared to the naturalized noninvasive taxa, the invasive taxa were present in significantly fewer online nurseries (Table 2 and Figure 2A), but there was no significant difference regarding the numbers of provinces and cities where these online nurseries were located (Table 2 and Figure 2B,C).

TABLE 1 Results of generalized linear model (GLM) testing effects of invasion status (nonnaturalized, naturalized noninvasive and invasive) on the online-nursery availability of cultivated alien plant taxa. The number of observations is 13,718.

Responses	df	χ^2	p
Online-nursery availability			
Nonnaturalized versus naturalized	1	**324.91**	**<0.001**
Naturalized noninvasive versus invasive	1	**6.07**	**0.014**

Note: Values are in bold where $p < 0.05$.

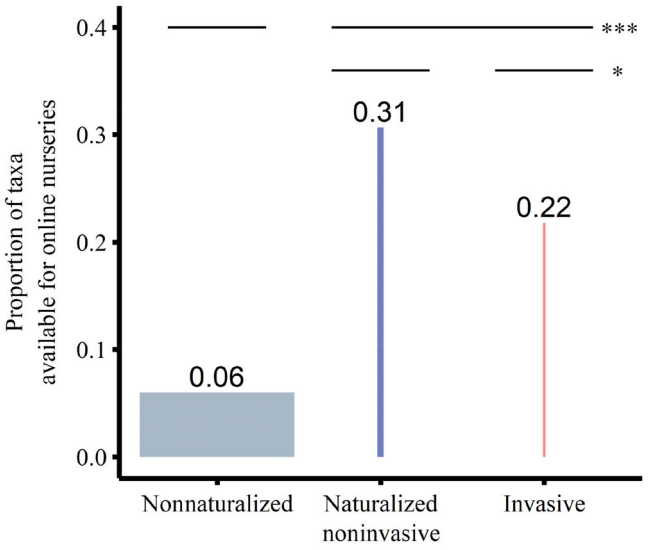

FIGURE 1 Barplots for effects of invasion status (nonnaturalized, naturalized noninvasive, and invasive) on online-nursery availability (presence, absence) of cultivated alien plant taxa. Horizontal lines and asterisks indicate p values (***<0.001, *<0.05) for contrasts of invasion status, that is, nonnaturalized versus naturalized (including invasive) and naturalized noninvasive versus invasive. The width of each bar is proportional to the number of cultivated alien taxa in each category (total $n = 13,718$).

TABLE 2 Results of vector generalized linear models (VGLMs) testing the effects of invasion status (nonnaturalized, naturalized noninvasive, and invasive) on the number of online nurseries that offered a taxon for sale and the number of provinces and cities where these online nurseries were located. The number of observations is 987.

Responses	df	χ^2	*p*
No. online nurseries			
Nonnaturalized versus naturalized	1	**1106.61**	**<0.001**
Naturalized noninvasive versus invasive	1	**20.62**	**<0.001**
No. provinces			
Nonnaturalized versus naturalized	1	**147.37**	**<0.001**
Naturalized noninvasive versus invasive	1	0.01	0.935
No. cities			
Nonnaturalized versus naturalized	1	**245.64**	**<0.001**
Naturalized noninvasive versus invasive	1	2.12	0.146

Note: Values are in bold where $p < 0.05$.

The proportion of online nurseries that had a taxon for sale as seeds was significantly higher for naturalized than for nonnaturalized taxa (60.6% vs. 18.7%), and among naturalized taxa it was higher for invasive than for noninvasive taxa (68.1% vs. 53.2%; Table 3 and Figure 3A). The opposite pattern was found for the proportions of online nurseries that sold a taxon as live plants or as vegetative organs (Table 3 and Figure 3B,C). However, the difference in the proportion of online nurseries that sold a taxon as vegetative organs between invasive and naturalized noninvasive taxa was statistically not significant (Table 3 and Figure 3C).

DISCUSSION

Wholesalers and retailers in the horticultural supply chain in China have increasingly entered the e-commerce market over the last decades (Tang, 2016). Among the 13,718 alien plant taxa known to be cultivated in China (Lin, 2018), we found 987 taxa (7.3% of the total) for sale on 1688.com (data available till August 2019). Taxa that are already naturalized in China, including invasive ones, were four to five times more likely to be on offer than nonnaturalized taxa, and they were for sale in more nurseries, cities, and provinces. Although naturalized and invasive taxa were more likely to be on offer as seeds, nonnaturalized taxa were more likely to be on offer as live plants or vegetative organs. The latter fact likely reflects that plants that are easily propagated from

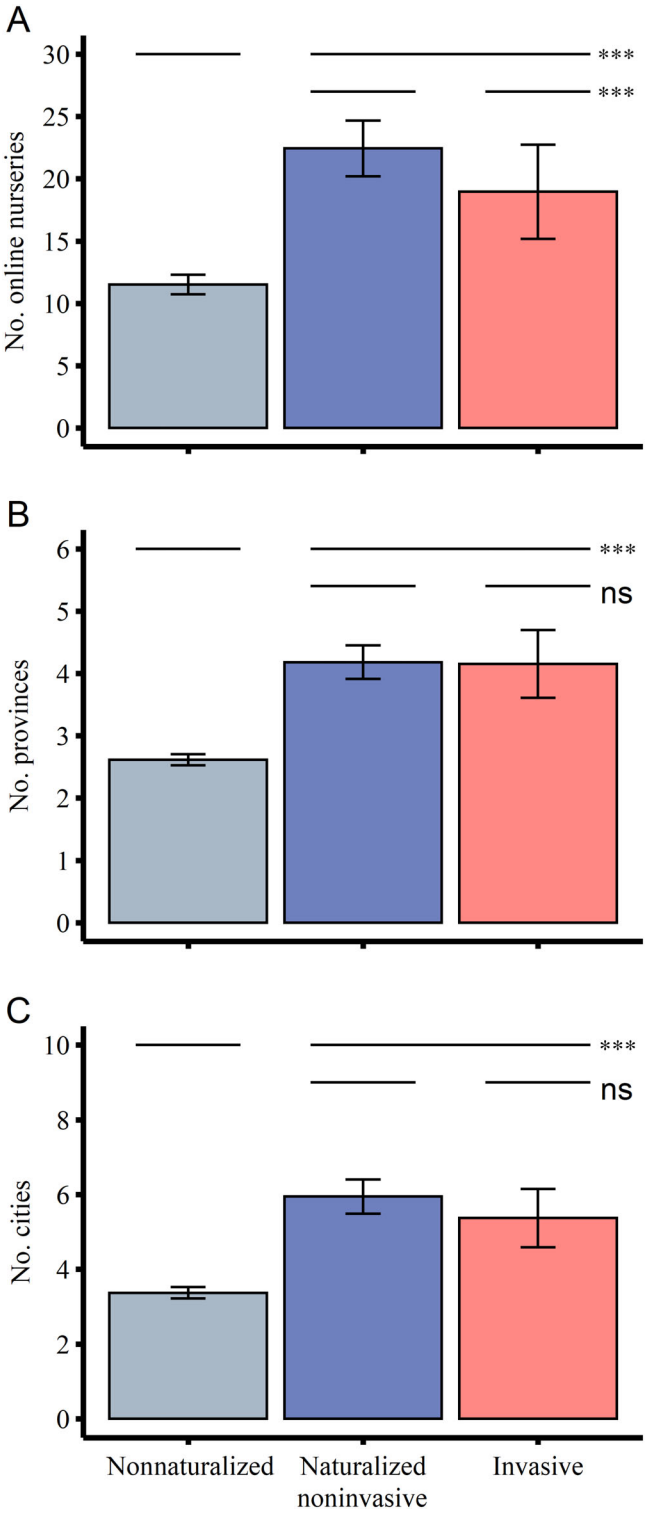

FIGURE 2 Barplots for effects of invasion status (nonnaturalized, naturalized noninvasive, and invasive) on (A) number of online nurseries that offered a taxon for sale, (B) number of provinces where these online nurseries were located, and (C) number of cities where they were located. The bar height and error bar represent mean ± SE. Horizontal lines and asterisks indicate *p* values (***<0.001, ns >0.05) for contrasts of invasion status, that is, nonnaturalized versus naturalized (including invasive) and naturalized noninvasive versus invasive.

TABLE 3 Results of generalized linear models (GLMs) testing effects of invasion status (nonnaturalized, naturalized noninvasive, and invasive) on the proportions of online nurseries that offered a taxon for sale as seeds, live plants, or vegetative organs. The number of observations is 987.

Responses	df	χ^2	*p*
Proportion of nurseries that sold seeds			
Nonnaturalized versus naturalized	1	**109.31**	**<0.001**
Naturalized noninvasive versus invasive	1	**3.33**	**0.045**
Proportion of nurseries that sold live plants			
Nonnaturalized versus naturalized	1	**100.49**	**<0.001**
Naturalized noninvasive versus invasive	1	**3.28**	**0.047**
Proportion of nurseries that sold vegetative organs			
Nonnaturalized versus naturalized	1	**3.51**	**0.013**
Naturalized noninvasive versus invasive	1	0.32	0.448

Note: Values are in bold where $p < 0.05$.

seeds are also the ones that have the highest naturalization potential.

Online-nursery availability of naturalized and invasive taxa

Naturalized and invasive cultivated taxa were more likely to be on offer on 1688.com than nonnaturalized ones, and they were on offer at almost twice the number of online nurseries. Similarly, Humair et al. (2015) found that invasive plants were overrepresented on the international e-commerce platform eBay.com (Humair et al., 2015). These findings most likely reflect that taxa that are more widely available on the market, and therefore have higher current and most likely also historical propagule pressures, are more likely to naturalize and become invasive. Previous studies have shown that naturalized alien plants have often also been introduced earlier into cultivation than nonnaturalized plants (Feng et al., 2016; Kinlock et al., 2022; Maurel et al., 2016). This suggests that cultivated alien plants that are now naturalized may have been more prevalent in the early horticulture markets than those that have not yet become naturalized, and this early availability may also have resulted in more marketing for those species by plant nurseries (Pemberton & Liu, 2009). For example, among the *Acacia* species (family Leguminosae) that are available on 1688.com, the naturalized *Acacia farnesiana* (L.) Willd., which was introduced at least 115 years ago, has been sold at 50 online nurseries, whereas the nonnaturalized *Acacia mangium* Willd.,

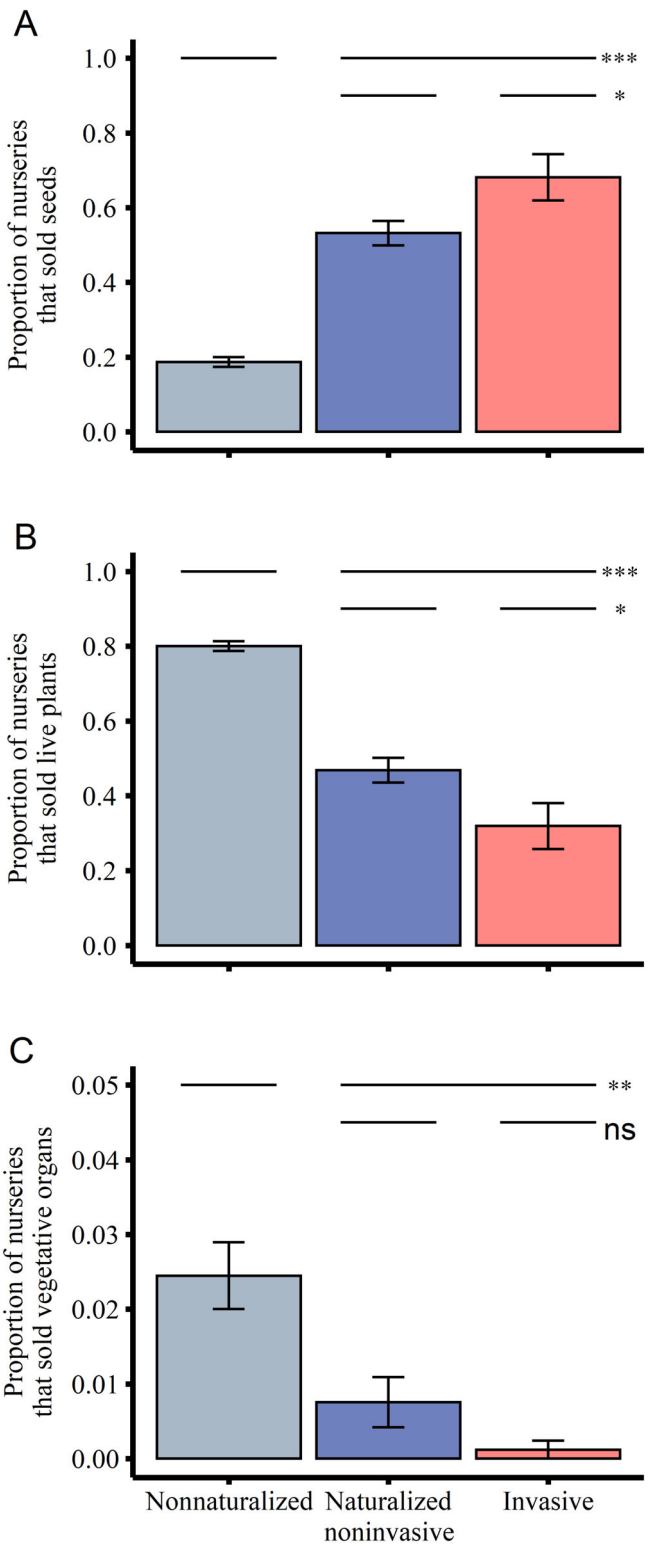

FIGURE 3 Barplots for effects of invasion status (nonnaturalized, naturalized noninvasive, and invasive) on proportion of online nurseries that offered a taxon for sale as (A) seeds, (B) live plants, or (C) vegetative organs. The bar height and error bar represent mean ± SE. Horizontal lines and asterisks indicate *p* values (***<0.001, **<0.01, *<0.05, ns >0.05) for contrasts of invasion status, that is, nonnaturalized versus naturalized (including invasive) and naturalized noninvasive versus invasive.

which was introduced only about 35 years ago, has only been found for sale at one online nursery. Although the year of first cultivation is not known for most alien plant taxa in China, available data on first records in the wild show that naturalized and nonnaturalized cultivated plants in China had average minimum residence times of 89 and 69 years, respectively (Appendix S1: Figure S8A and Table S1). A high availability in online nurseries indicates not only a likely high propagule pressure but also a wide spatial distribution of traded plants (Dehnen-Schmutz et al., 2007a). Indeed, the numbers of cities and provinces where the online nurseries reside were 1.6–1.7 times larger for naturalized than for nonnaturalized taxa.

Another reason why naturalized and invasive taxa have higher nursery availabilities could be that some of the species characteristics that promote invasion success also make them more attractive or suitable for cultivation. Previous studies that related species' scores in Grime's CSR (competitors, stress-tolerators, and ruderals) triangle of adaptive strategies found that species with high scores along the C and R axes were both more likely to be grown in gardens and to have higher naturalization success (Guo et al., 2019, 2022). For example, *Papaver rhoeas* L. (family Papaveraceae), a naturalized herb with high C and R values (55.0% and 45.0% in Guo et al., 2022), was available in 61 online nurseries. Similarly, species with a high climatic suitability in a region are more likely to be cultivated there and have a higher naturalization probability (Feng et al., 2016; Kinlock et al., 2022; Maurel et al., 2016). Indeed, among the cultivated alien species of China, the naturalized ones also have higher climatic suitability than the nonnaturalized ones (Appendix S1: Figure S8B and Table S1).

As most cultivated plants that have become naturalized in China were recorded there in the wild more than 50 years ago, the recent increase in online trade cannot be responsible for the majority of naturalizations. However, although nursery availability is sensitive to gardening fashions (van Kleunen et al., 2018), it is likely that many of the species that are popular as gardening plants now were also popular decades to centuries earlier when all plant trade was still offline (Dehnen-Schmutz et al., 2007b). For example, *Punica granatum* L. (family Lythraceae) *and Aloe vera* (L.) Burm. f. (family Xanthorrhoeaceae) are two naturalized species with extremely long histories of cultivation as economic plants (they were introduced into China in 126 BC and AD 739, respectively) and featured prominently in both historical and modern markets (Xie et al., 2001). Thus, historical nursery trade is likely a main determinant of the current naturalization success of cultivated alien plants in China. Nevertheless, the current high availability of plants that are already known to be naturalized in parts of China might promote their further spread and ecological impacts.

The naturalized and invasive taxa in our dataset had a higher online-nursery availability than the nonnaturalized ones. However, the availability of invasive taxa was slightly lower than that of naturalized noninvasive ones, although the numbers of provinces and cities where the online nurseries were located did not differ. In other words, the online marketplace may be less likely to offer invasive species, possibly because some nurseries have already banned them voluntarily or in response to government actions against invasive species (Wang et al., 2017). Indeed, government agencies have campaigned to raise awareness among the general public about the negative impacts of invasive species, supported scientific research, and encouraged knowledge sharing to strengthen the response capacities of local enforcement agencies (Ding et al., 2006; Wang et al., 2017). Moreover, China has now implemented its first national policies dedicated to biosafety (the Biosecurity Law of the People's Republic of China of 2021) and management of invasive species (the Management Measures on Alien Invasive Species of 2022). These could be a major first step in providing an integrated regulatory framework for preventing and controlling plant invasions in China.

Type of plant material on offer

There are three main types of living plant material on offer on 1688.com. Most taxa are offered as seeds or as live plants and only a few of them as vegetative organs, but the proportions vary among the three invasion-status categories (Appendix S1: Figure S7). Naturalized taxa, and particularly the invasive ones, were predominantly offered as seeds, whereas the nonnaturalized taxa were predominantly offered as live plants. This might partly reflect the fact that particularly short-lived herbs are propagated from seeds and that those species with short generation times are also more likely to become naturalized (Appendix S1: Figures S5 and S7, also see Kinlock et al., 2022; Omer et al., 2021). Indeed, seeds were available on 1688.com for more than 97% of the short-lived herbs, while this was the case for only 44% of the long-lived herbs and 30% of the woody species. Nevertheless, also for the two latter life forms, taxa that were on offer as seeds were more likely to be naturalized or invasive (Appendix S1: Figure S7). For example, for the invasive long-lived grass *Paspalum notatum* Flüggé (family Poaceae), 47 out of 48 nurseries offered its seeds in the online marketplace. These results suggest that naturalized and invasive plants are frequently on offer in the marketplaces as seeds, irrespective of their life form. Therefore, early detection of alien species in online

marketplaces that produce large amounts of seeds with high germination rates may become necessary to reduce the risk of further plant invasions.

The list of taxa for sale as live plants, on the contrary, included mainly woody species and long-lived herbs and hardly any short-lived herbs (Appendix S1: Figure S5B). Of the taxa for sale as live plants, 80.7% were nonnaturalized, including 183 succulent taxa in the families Cactaceae and Crassulaceae (Appendix S1: Figure S4). Although many succulent species from these families have become highly invasive in some countries (e.g., *Opuntia* species in many countries with Mediterranean climates, Novoa et al., 2019), most of them have failed to establish themselves in China, most likely because of their short introduction histories (34 years on average) and lack of climatic suitability (2.4% on average). The list of taxa for sale as vegetative organs included only woody species and long-lived herbs (Appendix S1: Figure S5), as short-lived herbs do not have perennating vegetative organs from which they can be propagated. Of the taxa for sale as vegetative organs, 86.6% were nonnaturalized (e.g., *Crinum moorei* Hook. f. [family Amaryllidaceae], *Gloriosa superba* L. [family Colchicaceae], and *Nymphaea odorata* Aiton [family Nymphaeaceae]). Thus, overall, naturalized and invasive species are preferentially sold as seeds and less likely as live plants or vegetative organs.

It is thus likely that many alien long-lived herbs and woody species have not escaped cultivation yet because they have long generation times. In other words, it can take many years for them to produce seeds. Therefore, to produce live plants of those taxa, horticulturalists will primarily rely on asexual propagation methods (e.g., cuttings, tissue culture; Roberto & Colombo, 2020). In the case of varieties of *Acer palmatum* (family Sapindaceae) and many other woody ornamental plants, softwood and semi-hardwood cuttings have become an effective and simple way to propagate large numbers of plants while shortening their precultivation times in the commercial nurseries (Ding, 2010). On the other hand, vegetative propagation reduces the genetic diversity of those species, and because long-lived species are more likely to be self-incompatible than short-lived species (Baker, 1974; Razanajatovo et al., 2016), the genetic uniformity reduces available mating partners, thereby reducing seed production even more. Overall, for the alien species that are for sale as live plants or as vegetative organs in the online marketplace, optimizing the detection of species with invasion potential based on available horticultural information (e.g., propagation methods and diversity of plant genetic resources) may greatly improve the effectiveness of invasive species management (Schmidt et al., 2012).

Current legislation for management of invasive aliens in China

Among the naturalized species, the invasive ones were slightly less likely to be on offer than the noninvasive ones, which suggests that some nurseries have voluntarily decided to remove invasive species from their assortment (e.g., the invasive macrophyte *Eichhornia crassipes* [Mart.] Solms [family Pontederiaceae] was found for sale at only two online nurseries). However, overall both naturalized and invasive species were far more likely to be on offer than nonnaturalized aliens, which suggests that national legislation and regulations intended to prevent and control plant invasions in China are still inadequate.

Prior to 2021, a legal framework that exclusively dealt with invasive species in China was nonexistent, and most of the existing relevant regulations were scattered over several phytosanitary policies, for example, the Regulations on Plant Quarantine of 1983 and the Law of the People's Republic of China on the Entry and Exit Animal and Plant Quarantine of 1991 (Cao, 2021; Eschen et al., 2015). In comparison to integrated invasive species policy frameworks adopted by other countries or political unions (e.g., the regulations of invasive species under the Biosecurity Act in Australia and New Zealand and the EU Regulation no. 1143/2014 in the European Union), the scattered regulations on invasive species in China unavoidably resulted in poor response capabilities, low awareness among stakeholders, and limited coordination among enforcement agencies (Early et al., 2016). The recently issued first national policies dedicated to biosafety (the Biosecurity Law of the People's Republic of China of 2021) and the management of invasive species (the Management Measures on Alien Invasive Species of 2022) might remedy this situation. However, they do not yet target the online trade of alien plants in China.

Conclusions and future management suggestions

Of the 13,718 alien taxa that are known to be cultivated in China, 987 are available through online nurseries on 1688.com. This number was surprisingly low but might reflect that 1688.com mostly offers the most popular cultivated plants. Most of the other 12,731 cultivated alien taxa are probably available through specialist nurseries that do not use the 1688.com e-commerce platform or through direct exchange of plant material among gardeners. Nevertheless, because 1688.com is the most widely used e-commerce platform in China, our work provides strong evidence that the online-nursery availability of cultivated alien plants is strongly associated with their

invasion status. In other words, many taxa that are already known to be naturalized or invasive in China can still be ordered through 1688.com, frequently as seeds. This allows these taxa to spread even more widely, and it could also allow new genotypes to admix with the genotypes that are already growing in the wild. Such admixture could, through heterosis, increase offspring performance and thereby increase invasiveness (Li et al., 2018). A glimmer of hope, however, is provided by our finding that among naturalized plants, the invasive ones had a slightly lower availability than the noninvasive ones. Nevertheless, since the invasive species still had a higher availability than the nonnaturalized alien species, stricter regulations of the online plant trade are required.

Based on our findings, we recommend the following measures to prevent the further spread of species that are already naturalized and the dissemination of species with naturalization potential through the novel pathway of e-commerce: (1) provisioning of comprehensive "white" lists of taxa with low invasion potential and "black" lists of species that are not allowed to be traded in online marketplaces; (2) collaboration with leading e-commerce companies to develop new technologies (i.e., algorithms) that allow identification of alien plant taxa with high invasion potential from photos and species descriptions (also when incorrect species names are provided) and fining sellers, buyers, and suppliers engaged in the illegal trade of blacklisted species; (3) implementation of an integrated surveillance and response system involving the participation of nongovernmental organizations, stakeholders, and the general public to improve response capacities; and (4) launching marketing campaigns promoting the planting of native species. For the latter, there is already a huge selection of plant species; for example, ca. 14,000 native plant species are included in the Cultivated Flora of China (Lin, 2018). However, also here care should be taken that species native to one part of China not become invasive in parts of China where they are not native.

AUTHOR CONTRIBUTIONS

Bi-Cheng Dong, Fei-Hai Yu, and Mark van Kleunen conceived and designed the experiment. Ran Dong, Qiu-Yue Fu, and Bi-Cheng Dong collected and analyzed the data. Ran Dong and Bi-Cheng Dong wrote the first draft of the manuscript, with further inputs from Qiang Yang, Zhi-Cong Dai, Fang-Li Luo, Jun-Qin Gao, Fei-Hai Yu, and Mark van Kleunen.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and R codes (Dong et al., 2022) are available in Zenodo at https://doi.org/10.5281/zenodo.7451903. Data on the year of first collection in the wild for the cultivated alien plant taxa were extracted from the Chinese Virtual Herbarium by searching for their taxon names (http://www.cvh.ac.cn/; accessed 9 June–2 September 2019). Data on the global occurrence data of the cultivated alien plant taxa, outside of China, were downloaded from the GBIF by searching for their taxon names (https://www.gbif.org/; accessed 24 June–12 August 2019). Data on current climate were directly downloaded from the WorldClim database version 2.1 (https://worldclim.org/current/).

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SUPPORTING INFORMATION

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

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