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The changing role of ornamental horticulture in alien plant invasions

Mark van Kleunen[1,2,*], Franz Essl[3], Jan Pergl[4], Giuseppe Brundu[5], Marta Carboni[6], Stefan Dullinger[3], Regan Early[7], Pablo González-Moreno[8], Quentin J. Groom[9], Philip E. Hulme[10], Christoph Kueffer[11,12], Ingolf Kühn[13,14], Cristina Máguas[15], Noëlie Maurel[2], Ana Novoa[4,12,16], Madalin Parepa[17], Petr Pyšek[4,18], Hanno Seebens[19], Rob Tanner[20], Julia Touza[21], Laura Verbrugge[22,23], Ewald Weber[24], Wayne Dawson[25], Holger Kreft[26], Patrick Weigelt[26], Marten Winter[14], Günther Klonner[3], Matthew V. Talluto[6] & Katharina Dehnen-Schmutz[27]

[1]*Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou 318000, China*

[2]*Ecology, Department of Biology, University of Konstanz, Universitätsstrasse 10, D-78457 Konstanz, Germany*

[3]*Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, 1030 Vienna, Austria*

[4]*Institute of Botany, Department of Invasion Ecology, The Czech Academy of Sciences, CZ-252 43 Průhonice, Czech Republic*

[5]*Department of Agriculture, University of Sassari, Viale Italia 39, 07100 Sassari, Italy*

[6]*Université Grenoble Alpes, CNRS, LECA, Laboratoire d'Écologie Alpine, F-38000 Grenoble, France*

[7]*Centre for Ecology and Conservation, University of Exeter, Penryn Campus, UK*

[8]*CABI, Bakeham Lane, Egham TW20 9TY, UK*
[9]*Botanical Garden Meise, Bouchout Domain, Nieuwelaan 38, 1860 Meise, Belgium*
[10]*Bio-Protection Research Centre, Lincoln University, Lincoln 7648, Canterbury, New Zealand*
[11]*Institute of Integrative Biology, ETH Zurich, Universitätstrasse 16, 8092 Zurich, Switzerland*
[12]*Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Matieland 7602, South Africa*
[13]*Helmholtz Centre for Environmental Research – UFZ, Dept. Community Ecology, Theodor-Lieser-Str. 4, 06120 Halle, Germany*
[14]*German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany*
[15]*Centre for Ecology, Evolution and Environmental Changes (cE3c), Faculty of Sciences, University of Lisbon, Campo Grande, 1749-016 Lisboa, Portugal*
[16]*Invasive Species Programme, South African National Biodiversity Institute, Kirstenbosch Research Centre, South Africa*
[17]*Institute of Evolution & Ecology, University of Tübingen, Auf der Morgenstelle 5, 72076 Tübingen, Germany*
[18]*Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 44 Prague, Czech Republic*
[19]*Senckenberg Biodiversity and Climate Research Centre, Georg-Voigt-Straße 14-16, 60325 Frankfurt, Germany*
[20]*European and Mediterranean Plant Protection Organization, 21 boulevard Richard Lenoir 75011, Paris, France*

[21]*Environment Department, University of York, Wentworth Way, Heslington, YO10 5NG, York, UK*

[22]*Institute for Science in Society, Radboud University, PO Box 9010, 6500 GL Nijmegen, The Netherlands*

[23]*Netherlands Centre of Expertise for Exotic Species, Nijmegen, The Netherlands*

[24]*Biodiversity Research, University of Potsdam, Maulbeerallee 1, Potsdam D-14469, Germany*

[25]*Department of Biosciences, Durham University, South Road, Durham DH1 2LF, UK*

[26]*Biodiversity, Macroecology & Biogeography, University of Goettingen, Büsgenweg 1, 37077 Göttingen, Germany*

[27]*Centre for Agroecology, Water and Resilience, Coventry University, Ryton Gardens, Coventry, CV8 3LG, UK*

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[*]Author for correspondence (E-mail: mark.vankleunen@uni-konstanz.de; Tel.: +49 7531 88 2997).

ABSTRACT

The number of alien plants escaping from cultivation into native ecosystems is increasing steadily. We provide an overview of the historical, contemporary and potential future roles of ornamental horticulture in plant invasions. We show that currently at least 75% and 93% of the global naturalised alien flora is grown in domestic and botanical gardens, respectively. Species grown in gardens also have a larger naturalised range than those that are not. After the Middle Ages, particularly in the 18th and 19th centuries, a global trade network in plants emerged. Since then, cultivated alien species also started to appear in the wild more frequently than non-cultivated aliens globally, particularly during the 19th century. Horticulture still plays a prominent role in current plant introduction, and the monetary value of live-plant imports in different parts of the world is steadily increasing. Historically, botanical gardens – an important component of horticulture – played a major role in displaying, cultivating and distributing new plant discoveries. While the role of botanical gardens in the horticultural supply chain has declined, they are still a significant link, with one-third of institutions involved in retail-plant sales and horticultural research. However, botanical gardens have also become more dependent on commercial nurseries as plant sources, particularly in North America. Plants selected for ornamental purposes are not a random selection of the global flora, and some of the plant characteristics promoted through horticulture, such as fast growth, also promote invasion. Efforts to breed non-invasive plant cultivars are still rare. Socio-economical, technological, and environmental changes will lead to novel patterns of plant introductions and invasion opportunities for the species that are already cultivated. We describe the role that horticulture could play in mediating these changes. We identify current research challenges, and call for more research efforts on the past and current role of horticulture in plant invasions. This is required to develop science-based regulatory frameworks to prevent further plant invasions.

Key words: botanical gardens, climate change, horticulture, naturalised plants, ornamental plants, pathways, plant invasions, plant nurseries, trade, weeds.

CONTENTS

I. INTRODUCTION

With increasing globalisation, many plant species have been introduced beyond their natural ranges, and some of these have established and sustain persistent populations without human assistance (van Kleunen *et al.*, 2015; Pyšek *et al.*, 2017). Most of these alien species (*sensu* Richardson *et al.*, 2000) have comparatively small naturalised ranges (Pyšek *et al.*, 2017) and do not cause major ecological or economic damage. Some alien species, however, have become invasive (*sensu* Richardson *et al.*, 2000), impact upon native species, and can result in a significant burden on global economies, ecosystem services and public health (Pimentel, Zuniga & Morrison, 2005; Vilà *et al.*, 2011; Pyšek *et al.*, 2012*b*). Alien species introductions have sometimes occurred unintentionally through various pathways (e.g. as seed contaminants), but most invasive alien plants have been introduced intentionally, particularly for cultivation as ornamentals in public and private gardens (Hulme *et al.*, 2008; Pyšek, Jarošík & Pergl, 2011).

Alien plant invasions have been facilitated by an increase in species traded and trade volumes, complexity of the trade network, improved long-distance connections, and new ways of trading (Humair *et al.*, 2015; Pergl *et al.*, 2017). The horticultural introduction pathway is characterised by a wide range of supply-chain actors (Fig. 1; also see Drew, Anderson & Andow, 2010; Hulme *et al.*, 2018), whose roles have changed over time (Daehler, 2008). Some of the first actors were professional 'plant hunters' – individuals who collected seeds, bulbs, roots and tubers of wild species for cultivation and trade. Although the heydays of plant hunting were in the 18th and 19th century, such practices continue today (Ward, 2004). Many of the species collected by plant hunters are not grown easily or are not chosen by breeders and propagators, limiting the eventual size of the cultivated species pool (Fig. 1). Through selection and hybridisation, however, breeders also create novel ornamental cultivars and species, increasing the gene pool for cultivation (Fig. 1). The availability of plant species through wholesalers and retailers largely determines the alien species that are cultivated in botanical gardens, public green spaces and domestic gardens, from which some of these alien species may escape into the wild and become invasive. While certain native species show similar behaviour to invasive alien species, we use the term 'invasive' exclusively to refer to species that spread outside their native range through human intervention (Richardson *et al.*, 2000).

To interpret current trends and to predict likely future developments, we need a better understanding of the number and diversity of alien plants grown in gardens. Furthermore, we also need to know their introduction history and the species characteristics that promote both their horticultural usage and potential invasion success. Therefore, we here integrate information from invasion biology and horticulture to provide a broad overview of the role of ornamental horticulture in alien plant invasions. We do this by (*i*) using a scheme describing the pathways and processes involved in ornamental plant invasions (Fig. 1; also see Drew *et al.*, 2010), (*ii*) covering a wide range of relevant issues, such as introduction dynamics, garden fashions and plant traits promoted by horticulture, from both historical and contemporary perspectives, (*iii*) discussing the potential future role of horticulture, and (*iv*) highlighting research needs.

II. CONTEMPORARY GARDENS AND THE NATURALISED ALIEN FLORA OF THE WORLD

Regional analyses of alien naturalised floras have shown that usually more than half of these species were introduced for ornamental horticulture purposes (e.g. Germany: Kühn & Klotz, 2002; Czech Republic: Pyšek *et al.*, 2012*a*; Britain: Clement & Foster, 1994; USA: Mack & Erneberg, 2002; Australia: Groves, 1998; South Africa: Faulkner *et al.*, 2016). Furthermore, a comparison of the frequency of invasive species across the world reveals that most have originated from ornamental horticulture (Hulme *et al.*, 2018). However, a global analysis of naturalised alien plants is still missing. In order to obtain a benchmark estimate of the proportion of naturalised species that have been introduced as garden plants globally, we compared the naturalised alien flora and the cultivated garden flora. The recently compiled Global Naturalized Alien Flora (GloNAF) database revealed that more than 13,000 vascular plant species have become naturalised somewhere in the world (van Kleunen *et al.*, 2015; Pyšek *et al.*, 2017). The number of plant species grown in domestic gardens, public green spaces and botanical gardens is much larger but precise numbers are yet unknown (Khoshbakht & Hammer, 2008). In order to obtain a minimum estimate of the size of the global domestic garden flora, we extracted the lists of species in Dave's Garden PlantFiles (http://davesgarden.com/guides/pf/, accessed 23 March 2016) and in the Plant Information Online database (https://plantinfo.umn.edu/, accessed 22 November 2017). Furthermore, to obtain a minimum estimate of the number of species planted in botanical gardens, we extracted the list of species in the PlantSearch database of Botanic Gardens Conservation International (http://www.bgci.org/plant_search.php, accessed 25 May 2016), which includes species accessions of 1,144 botanical institutions worldwide. All species names were taxonomically harmonised using The Plant List (version 1.1; http://www.theplantlist.org/, accessed in December 2017), which also provided us with an estimate of the number of species in the global vascular plant flora. Ornamental cultivars that could not be assigned to species were not considered as they are not included in The Plant List.

At least 51% of all known species of vascular plants worldwide (337,137) are grown in domestic (70,108) or botanical gardens (162,846; Fig. 2). Most of the species grown in domestic gardens are also grown in botanical gardens (88%; Fig. 2), and it is likely that most, if not all species grown in public green spaces, for which we have no estimates, are also grown in domestic or botanical gardens (Mayer *et al.*, 2017). Although not all species in these gardens are cultivated for decorative purposes, and not all of them are cultivated outside their native ranges, these large numbers of garden species suggest that ornamental horticulture is the major pathway of alien plant introduction. Thus, it is not surprising that at least 75% and 93%, respectively, of the naturalised alien plants worldwide are grown in domestic and botanical gardens (Fig. 2). Moreover, among the naturalised species, those grown in domestic or botanical gardens are also naturalised in more regions around the globe (Fig. 3). Furthermore, Hulme (2011) showed for the 450 invasive alien plant species listed in Weber (2003) that the number of regions in which each of these species is invasive is positively correlated with their frequency in botanical garden collections worldwide. Some of these species may also have been introduced via additional pathways (e.g. agriculture or forestry). For example, *Robinia pseudoacacia* has been introduced as ornamental plant, forestry tree and nectar source, and for soil stabilization (Vítková *et al.*, 2017). Particularly, during the so-called utilitarian phase of the history of global weed movement (Mack & Lonsdale, 2001), the chances of becoming invasive may be high. So, while other deliberate introduction pathways are also important, there is strong evidence that ornamental horticulture remains a major contributor to plant invasions (Mack & Erneberg, 2002; Dehnen-Schmutz *et al.*, 2007; Hanspach *et al.*, 2008; Lambdon *et al.*, 2008; Hulme, 2011, Pyšek *et al.*, 2011; Pergl *et al.*, 2016; Saul *et al.*, 2017; Hulme *et al.*, 2018).

III. THE HISTORY OF ORNAMENTAL HORTICULTURE AND IMPLICATIONS FOR CURRENT PLANT INVASIONS

(1) Garden-plant introductions

Archaeological evidence has revealed that plant species were transported by modern humans when humans expanded their range from the Late Pleistocene onwards (Bolvin *et al.*, 2016). Most of these alien species were used as food crops or as medicinal plants. It has also been speculated that Pleistocene people, and even Neanderthals, used ornamental flowers in burial sites (Leroi-Gourham, 1975). However, these claims are very controversial (Fiaconni & Hunt, 1995) and there is no evidence that these ornamentals were alien species. In the Americas, there is evidence for the existence of intensive trade of agricultural crops between areas in current Mexico and the coastal areas of Peru approximately 3000 years ago (Manrique, 2010). Around the same time, regions in current Panama had established a trade of plants with regions in current Ecuador, Colombia, Guatemala or Mexico (Sánchez, 1997). To what extent these traded plants included ornamentals remains unknown.

Since pre-Roman times, and increasingly with the Romans and in the Middle Ages, plant species were transported across Europe. In particular, Mediterranean plants were carried to other parts of Europe, and occasionally plants from more distant regions, such as Central and East Asia, were introduced to Europe (e.g. Jacomet & Kreuz, 1999; Campbell-Culver, 2001). In their colonisation of Pacific islands, Polynesians introduced several crop and fibre species to Hawaii and later New Zealand (Cox & Barnack, 1991; Roullier *et al.*, 2013). From China, there is evidence of the early use of alien plants during the Han-Dynasty, where the new long-distance trade network of the 'silk road' was used to introduce ornamental alien plants for the extensive park created by Emperor Wu-Ti (140–89 BC; Hill, 1915; Keller, 1994). In pre-Columbian Mexico, there were already gardens, such as that of the Acolhua king Netzahualcóyotl (1402–1472) and those of the Aztec kings Moctezuma I (1390–1469) and Moctezuma II (1465–1520), with plants collected in Mexico and elsewhere in the Americas (Hill, 1915; Sánchez, 1997). For other parts of the world, little or no information is available on such historical plant introductions.

It is known that roses were cultivated and traded as early as in the times of the ancient Romans, Greeks and Phoenicians (Harkness, 2003). For the medieval period, there are documents that detail the plants grown in the gardens of monasteries and castles. An example is Walafried Strabo's *Liber de cultura hortorum*, published around the year 840 and describing 24 garden herbs. Although most of the species listed in these works were used as spices or as medicinal plants, some also had symbolic value and were appreciated as ornamentals (e.g. roses, lavender and poppies). Certain alien plant species introduced to medieval European castle gardens still persist as naturalised species in the areas around these castles today (e.g. *Erysimum cheiri*; Dehnen-Schmutz, 2004).

After the Middle Ages, global exploration by European nations expanded rapidly, the intercontinental exchange of species gained momentum, and eventually a truly global network of plant species trade and exchange emerged (Mack, 2000). The explorers and plant hunters sent out by the different European countries in the 15^{th} and 16^{th} century were instructed to collect (economically) interesting plants (e.g. Stöcklin, Schaub & Ojala, 2003). Driven by the discoveries of new lands and the growing demands of private collectors, nurseries and botanical gardens for botanical novelties, plant hunting became a recognized occupation in Europe during the mid-16^{th} century (Janick, 2007). In the 17^{th} century, John Tradescant the elder and his son were among the first Europeans to explore the floras of the Middle East and Russia, and later North America (Reichard & White, 2001). They collected for example *Rhus typhina*, *Tradescantia virginiana* and *Liriodendron tulipifera* (Musgrave, Gardner & Musgrave, 1999), species that are now widely naturalised in different parts of the world. During the 18^{th} and 19^{th} centuries, many plant hunters collected plants for botanical institutions such as the Royal Botanical Gardens, Kew in the UK, the Leiden Hortus Botanicus in the Netherlands and the Jardin du Roi in France (Whittle, 1970), and for clubs of plant enthusiasts such as Der Esslinger Botanische Reiseverein in Germany (Wörz, 2016). During this period, plant exploration became very popular. For example, by the 18^{th} century almost 9,000 ornamental plant species from all over the world were introduced to the British Isles (Clement & Foster, 1994). Many of the ornamental species currently naturalised in Europe were introduced in this period (e.g. Maurel *et al.*, 2016).

Similarly, many new ornamentals were introduced to North America from the 18^{th} to the 20^{th} centuries from plant-collection expeditions in Eastern and Central Asia, North Africa and the Middle East (Stoner & Hummer, 2007). During the first expedition of this kind funded by the federal government of the USA, Robert Fortune (1812–1880) introduced species of *Chrysanthemum*, *Paeonia* and *Rhododendron* (azaleas) as ornamentals into the USA (Musgrave *et al.*, 1999). Another noteworthy plant hunter was Ernest Henry Wilson (1876–1930), who introduced >2,000 plant species from Asia to Europe and North America.

Some of these species, such as *Lonicera maackii* and *Pyrus calleryana* (Farrington, 1931), are now widely naturalised in North America (http://bonap.org/). Taken together, the efforts of plant hunters brought many new species to botanical gardens and private collections, and fuelled the horticultural trade from the 16th until the early 20th century.

Governments also played active roles in alien plant introductions. For example, US President John Quincy Adams (1767–1829) requested all US consuls to forward rare seeds to Washington for distribution (Hodge & Erlanson, 1956). In 1839, the US Congress appropriated $1000 for the handling and distribution of seeds of introduced alien plants, and the United States Department of Agriculture (USDA) created in 1898 the Office of Foreign Plant Introductions with the aim of building up new plant industries (Fairchild, 1898; Hodge & Erlanson, 1956). Until the end of World War II, the USDA office introduced approximately 250,000 accessions (i.e. species and varieties combined), and coordinated the initial propagation, testing and distribution of the plants (Hodge & Erlanson, 1956). Most of these plants were introduced for agricultural purposes, but they also included species for ornamental horticulture (Fairchild, 1898; Dorsett, 1917). Similarly, government agencies were responsible for the introduction of alien plant species in countries like Australia (Cook & Dias, 2006) and New Zealand (Kirkland & Berg 1997).

Ornamental alien plants were not only introduced to the home countries of the predominantly European plant hunters, but plants native to Europe were also introduced into, and exchanged among the colonies. An important role in this exchange was played by the acclimatisation societies, which arose in Europe and its colonies during the 19th century. Initially, the acclimatisation societies were fuelled by interest in novel flora and fauna from the colonies for introduction into European gardens and zoos (Dunlap, 1997). Later, the focus changed to transplanting the biotic landscape from the mother country into the colonies and the exchange of ornamental and crop species among colonies (di Castri, 1989; Osborne, 2001). Subsidies and free transport of explorers, plants and animals on cargo ships to and from the colonies was offered by supporting governments (Grove, 1995). Many crops but also ornamentals were transported this way, including bamboos and species of *Araucaria*, *Acacia* and *Camellia* (Bennett, 1870). Soon after their foundation, popularity of the acclimatisation societies waned due to growing concerns for the preservation of indigenous biota (Dunlap, 1997). Twenty years after their rapid appearance, most acclimatisation societies had been dissolved, and the few remaining ones started to focus on reintroduction of threatened native species.

While botanical gardens were used as showcases by the acclimatisation societies in the second half of the 19th century, their role in introducing and cultivating alien plants started much earlier and continues today. Particularly, during the 17th and 18th century, botanical gardens were part of the colonial infrastructure that facilitated the distribution of useful plants around the world (Hulme, 2011). Between 1750 and 1850, the first botanical gardens were founded in all non-European continents (with the exception of Antarctica): Bartram's Garden (1728) in North America, the Calcutta Botanic Garden (1786) in Asia, the Sydney Gardens (1788) in Australia, the Rio de Janeiro Botanical Garden (1808) in South America, and Cape Town Botanic Garden (1848) in Africa (Hill, 1915). Botanical gardens were also instrumental in the collation, evaluation and dissemination of new discoveries of foods, agricultural products and ornamentals, generally sponsored by governments and commercial enterprises (e.g. Diagre-Vanderpelen, 2011). Unsurprisingly, many of the currently naturalised and invasive alien plant species were first planted in botanical gardens. For example, in Europe, *Solidago canadensis* and *S. gigantea* were first planted in Paris and London, respectively (Wagenitz, 1964; Weber, 1998), and *Agave americana* was first planted in the Padua Botanical Garden (Italy; http://www.ortobotanicopd.it/en/piante-introdotte-italia-dallorto-botanico; accessed 23 March 2017). Many of the species introduced to botanical gardens may first have been distributed to other gardens and public green spaces before they escaped into the wild. However, some alien species escaped directly from botanical gardens (Harris, 2002; Sukopp, 2006), including several listed among the worst aliens worldwide (Hulme, 2011).

With the emergence and intensification of the global network of ornamental plant species trade after the Middle Ages, it is not surprising that the rate at which new alien species established in the wild increased dramatically (Seebens *et al.*, 2017). Some of these species were not introduced intentionally for their economic and ornamental value, but were accidentally transported with other cargo or in ballast soil (e.g. Brown, 1878; Hulme *et al.*, 2008). The exact role of ornamental horticulture in the temporal dynamics of naturalisation events is therefore difficult to quantify. To gain some insights, we used the database of Seebens *et al.* (2017) on first-record rates of established alien plants in combination with data on their cultivation in domestic (data from Dave's Garden PlantFiles and the Plant Information Online database) and botanical (data from Botanic Gardens Conservation International PlantSearch database) gardens. The first-record rate in the 19th century increased faster for species that are now cultivated in gardens, particularly in botanical gardens, than for species not known to be cultivated (Fig. 4). This suggests that species introduced for horticultural purposes naturalised earlier than alien species introduced by other pathways. However, while the first-record rates of species grown in domestic gardens only and species not known to be cultivated are still increasing rapidly, the first-record rate appears to slow down for species grown in botanical gardens (Fig. 4). Possibly, this is partly a consequence of the increasing awareness about invasive plants among botanical gardens and their stronger focus on native plants in recent times (Hulme, 2015).

(2) Historical garden-fashion trends

Changing garden and landscaping fashions impact on plant introductions and subsequent invasions through floral design, style elements and layouts of gardens, parks and other green spaces, as well as through the choice of plants they promote (e.g. Müller & Sukopp, 2016). Historic fashion trends were not only driven by demand but also by the chronological order in which plants from different parts of the world became available. For example, with the discovery of the New World, novel ornamental plants were introduced into European horticulture as early as the 16th century, many of which are still common in today's gardens – e.g. *Helianthus* spp., *Amaranthus caudatus* and *Mirabilis jalapa*. Increased trade with the Orient also opened the door to plants from Asia (e.g. *Hemerocallis* spp.) into Europe. While most of these species are herbaceous, the development of landscape gardens and arboreta in the 18th and 19th centuries marked the start of the widespread introduction of ornamental trees to Europe (see e.g. Goeze, 1916). Landscape gardens were characterised by the opening up of gardens into a wider landscape accompanied by careful positioning of artificial lakes, trees and hedges. Many alien trees introduced to create such gardens still characterise urban parks today, and some of them – such as the North American species *Acer negundo*, *Robinia pseudoacacia*, *Pinus strobus*, *Prunus serotina* and *Quercus rubra* – have also become naturalised in Europe and elsewhere (Brundu & Richardson, 2016; Richardson & Rejmánek, 2011; Campagnaro, Brundu & Sitzia, 2017).

The second half of the 19th century saw the development of ecologically and biogeographically focused plantings that aimed to recreate representative examples of specific vegetation types from around the world (Woudstra, 2003). This period also saw a broadening interest in different growth forms besides plantings of woody species, with an increasing representation of perennial forbs and later also grasses. Specific habitats such as rockeries, bogs and woodlands were created in gardens to accommodate high plant diversity.

Plant recommendations for these habitats in Britain were provided by William Robinson with his influential book *The wild garden or, our groves and shrubberies made beautiful by the naturalization of hardy alien plants* (Robinson, 1870). The trend of using hardy perennial plants continued into the 20th century, first driven by the desire to create *Colour in the flower garden* as Gertrude Jekyll (1908) titled her influential book. It was also influenced by the ornamental plant breeder Karl Foerster (1874–1970), one of the first to promote the use of grasses as ornamentals in Germany (Hottenträger, 1992). These are just a few of the individuals that influenced garden fashions in Europe. Examples of influential people in the Americas are Andrew Jackson Downing (1815–1852) and Frederick Law Olmsted (1822–1903), who both preached the English or natural style of landscape gardening, and more recently Thomas Church (1902–1978), who designed the 'California Style' of garden landscapes (https://www.gardenvisit.com, accessed 28 November 2017). The consequences of these different 'garden fashions' initiated by these people on plant invasions in different regions of the world still need more research.

IV. THE RECENT ROLE OF HORTICULTURE IN PLANT INVASIONS

(1) Global patterns, changing dynamics and likely future trends

Horticulture continues to play a prominent role in alien plant introductions (Reichard & White, 2001; Bradley *et al.*, 2011; Humair *et al.*, 2015). This is confirmed by analyses of the monetary value of live-plant imports in different parts of the world, which show a steady increase in live-plant imports in Europe and North America (Fig. 5). This may, however, not necessarily translate into a higher diversity of species traded, as such trade statistics do not specify the number of species traded, and include non-ornamental plants. Live-plant imports in South and Central Asia are rising at an increasing rate, and, while imports to East Asia appear to have undergone a rise and fall at the end of the 1990s, imports are increasing once again (Fig. 5). Understanding who is involved in horticulture in these regions would help invasive-plant management plans to be targeted to the appropriate audience.

The most data on the role of ornamental horticulture in plant invasions are available for Europe and North America. However, horticulture was recently identified as a strong driver of invasions in Argentina (Giorgis & Tecco, 2014), Brazil (Zenni, 2014), and Puerto Rico and the Virgin Islands (Rojas-Sandoval & Acevedo-Rodríguez, 2014). This is despite slow growth of live-plant imports to the Caribbean, Central and South America (Fig. 5). Furthermore, while gardening is a popular hobby in North America, Australasia and Europe (Bradbury, 1995; Crespo *et al.*, 1996; Soga, Gaston & Yamaura, 2017), information on the prevalence of recreational gardening outside these regions is harder to find. In Japan, one in four people gardens daily, and at least five studies have assessed the effect of gardening on mental health in Asia (Soga *et al.*, 2017), suggesting public interest in this hobby.

The establishment of botanical gardens was historically driven by the needs of economic botany and ornamental horticulture. This role has decreased with the increasing importance of many botanical gardens in global plant conservation (Havens *et al.*, 2006). Currently, private and public sector breeding programs play major roles in the release of alien plants through the ornamental nursery supply-chain. The role of botanical gardens in the ornamental nursery supply-chain, however, is not negligible (Fig. 1; Hulme 2011, 2015). An analysis of the Botanic Garden Conservation International (BGCI) Garden Search database (http://www.bgci.org/garden_search.php, accessed on 1 November 2016) shows that approximately one-third of botanical gardens worldwide are involved in retail-plant sales, particularly in developing countries (Fig. 6). Similarly, approximately one-third of botanical gardens undertake horticultural research and around 10% are involved in plant breeding (Fig. 6). In both cases, the levels of participation in this research seem particularly high in Asia, and low in North America (χ^2=28.02 and 26.03, df=5, P < 0.0001, respectively).

Nevertheless, North American botanical gardens play a leading role in using their living collections of alien ornamentals as a basis for commercial breeding and marketing (Pooler, 2001; Kintgen, Krishnan & Hayward, 2013; Ault & Thomas, 2014).

The participation of botanical gardens in plant exploration varies among continents (χ^2=48.02, df=5, $P < 0.0001$), and is most important in continents with many developing countries, Asia in particular (Fig. 6). While much of this exploration advances the knowledge of the native flora, it also highlights a potential route for new ornamental plants to enter the global horticulture market. The combination of a rapid growth in numbers and importance of botanical gardens in Asia (Hulme, 2015), an increased emphasis on horticulture and breeding research in these institutions and a significant role of retail-plant sales suggest that Asia will contribute to increasing global trade in ornamental plants in the future. This is certainly the philosophy and expectation of botanical gardens in China (Zhao & Zhang, 2003). Given the increasing evidence that alien plants from Asia are particularly successful invaders elsewhere in the world (Lambdon *et al.*, 2008; Fridley & Sax, 2014; van Kleunen *et al.*, 2015), we can expect even more horticulture-driven plant invasions from Asia in the future.

With already a significant proportion of the global flora in cultivation (Fig. 2) and increased availability of plant propagules through other sources, wild collection has probably decreased in the last decades. It is likely to decrease further due to global restrictions on collecting wild plants imposed by the Nagoya Protocol on access and benefit-sharing of the Convention of Biological Diversity (2011; https://www.cbd.int/abs/). This means that home gardens and plantings in public green spaces will rely on nurseries, but also that botanical gardens will have to maintain or expand their collections using commercially bought plant material or through exchange with other botanical gardens. To obtain an impression of the importance of different plant sources for current botanical garden collections, we sent a questionnaire to botanical gardens around the globe (Appendix 1). Of the 161 respondents, 37%, 29% and 27% indicated that their major sources of plants are commercial nurseries, other botanical gardens and collections from the wild, respectively (Fig. 7). Commercial nurseries were particularly important sources for North American botanical gardens, whereas other botanical gardens were particularly important sources for European botanical gardens (Fig. 7). The latter might reflect that many European botanical gardens produce an Index Seminum (i.e. seed catalogue) of the species available for exchange.

(2) Modern garden-fashion trends

Since the 1990s, there has been a resurgence in cultivating herbaceous perennials, frequently prairie species from North America, in more naturalistic plantings. This is motivated by the ease and low costs of management and by an increased interest in species-rich gardens (Hitchmough & Woudstra, 1999). These plantings often combine native and alien species that originate from different continents but belong to the same habitat type (e.g. prairies). Regarding other more recent gardening fashions, few formal studies exist that document them, and even fewer link them to plant invasions (e.g. Dehnen-Schmutz, 2011; Humair, Kueffer & Siegrist, 2014*a*; Pergl *et al.*, 2016). For example, although the surge in invasive aquatic plants is most likely the result of increasing interest in water gardening since the middle of the 20th century, robust data are hard to find (Maki & Galatowitsch, 2004). Other recent fashions are 'jungle' and desert gardens, living walls, and guerrilla gardening (i.e. gardening on land not owned by the gardener), all of which depend on and promote their own selection of mainly alien plants (Dunnett & Kingsbury, 2008; Reynolds, 2014). There is also a rising interest in increasing the services provided by urban vegetation, such as food production (Smardon, 1988), and therefore an increasing number of urban parks include ornamental aliens that are edible (Viljoen, Bohn & Howe, 2005). In addition to the fashion trends that mainly use alien plants, there is also an increasing interest in gardening with native species (e.g. Kruckeberg, 2001; Shaw, Miller & Wescott, 2017). This is likely due to awareness of biological invasions but also because people want to have gardens that promote diversity and wildlife, and are less labour intensive.

(3) Horticultural selection favours traits related to invasiveness

The horticultural industry identifies particularly prized species, varieties or cultivars through specific accolades, e.g. Awards of Garden Merit (Great Britain), Mérites de Courson (France), All-America Selection Winners (USA), Gold Medal Plant (Pennsylvania). Such accolades are an important marketing strategy to promote specific plants, and are an important aspiration for many ornamental plant breeders. While the criteria differ for individual accolades, in general the plants must be excellent for garden use, exhibit consistently good performance in different garden environments and climates, should be easy to grow, and should not be particularly susceptible to insect pests or pathogens (Hulme, 2011). Such characteristics, together with the higher market frequency of these species may have contributed to the high propensity of award-winning plants to become invasive (Hulme, 2015).

There are several plant characteristics that might promote both horticultural use and invasion. Environmental matching is an obvious criterion when considering a species for horticulture (Reichard, 2011), and at the same time is also important for naturalisation and invasiveness (Richardson & Pyšek, 2012). For example, in Germany – a temperate region with winter frost – hardier species are planted more frequently (Maurel *et al.*, 2016) and have a higher probability of naturalisation (Hanspach *et al.*, 2008; Maurel *et al.*, 2016) than less hardy species. Horticultural usage should also be favoured by ease of propagation (Mack, 2005; Reichard, 2011), and alien species with rapid and profuse seedling emergence are also more likely to naturalise (van Kleunen & Johnson, 2007). Similarly, fast vegetative growth is promoted by the horticultural industry (Reichard, 2011), and also promotes invasiveness of plants (Dawson, Fischer & van Kleunen, 2011; Grotkopp, Erskine-Ogden, & Rejmánek, 2010). Furthermore, early-flowering species and genotypes often have a long flowering period or have repeated bouts of flowering (Mack, 2005) and can be sold sooner or for a longer time, thus increasing profit (Reichard, 2011). At the same time, a longer flowering period has also been found to be associated with invasiveness (Lloret *et al.*, 2005; Gallagher, Randall & Leishman, 2015). So, horticulture may facilitate plant invasions by screening species and genotypes of ornamental value based on traits that inadvertently promote spread (Drew *et al.*, 2010; Knapp *et al.*, 2012).

Although horticulture seems to foster plant invasions overall by filtering species based on characteristics that increase their success inside and outside of gardens, this is not systematically the case. In some taxonomic groups, the most valued species are actually the ones with traits that make them less successful outside of gardens. For example, among cacti, slow-growing species are usually favoured by gardeners (Novoa *et al.*, 2017), and they should be less likely to naturalise and become invasive (Novoa *et al.*, 2015*b*). For orchids, which are strongly underrepresented in the global naturalised flora (Pyšek *et al.*, 2017), some hobby growers are willing to pay more for species that are rare in trade and most likely difficult to cultivate (Hinsley, Verissimo & Roberts, 2015). Furthermore, many ornamental cultivars have showy flowers that are sterile (e.g. in roses; Debener *et al.*, 2001), which diminishes their invasion potential. Thus, there is potential to select ornamental species or breed cultigens that are less likely to become invasive.

To date there has been very limited involvement of plant breeders in reducing invasion risk of ornamental plants (e.g. Burt *et al.*, 2007; Novoa *et al.*, 2015*a*). Anderson, Gomez & Galatowitsch (2006) proposed 10 traits to reduce invasiveness while retaining commercial value of ornamentals: reduced genetic variation in propagules, slowed growth rates, non-flowering, elimination of asexual propagules, lack of pollinator rewards, non-dehiscing fruits (to prevent seed dispersal), lack of edible fruit flesh, lack of seed germination, sterility and programmed death prior to seed production. So far, most effort in producing non-invasive cultivars has focussed on reduced fecundity (e.g. Freyre *et al.*, 2016). Unfortunately, for perennial species, even relatively low levels of seed production may be sufficient for plant invasions (Knight, Havens & Vitt, 2011). Furthermore, traits such as seed sterility and dwarfism, bred into cultivars to reduce invasion potential, may revert back to their original states (Brand, Lehrer & Lubell, 2012). Perhaps the way forward is for horticultural accolades to recognise the risk of invasiveness more formally and at least account for this in field trials and subsequent selection of award-winning taxa.

V. THE NEXT GENERATION OF INVADING ALIEN HORTICULTURAL PLANTS

(1) New pathways and horticultural practices

A major future challenge might be that social, technological and environmental changes will lead to fundamentally novel patterns of plant introductions resulting in invasion risks by new types of plants for which past invasions give only partial guidance (Kueffer, 2010). Through internet trade, a much broader range of taxa from many more source regions becomes available for buyers worldwide (Humair *et al.*, 2015). Many of these new species might initially be traded in low numbers, but marketing, promotion by celebrity gardeners, and popularity in social media of specialised gardening groups can result in sudden interest in a new plant species. One example is the recent rise in trade and illegal import into Europe of *Lycium barbarum*, the shrub that produces the putative 'superfood' goji berry (Giltrap, Eyre & Reed, 2009) and is widely naturalised in Europe (http://www.europe-aliens.org/speciesFactsheet.do?speciesId=20401#, accessed on 13 July 2017). Unsurprisingly, horticulturalists are continually searching for new plants with 'unique' features to be sold.

Seaton, Bettin & Grüneberg (2014) for instance wrote that "Introduction of new plants is critical to the survival and profitability of the horticultural industries" in their article on how to find new plant species in the world's existing plant diversity. Furthermore, new molecular-based breeding technologies have reached the horticultural industry (e.g. Chandler & Brugliera, 2011; Xiong, Ding & Li, 2015). One primary target of current breeding efforts is to increase resistance to diseases and herbivores, which could then also increase invasiveness of some cultivars.

(2) Climate change

Environmental changes, such as atmospheric nitrogen deposition, habitat fragmentation and disturbance due to land-use change, have contributed to plant invasions and are likely to do so in the future (Bradley *et al.*, 2010; Sheppard, Burns & Stanley, 2014; Dullinger *et al.*, 2017; Liu *et al.*, 2017). In addition, it is commonly expected that climate change will increase plant invasions globally, although its impacts may vary considerably among geographic areas and species (Lambdon *et al.*, 2008; Hulme, 2009; Bradley *et al.*, 2010; Seebens *et al.*, 2015; Early *et al.*, 2016; Dullinger *et al.*, 2017). This expectation is mainly based on the anticipated destabilisation of resident native plant communities caused by an emerging disequilibrium with climatic conditions (Svenning & Sandel, 2013) and by increased frequencies of extreme events, such as droughts, hurricanes and heat waves (Diez *et al.*, 2012). Both will likely decrease the biotic resistance of resident vegetation against the establishment and spread of alien species (e.g. Eschtruth & Battles, 2009; Early *et al.*, 2016; Haeuser, Dawson & van Kleunen, 2017).

Although climatic suitability is an important criterion in horticulture, many ornamental species are grown beyond the climatic conditions they would be able to tolerate in the wild (Van der Veken *et al.*, 2008). A warming climate potentially increases the match between current cultivation areas and suitable climatic conditions, especially in temperate regions where many garden plants have been introduced from warmer parts of the world (Niinimets & Peñuelas, 2008; Bradley *et al.*, 2011; Dullinger *et al.*, 2017). Cultivated ornamental plants will have a 'head start' (Van der Veken *et al.*, 2008) allowing them to colonise newly suitable areas long before other range-shifting species arrive. This head-start advantage may become even more important in the coming decades. First, adaptation of gardeners' demands to anticipate changes in regional climates could improve the climatic match of newly planted species. Demand for drought-tolerant ornamental species is already growing in the USA in response to forecasted drier conditions (Bradley *et al.*, 2011). Second, rising urbanisation all around the world will lead to an increased concentration of demand for ornamental plants in metropolitan areas. These areas usually have higher temperatures than the surrounding rural areas (i.e. the urban heat-island effect). Consequently, warm-adapted garden plants will have the chance to establish naturalised populations in cities, which may facilitate their spread into the surrounding landscapes (e.g. Essl, 2007; but see Botham *et al.*, 2009).

A warming climate may also foster the establishment of ornamental plants in those ecosystems that have so far been less affected by biological invasions. Mountains, for example, have few invasive species so far due to climatic constraints and low human population densities, and hence low propagule pressure (Pauchard *et al.*, 2016). Indeed, the few alien species currently found in mountains are mostly lowland generalists able to cope with the cold climate (Alexander *et al.*, 2011). However, climate warming, in combination with changing land use and increased tourism, will potentially relax these constraints and increase invasion risks at higher elevations (Pyšek *et al.*, 2011; Petitpierre *et al.*, 2016; Dainese *et al.*, 2017). Specifically, ornamental plants currently cultivated in mountain villages and resorts will have a head start under a warming climate and profit from greater propagule availability with increasing human population (Pauchard *et al.*, 2009). Further, in order to satisfy the growing demands of tourism, nurseries selling into mountainous regions are also likely to increase the supply of garden plants pre-adapted to mountain conditions, i.e. originating from other alpine environments around the world (Kueffer *et al.*, 2013; Alexander *et al.*, 2017). The threat posed to mountains by escaping ornamental plants will thus probably increase in the future because of globalisation and climate change.

VI. RESEARCH OPPORTUNITIES AND NEEDS

To address new research frontiers identified in this overview, we provide an agenda of pressing research challenges that lie ahead in order to foster our understanding of the role of horticulture in plant invasions (Table 1). One overarching scientific challenge is advancing our understanding of how different practices, related features and characteristics of horticulture, and processes and impacts of plant invasions are linked to one another (Fig. 1). This will benefit greatly from an interdisciplinary scientific approach that jointly considers the human dimensions (e.g. behaviour, preferences, governance, culture), and their interactions with the biophysical environment. Addressing this topic in well-circumscribed study systems may be an appropriate way forward. *Inter alia* this can be achieved by focussing research questions on specific geographical regions or by focusing on subsets of ornamental species (e.g. certain families, or species with certain traits). This general research background can be broken down into eight specific research challenges (Table 1).

Topic 1: an improved understanding of the origins of ornamental alien species and the means by which they arrive and are distributed. Here, it is important to go beyond analyses on where from and by which pathway the most successful (most frequent) species, or those with the highest impacts arrived. It is crucial to take into account the species pool in the area of their origin and the trade pattern and volume to disentangle the effect of propagule pressure ('transport mass effect') from other factors related to invasion success or impact. In this light, it is also important to know how species are distributed through new ways of trading or social networks. For example, how important is garden-plant exchange among relatives and friends (Verbrugge *et al.*, 2014)? In addition, there might be certain plant traits associated with specific origins and pathways.

Topic 2: knowledge of temporal trends and fashions related to import and the consequences for invasion success and impact. For example, are species that were introduced earlier more likely to be invasive now because they have had more time to become invasive or because plant hunters initially introduced plant species that could be cultivated easily and thus are better pre-adapted and more competitive? How do changes in breeding, fashions, and cultivation patterns affect plant invasions and impacts?

Topic 3: improve understanding of the drivers of horticulture-related plant invasions including the identification of future invaders. For example, what are the roles of changing trade partners and consequently trade patterns, plant traits and environmental conditions in invasion success, and how can the different drivers be ranked in importance? This, to some degree, is different from, but can be dependent on, origins and pathways.

Topic 4: forecasting whether global environmental change will influence the naturalisation of ornamental species that were not a problem in the past. Emerging patterns in global environmental change, like for example increased landscape fragmentation and climate change impacts, might differ among regions and among habitats (i.e. some combinations of these changes may synergistically promote invasions, while other combinations may inhibit invasions). Moreover, some of the solutions proposed to help native species survive might also affect plant invasions. For example, the creation of habitat corridors to promote dispersal and migration of native species in the light of habitat fragmentation and climate change may also benefit invasive alien species (Procheș *et al.*, 2005). However, it is not known whether these corridors provide appropriate dispersal habitat for many ornamental alien species.

Topic 5: a much better understanding of the current and future impacts of horticulture-related plant invasions. For instance, what are the impacts of horticultural invaders on biodiversity, human livelihoods, and ecosystem services provision, including cultural ecosystem services; and where do they occur?

Topic 6: evaluation and development of tools for detecting, managing and monitoring of horticulture-driven plant invasions. Based on evaluations of current early-detection programs, this should involve developing best practices for comprehensive early-detection programs for colonising and spreading alien horticultural species. This should consider how effective monitoring and prevention strategies can be implemented, and which management methods would be most efficient and effective.

Topic 7: legal regulations that permit a thriving industry with a low risk of plant invasions. First, one would need to review the existing regulatory frameworks (Hulme *et al.*, 2018), identify gaps, address the demands of nature conservation to prevent the spread of ornamental species, and investigate how to promote the success of novel schemes (e.g. assurance schemes) in the industry that can incentivise behavioural changes. Given the diversity of stakeholders, this needs to be done sensitively to gain support from a diverse community. Importantly, sufficient long-term funding should be made available for monitoring by regulatory agents and land managers.

Topic 8: public awareness and building partnerships with stakeholders. Finally, we need to inform, educate and convince the public to promote native or benign alien plants as ornamentals rather than detrimental ones. Public awareness campaigns need to be underpinned by research on the role of cultural and social values in processes leading to new introductions. In addition to raising awareness, we need to build long-term, enduring partnerships with stakeholders, such as the plant industry, gardeners and the public (Humair, Siegrist & Kueffer, 2014*b*). They harness important knowledge about how to regulate trade and inform the involved actors. Moreover, they are also interested in avoiding unregulated trade that leads to the introduction of new plant diseases and pests.

VII. CONCLUSIONS

(1) It is clear that ornamental horticulture is the major introduction pathway of naturalised and invasive alien plants (Figs 2 and 3). Therefore, a better knowledge and understanding of the ornamental plant supply chain (Fig. 1) and historical changes therein might help us predict the potential next generation of plant invaders.

(2) The efforts of plant hunters brought many new species to botanical gardens and private collections, and fuelled the horticultural trade. Species that came in through this horticultural pathway naturalised earlier than alien species introduced by other pathways (Fig. 4).

(3) Garden fashions, and the plant species promoted by them, have changed in the last centuries, and differ among regions. However, the consequences of the different garden fashions on plant invasions still need more research.

(4) The horticultural industry continues to play a prominent role in alien plant introductions, as is evident from the high monetary value of the live-plant import market in different parts of the world (Fig. 5). Botanical gardens still play an important role in horticultural activities (Fig. 6), but their collections have become more dependent on commercial nurseries and exchange among botanical collections than on wild collection (Fig. 7).

(5) Some of the species traits promoted by horticulture, such as fast growth, are also likely to promote invasiveness. On the other hand, there is great potential to breed non-invasive ideotypes of ornamental plants, but the efforts of the horticultural industry in this regard are still very limited.

(6) A major future challenge is that social and technological changes, such as internet trade and molecular genetic breeding techniques, will lead to fundamentally novel patterns of plant introductions. In addition, environmental change, and climate change in particular, is likely to change the invasion opportunities of the ornamental species that have already been introduced.

(7) There is a need for analysis of current and future invasion risks for ornamental species in many regions of the world (Mayer *et al.*, 2017). Ecological and socio-economic impact-categorisation frameworks such as EICAT (Blackburn *et al.*, 2014) and SEICAT (Bacher *et al.*, 2017), as well as global lists of currently widely naturalised species (Pyšek *et al.*, 2017) will be very useful in this regard.

(8) There are still many open questions on the role of horticulture in plant invasions (Table 1). Therefore, more intensive research efforts on the role of horticulture are urgently needed to develop science-based regulatory frameworks that help to prevent further plant invasions.

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X. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. The questionnaire sent to botanical gardens.

Table 1. Eight key research topics proposed for studying horticulture and plant invasions, associated priority research questions, and the required data and methods.

#	Research topics	Priority questions	Required data and methods
1	Origins of ornamentals and routes of introduction and distribution	Why are new species being introduced? How are they selected? From where do they come? What is the import volume? How are introduced species distributed?	Qualitative and quantitative data on species introductions from the horticultural trade, customs duties, sales volume
2	Temporal dimensions, predicting new developments and emerging trends on horticultural trade and plant invasion	What will the future trends in horticulture be? Which species will be next to become invasive? How did and how will horticultural invaders change (fashions, traits, trade volume)?	Questionnaire to horticultural experts, qualitative and quantitative data and approaches from different scientific domains, phenomenological and mechanistic models
3	Identifying the drivers of horticulture-related plant invasions, identifying future invaders from the horticultural trade	How does trade volume and planting frequency affect invasiveness of horticultural species? How does this depend on habitat characteristics, species traits, and global change (habitat loss, land-use change, climate warming)?	Measuring propagule pressure, assessing ability to become naturalised by experimental means
4	Interactions with other features of global change: climate, land-use, urbanisation, eutrophication, habitat loss and fragmentation	How will global environmental change interact with horticulture on plant invasions?	Quantitative models on the current and future interactions of horticulture and other environmental changes
5	Assessing and predicting impacts of alien plants introduced by horticulture	What are the current impacts of alien plants introduced by horticulture? What will be the impacts of current and future ornamental plants?	Qualitative and quantitative data and approaches from different scientific domains, phenomenological and mechanistic models
6	Management: tools, effectiveness, monitoring and implementation	Do we have enough expertise to detect, monitor and manage invasive alien species introduced by horticulture? How can the	Data and models on monitoring and management measures, implementation, analysing and improving management efficiency

		relevant methods be improved? Are efficient management and methods species and site specific or can generalisations be made?	
7	Legal frameworks	Are current legal frameworks for combating invaders from the horticultural trade sufficient and effective? What roles do voluntary codes of conduct have?	Analyses of the coverage, implementation and effectiveness of current legislation, assessment of different legal tools
8	Raising public awareness, stakeholder partnerships, capacity building and promoting non-invasive species/cultivars	Are people sufficiently informed about invaders? How can communication tools be adapted to maximise the number of people reached? Who are the key people to reach? How to build mutually beneficial partnerships?	Qualitative and quantitative surveys and questionnaires of gardeners, authorities, and managers of invasive species

Fig. 1. The main pools (boxes) and flows (arrows) of species introduced for ornamental purposes, and the actors and processes involved. The width of the different species pools illustrate differences in their sizes: the cultivated species pool represents a subset of the wild species pool, and the escaped species pool is a subset of the cultivated species pool. Note that although we do not include arrows from breeders and propagators, and from wholesalers and retailers to the escaped species pool, alien plants may also escape at those stages of the supply chain. The dashed arrow indicates that the escaped alien species become part of the wild species pool, and thus that in certain regions alien species might subsequently be collected again for ornamental purposes. Across the different horticultural and ornamental trade stages, the size of the cultivated species pool changes; some of the species collected by plant hunters will not be used by breeders and propagators, but the latter will through breeding and hybridisation create new taxa, and some of the species offered by the nursery trade network of wholesalers and retailers will not be sold and planted. The thin arrows from plant hunters to botanical gardens and domestic gardens, indicate that some species planted in these gardens were collected in the wild, and by-passed the commercial ornamental plant industry. The looped arrow for botanical gardens indicates the exchange of seeds/plants among botanical gardens and the looped arrow for domestic gardens indicates the exchange of seeds/plants among hobby gardeners. Public spaces include both public green spaces (e.g. city parks) and infrastructure (e.g. road-side plantings). For similar diagrams, see Drew *et al.* (2010) and Hulme *et al.* (2018).

Fig. 2. Venn diagram illustrating that most of the species that have become naturalised somewhere in the world are grown in private gardens and in botanical gardens. A circle illustrating the size of the global vascular plant flora has been added for comparison. Data on the global naturalised flora were extracted from the Global Naturalized Alien Flora database

(GloNAF version 1.1; van Kleunen *et al.*, 2015). Data on species grown in private gardens were extracted from Dave's Garden PlantFiles (http://davesgarden.com/guides/pf/) and the Plant Information Online database (https://plantinfo.umn.edu/). Data on species grown in botanical gardens were extracted from the PlantSearch database of Botanic Gardens Conservation International (BGCI; http://www.bgci.org/plant_search.php). All species names were standardised according to The Plant List (http://www.theplantlist.org/), which also provided the number for the size of the global vascular plant flora.

Fig. 3. Among naturalised species, those grown in domestic or botanical gardens have become naturalised in more regions around the globe than species not known to be grown (labelled 'No' on figure) in gardens (Kruskal-Wallis χ^2= 1379.8, df = 3, $P < 0.001$). Data were taken from the Global Naturalized Alien Flora database (version 1.1; van Kleunen *et al.*, 2015), Dave's Garden PlantFiles (http://davesgarden.com/guides/pf/), the Plant Information Online database (https://plantinfo.umn.edu/) and PlantSearch of Botanic Gardens Conservation International (http://www.bgci.org/plant_search.php).

Fig. 4. (A) Absolute and (B) normalised first-record rates for naturalised species that are not known to be planted in gardens, and that are planted in domestic gardens (Dave's Garden PlantFiles, http://davesgarden.com/guides/pf/; the Plant Information Online database, https://plantinfo.umn.edu/), botanical gardens (PlantSearch of Botanic Gardens Conservation International, http://www.bgci.org/plant_search.php) or both. The data on first-record rates were taken from Seebens *et al.* (2017). First-record rates are defined as the number of first records of alien species per ten-year period. As the first-record rates for naturalised species that are only known to occur in domestic gardens or in no garden at all were very low, the inset of A zooms in on those species. In B, the data were normalised by setting the highest

first-record rate of each group equal to 1, and changing the other values proportionally. The trends in B are indicated by running medians (lines).

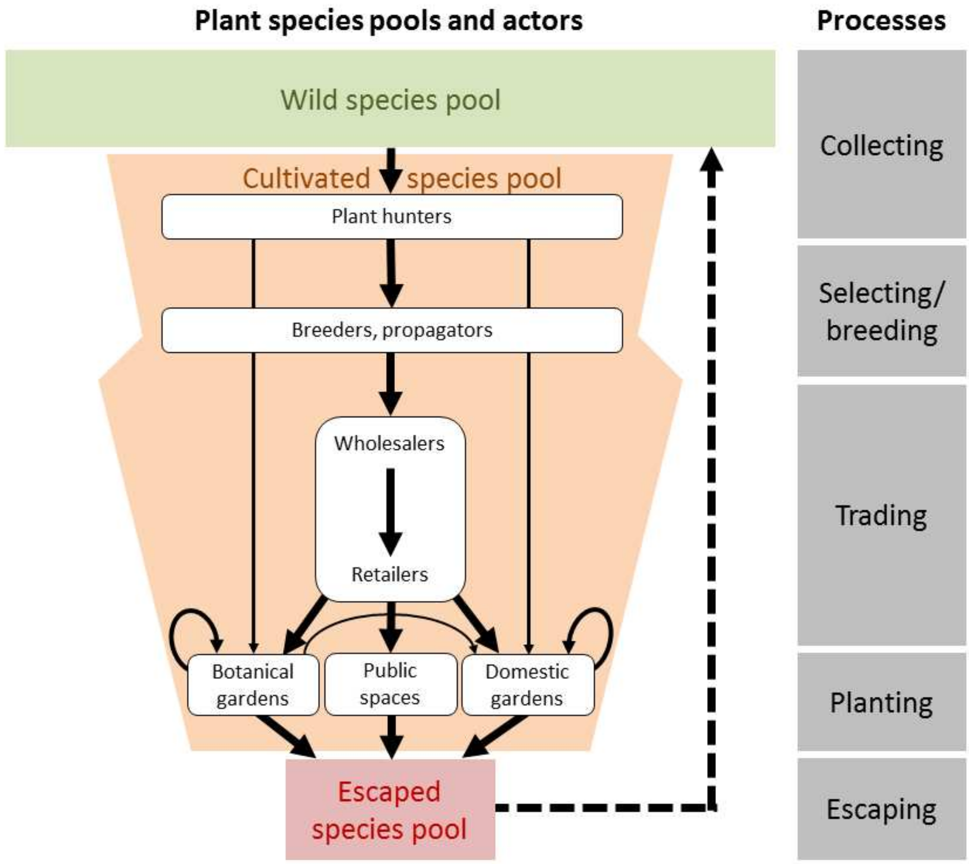
Fig. 5. (A) The import value (US$) of live plants to each country averaged for the period 2001–2010, and expressed per person. Plant import data were extracted from the United Nations Commodity Trade Statistics database (Comtrade; http://comtrade.un.org), and included commodity codes 0601 (bulbs and seeds) and 0602 (other live plants). Human population data were taken from CIESIN *et al.* (2011). Values are presented as 20% quantiles. (B) The increase in the imports of live plants expressed relative to the region with the greatest increase, Europe. Rates of increase were calculated as the area under the trend curve, and for East Asia was calculated from 2005 to 2015 due to the decrease in plant imports that occurred prior to that. (C, D) Change in import value (US$) of live plants (from 1995 to 2015, reliable plant import data were not available before 1995), for the highest four (C) and lowest five (D) importing regions shown in B. Colours correspond to the legend in B. As the rates of increase for Africa and Western Asia were identical, we distinguish Africa with white stippling on the map in panel B, and a dashed line on the graph in panel D. Import values were summed across all countries in a region, and regions were defined according to sub-continent and similarity among import trends. Import values and trends were very similar for some geographically disjunct regions, and so values were aggregated to reduce the number of lines and maximise colour differences: for Central-South America and Africa Pearson's r=0.81, P<0.00001, df=19; the combined import values for Central-north Asia, south and south-east Asia, and Oceania were grouped as they were relatively low.

Fig. 6. Proportion of 947 botanical gardens across six continents that participate in retail plant sales, horticulture or plant breeding research, or undertake plant explorations. Data from

Botanic Garden Conservation International Garden Search (www.bgci.org/garden_search.php; accessed on 1 November 2016).

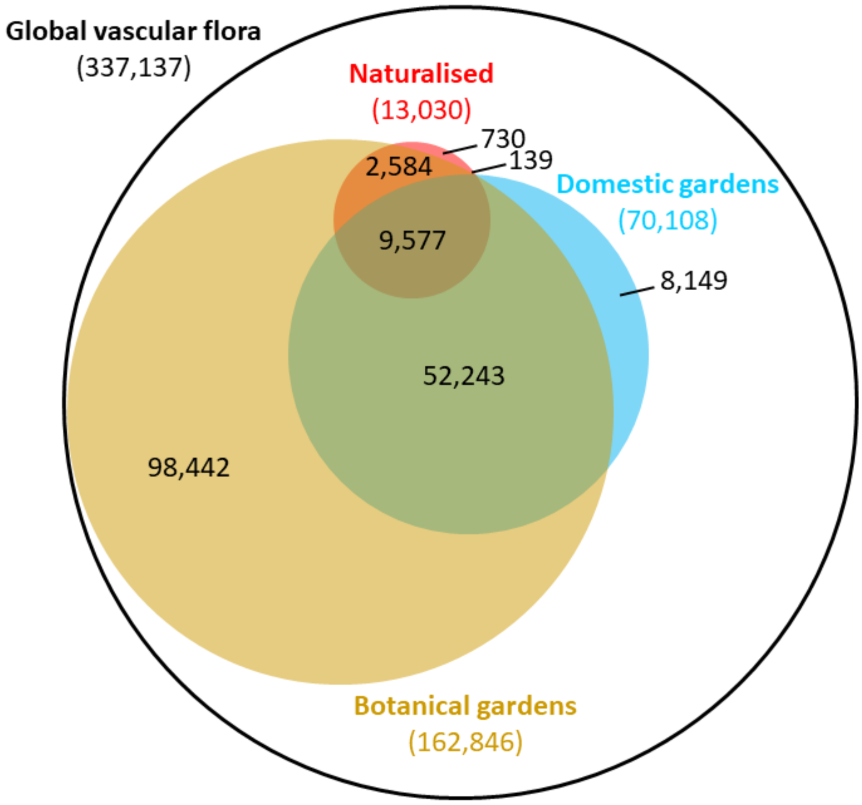
Fig. 7. Main sources of plants in botanical gardens, based on a questionnaire to which 161 botanical gardens responded. Six of the botanical gardens indicated two sources as the main ones; these were assigned to both sources. The botanical gardens were grouped according to continent (TDWG continent; Brummitt, 2001).

FIGURE 1

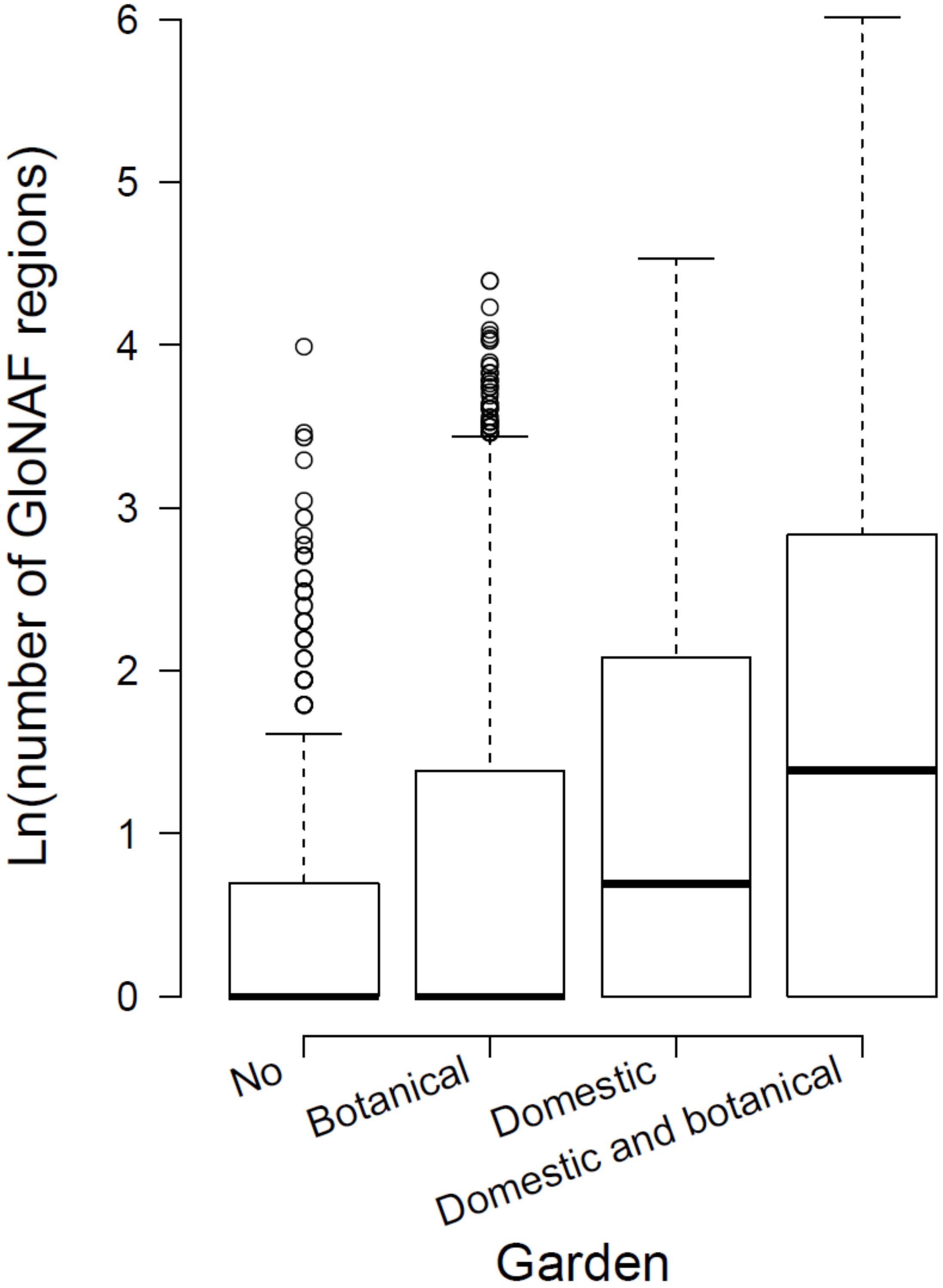


Plant species pools and actors
Processes
Wild species pool
Cultivated species pool
Plant hunters
Breeders, propagators
Wholesalers
Retailers
Botanical gardens
Public spaces
Domestic gardens
Escaped species pool
Collecting
Selecting/ breeding
Trading
Planting
Escaping

FIGURE 2


Global vascular flora
(337,137)
Naturalised
(13,030)
730
2,584
139
Domestic gardens
(70,108)
9,577
8,149
52,243
98,442
Botanical gardens
(162,846)

1250 **FIGURE 3**



1251

1252

FIGURE 4

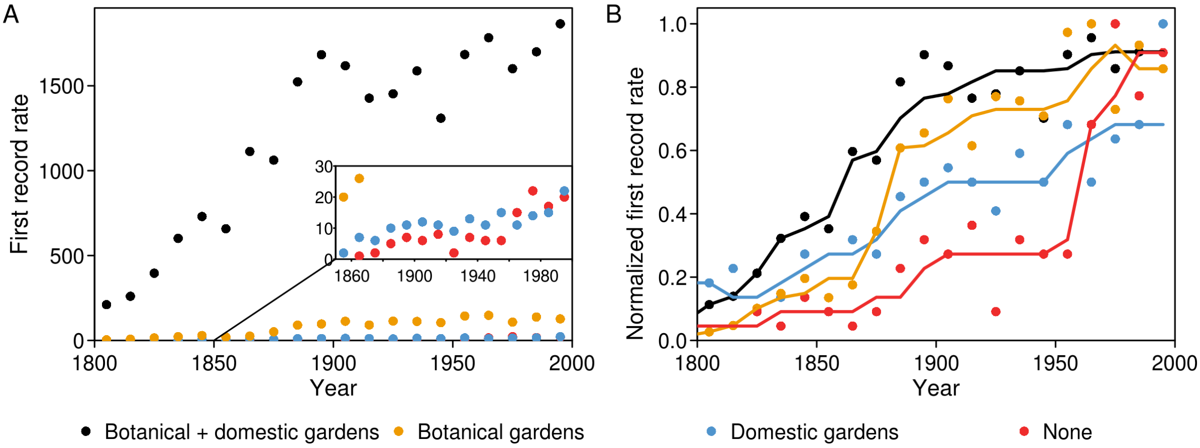

A
First record rate
1500
1000
500
0
1800
1850
1900
1950
2000
Year
30
20
10
0
1860
1900
1940
1980
B
Normalized first record rate
1.0
0.8
0.6
0.4
0.2
0.0
1800
1850
1900
1950
2000
Year
Botanical + domestic gardens
Botanical gardens
Domestic gardens
None

FIGURE 5

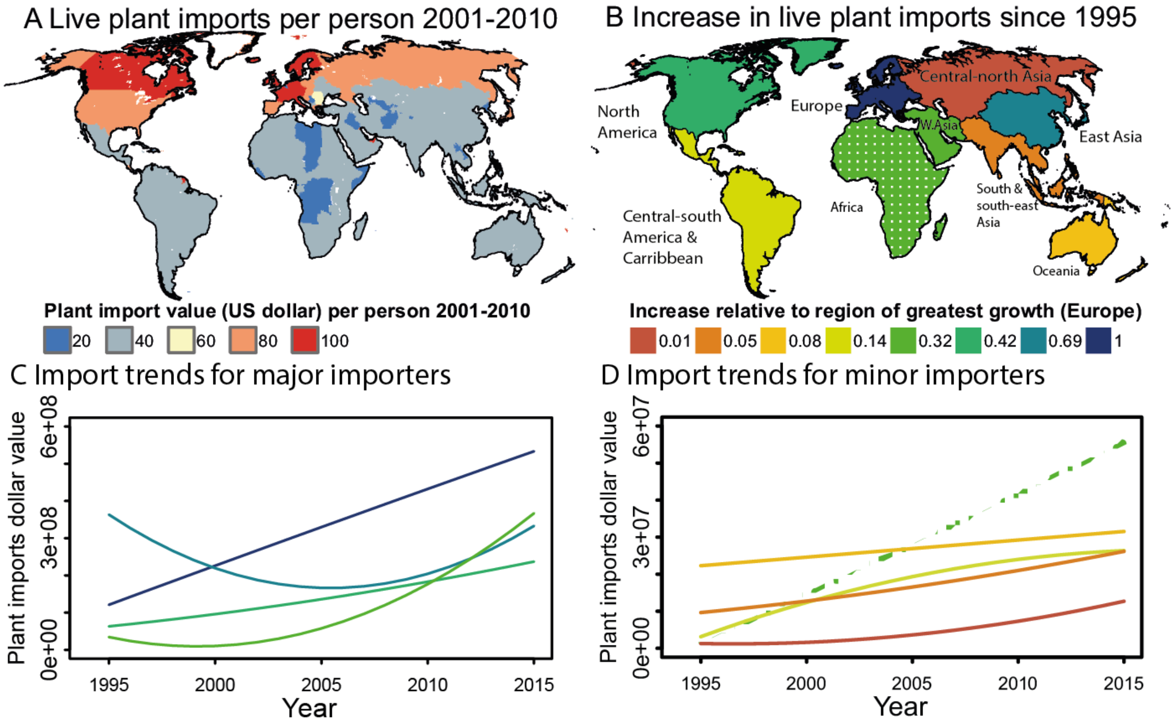

A Live plant imports per person 2001-2010
Plant import value (US dollar) per person 2001-2010
20
40
60
80
100
B Increase in live plant imports since 1995
North America
Europe
Central-north Asia
W.Asia
East Asia
Africa
South & south-east Asia
Central-south America & Carribbean
Oceania
Increase relative to region of greatest growth (Europe)
0.01
0.05
0.08
0.14
0.32
0.42
0.69
1
C Import trends for major importers
Plant imports dollar value
0e+00
3e+08
6e+08
1995
2000
2005
2010
2015
Year
D Import trends for minor importers
Plant imports dollar value
0e+00
3e+07
6e+07
1995
2000
2005
2010
2015
Year

FIGURE 6

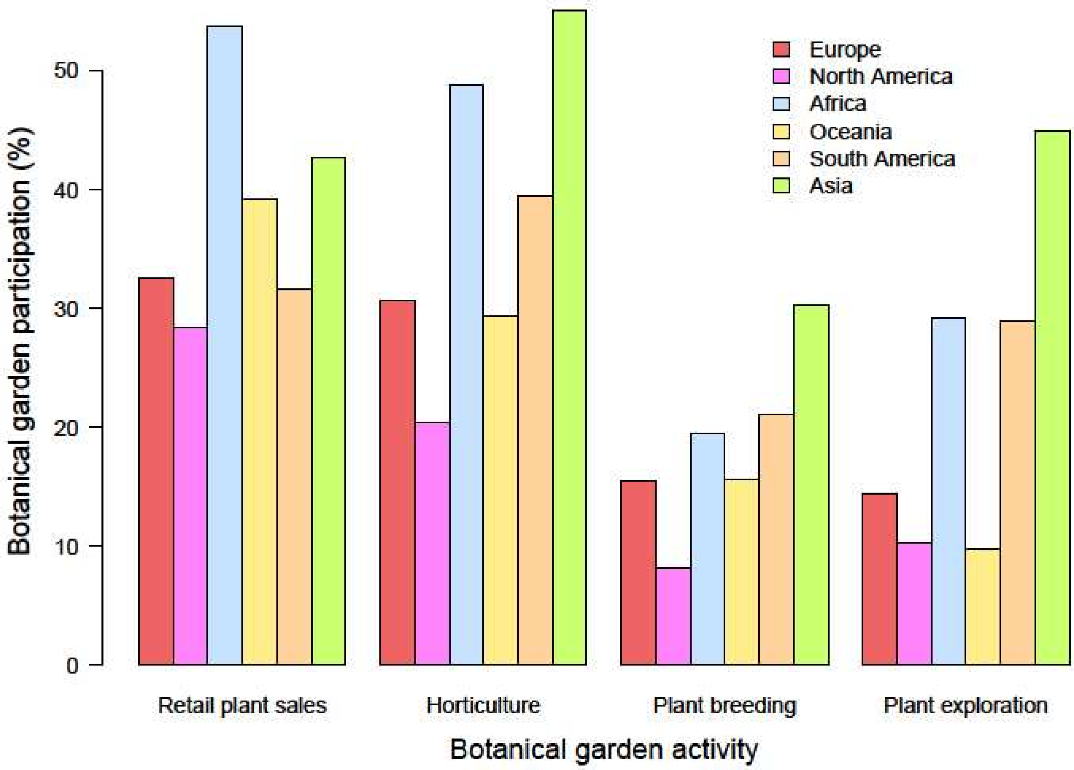
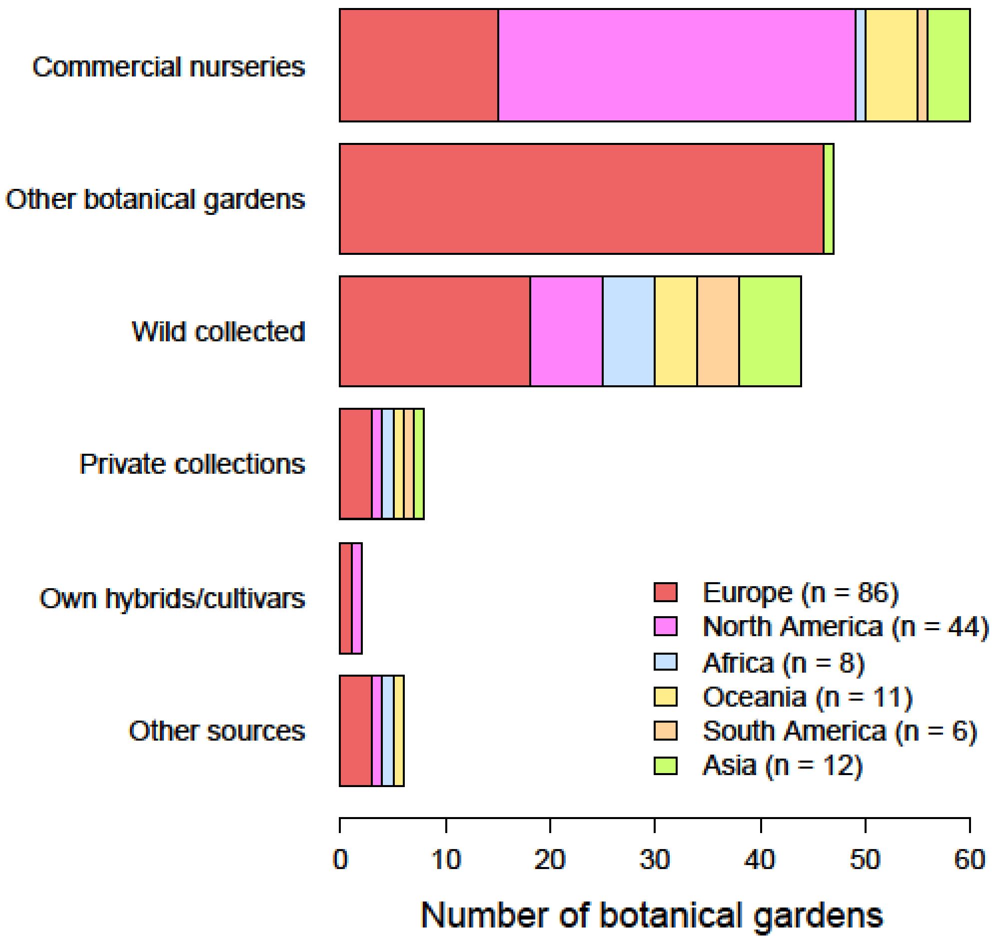

Europe
North America
Africa
Oceania
South America
Asia
Botanical garden participation (%)
0
10
20
30
40
50
Retail plant sales
Horticulture
Plant breeding
Plant exploration
Botanical garden activity

FIGURE 7


Commercial nurseries
Other botanical gardens
Wild collected
Private collections
Own hybrids/cultivars
Other sources
Europe (n = 86)
North America (n = 44)
Africa (n = 8)
Oceania (n = 11)
South America (n = 6)
Asia (n = 12)
0
10
20
30
40
50
60
Number of botanical gardens