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1 **The changing role of ornamental horticulture in alien plant**
2 **invasions**

3
4 Mark van Kleunen^{1,2,*}, Franz Essl³, Jan Pergl⁴, Giuseppe Brundu⁵, Marta
5 Carboni⁶, Stefan Dullinger³, Regan Early⁷, Pablo González-Moreno⁸, Quentin J.
6 Groom⁹, Philip E. Hulme¹⁰, Christoph Kueffer^{11,12}, Ingolf Kühn^{13,14}, Cristina
7 Máguas¹⁵, Noëlie Maurel², Ana Novoa^{4,12,16}, Madalin Parepa¹⁷, Petr Pyšek^{4,18},
8 Hanno Seebens¹⁹, Rob Tanner²⁰, Julia Touza²¹, Laura Verbrugge^{22,23}, Ewald
9 Weber²⁴, Wayne Dawson²⁵, Holger Kreft²⁶, Patrick Weigelt²⁶, Marten Winter¹⁴,
10 Günther Klöner³, Matthew V. Talluto⁶ & Katharina Dehnen-Schmutz²⁷

11
12 ¹*Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation,*
13 *Taizhou University, Taizhou 318000, China*

14 ²*Ecology, Department of Biology, University of Konstanz, Universitätsstrasse 10, D-78457*
15 *Konstanz, Germany*

16 ³*Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, 1030*
17 *Vienna, Austria*

18 ⁴*Institute of Botany, Department of Invasion Ecology, The Czech Academy of Sciences, CZ-*
19 *252 43 Průhonice, Czech Republic*

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

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

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

24 ⁸*CABI, Bakeham Lane, Egham TW20 9TY, UK*

25 ⁹*Botanical Garden Meise, Bouchout Domain, Nieuwelaan 38, 1860 Meise, Belgium*

26 ¹⁰*Bio-Protection Research Centre, Lincoln University, Lincoln 7648, Canterbury, New*
27 *Zealand*

28 ¹¹*Institute of Integrative Biology, ETH Zurich, Universitätsstrasse 16, 8092 Zurich,*
29 *Switzerland*

30 ¹²*Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University,*
31 *Matieland 7602, South Africa*

32 ¹³*Helmholtz Centre for Environmental Research – UFZ, Dept. Community Ecology, Theodor-*
33 *Lieser-Str. 4, 06120 Halle, Germany*

34 ¹⁴*German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher*
35 *Platz 5e, 04103 Leipzig, Germany*

36 ¹⁵*Centre for Ecology, Evolution and Environmental Changes (cE3c), Faculty of Sciences,*
37 *University of Lisbon, Campo Grande, 1749-016 Lisboa, Portugal*

38 ¹⁶*Invasive Species Programme, South African National Biodiversity Institute, Kirstenbosch*
39 *Research Centre, South Africa*

40 ¹⁷*Institute of Evolution & Ecology, University of Tübingen, Auf der Morgenstelle 5, 72076*
41 *Tübingen, Germany*

42 ¹⁸*Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 44*
43 *Prague, Czech Republic*

44 ¹⁹*Senckenberg Biodiversity and Climate Research Centre, Georg-Voigt-Straße 14-16, 60325*
45 *Frankfurt, Germany*

46 ²⁰*European and Mediterranean Plant Protection Organization, 21 boulevard Richard Lenoir*
47 *75011, Paris, France*

48 ²¹*Environment Department, University of York, Wentworth Way, Heslington, YO10 5NG,*
49 *York, UK*

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

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

53 ²⁴*Biodiversity Research, University of Potsdam, Maulbeerallee 1, Potsdam D-14469,*
54 *Germany*

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

56 ²⁶*Biodiversity, Macroecology & Biogeography, University of Goettingen, Büsgenweg 1,*
57 *37077 Göttingen, Germany*

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

60

61 **Running head:** Horticulture and plant invasions

62

63 * Author for correspondence (E-mail: mark.vankleunen@uni-konstanz.de; Tel.: +49 7531 88
64 2997).

65

66 **ABSTRACT**

67 The number of alien plants escaping from cultivation into native ecosystems is increasing
68 steadily. We provide an overview of the historical, contemporary and potential future roles of
69 ornamental horticulture in plant invasions. We show that currently at least 75% and 93% of
70 the global naturalised alien flora is grown in domestic and botanical gardens, respectively.
71 Species grown in gardens also have a larger naturalised range than those that are not. After
72 the Middle Ages, particularly in the 18th and 19th centuries, a global trade network in plants

73 emerged. Since then, cultivated alien species also started to appear in the wild more
74 frequently than non-cultivated aliens globally, particularly during the 19th century.
75 Horticulture still plays a prominent role in current plant introduction, and the monetary value
76 of live-plant imports in different parts of the world is steadily increasing. Historically,
77 botanical gardens – an important component of horticulture – played a major role in
78 displaying, cultivating and distributing new plant discoveries. While the role of botanical
79 gardens in the horticultural supply chain has declined, they are still a significant link, with
80 one-third of institutions involved in retail-plant sales and horticultural research. However,
81 botanical gardens have also become more dependent on commercial nurseries as plant
82 sources, particularly in North America. Plants selected for ornamental purposes are not a
83 random selection of the global flora, and some of the plant characteristics promoted through
84 horticulture, such as fast growth, also promote invasion. Efforts to breed non-invasive plant
85 cultivars are still rare. Socio-economical, technological, and environmental changes will lead
86 to novel patterns of plant introductions and invasion opportunities for the species that are
87 already cultivated. We describe the role that horticulture could play in mediating these
88 changes. We identify current research challenges, and call for more research efforts on the
89 past and current role of horticulture in plant invasions. This is required to develop science-
90 based regulatory frameworks to prevent further plant invasions.

91

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

94

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113

114 I. INTRODUCTION

115 With increasing globalisation, many plant species have been introduced beyond their natural
116 ranges, and some of these have established and sustain persistent populations without human
117 assistance (van Kleunen *et al.*, 2015; Pyšek *et al.*, 2017). Most of these alien species (*sensu*
118 Richardson *et al.*, 2000) have comparatively small naturalised ranges (Pyšek *et al.*, 2017) and
119 do not cause major ecological or economic damage. Some alien species, however, have
120 become invasive (*sensu* Richardson *et al.*, 2000), impact upon native species, and can result
121 in a significant burden on global economies, ecosystem services and public health (Pimentel,
122 Zuniga & Morrison, 2005; Vilà *et al.*, 2011; Pyšek *et al.*, 2012*b*). Alien species introductions

123 have sometimes occurred unintentionally through various pathways (e.g. as seed
124 contaminants), but most invasive alien plants have been introduced intentionally, particularly
125 for cultivation as ornamentals in public and private gardens (Hulme *et al.*, 2008; Pyšek,
126 Jarošík & Pergl, 2011).

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

145 To interpret current trends and to predict likely future developments, we need a better
146 understanding of the number and diversity of alien plants grown in gardens. Furthermore, we
147 also need to know their introduction history and the species characteristics that promote both

148 their horticultural usage and potential invasion success. Therefore, we here integrate
149 information from invasion biology and horticulture to provide a broad overview of the role of
150 ornamental horticulture in alien plant invasions. We do this by (i) using a scheme describing
151 the pathways and processes involved in ornamental plant invasions (Fig. 1; also see Drew *et*
152 *al.*, 2010), (ii) covering a wide range of relevant issues, such as introduction dynamics,
153 garden fashions and plant traits promoted by horticulture, from both historical and
154 contemporary perspectives, (iii) discussing the potential future role of horticulture, and (iv)
155 highlighting research needs.

156

157 **II. CONTEMPORARY GARDENS AND THE NATURALISED ALIEN FLORA OF** 158 **THE WORLD**

159 Regional analyses of alien naturalised floras have shown that usually more than half of these
160 species were introduced for ornamental horticulture purposes (e.g. Germany: Kühn & Klotz,
161 2002; Czech Republic: Pyšek *et al.*, 2012a; Britain: Clement & Foster, 1994; USA: Mack &
162 Erneberg, 2002; Australia: Groves, 1998; South Africa: Faulkner *et al.*, 2016). Furthermore, a
163 comparison of the frequency of invasive species across the world reveals that most have
164 originated from ornamental horticulture (Hulme *et al.*, 2018). However, a global analysis of
165 naturalised alien plants is still missing. In order to obtain a benchmark estimate of the
166 proportion of naturalised species that have been introduced as garden plants globally, we
167 compared the naturalised alien flora and the cultivated garden flora. The recently compiled
168 Global Naturalized Alien Flora (GloNAF) database revealed that more than 13,000 vascular
169 plant species have become naturalised somewhere in the world (van Kleunen *et al.*, 2015;
170 Pyšek *et al.*, 2017). The number of plant species grown in domestic gardens, public green
171 spaces and botanical gardens is much larger but precise numbers are yet unknown
172 (Khoshbakht & Hammer, 2008). In order to obtain a minimum estimate of the size of the

173 global domestic garden flora, we extracted the lists of species in Dave's Garden PlantFiles
174 (<http://davesgarden.com/guides/pf/>, accessed 23 March 2016) and in the Plant Information
175 Online database (<https://plantinfo.umn.edu/>, accessed 22 November 2017). Furthermore, to
176 obtain a minimum estimate of the number of species planted in botanical gardens, we
177 extracted the list of species in the PlantSearch database of Botanic Gardens Conservation
178 International (http://www.bgci.org/plant_search.php, accessed 25 May 2016), which includes
179 species accessions of 1,144 botanical institutions worldwide. All species names were
180 taxonomically harmonised using The Plant List (version 1.1; <http://www.theplantlist.org/>,
181 accessed in December 2017), which also provided us with an estimate of the number of
182 species in the global vascular plant flora. Ornamental cultivars that could not be assigned to
183 species were not considered as they are not included in The Plant List.

184 At least 51% of all known species of vascular plants worldwide (337,137) are grown
185 in domestic (70,108) or botanical gardens (162,846; Fig. 2). Most of the species grown in
186 domestic gardens are also grown in botanical gardens (88%; Fig. 2), and it is likely that most,
187 if not all species grown in public green spaces, for which we have no estimates, are also
188 grown in domestic or botanical gardens (Mayer *et al.*, 2017). Although not all species in these
189 gardens are cultivated for decorative purposes, and not all of them are cultivated outside their
190 native ranges, these large numbers of garden species suggest that ornamental horticulture is
191 the major pathway of alien plant introduction. Thus, it is not surprising that at least 75% and
192 93%, respectively, of the naturalised alien plants worldwide are grown in domestic and
193 botanical gardens (Fig. 2). Moreover, among the naturalised species, those grown in domestic
194 or botanical gardens are also naturalised in more regions around the globe (Fig. 3).
195 Furthermore, Hulme (2011) showed for the 450 invasive alien plant species listed in Weber
196 (2003) that the number of regions in which each of these species is invasive is positively
197 correlated with their frequency in botanical garden collections worldwide. Some of these

198 species may also have been introduced via additional pathways (e.g. agriculture or forestry).
199 For example, *Robinia pseudoacacia* has been introduced as ornamental plant, forestry tree
200 and nectar source, and for soil stabilization (Vítková *et al.*, 2017). Particularly, during the so-
201 called utilitarian phase of the history of global weed movement (Mack & Lonsdale, 2001),
202 the chances of becoming invasive may be high. So, while other deliberate introduction
203 pathways are also important, there is strong evidence that ornamental horticulture remains a
204 major contributor to plant invasions (Mack & Erneberg, 2002; Dehnen-Schmutz *et al.*, 2007;
205 Hanspach *et al.*, 2008; Lambdon *et al.*, 2008; Hulme, 2011, Pyšek *et al.*, 2011; Pergl *et al.*,
206 2016; Saul *et al.*, 2017; Hulme *et al.*, 2018).

207

208 **III. THE HISTORY OF ORNAMENTAL HORTICULTURE AND IMPLICATIONS** 209 **FOR CURRENT PLANT INVASIONS**

210 **(1) Garden-plant introductions**

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

222 Since pre-Roman times, and increasingly with the Romans and in the Middle Ages,
223 plant species were transported across Europe. In particular, Mediterranean plants were carried
224 to other parts of Europe, and occasionally plants from more distant regions, such as Central
225 and East Asia, were introduced to Europe (e.g. Jacomet & Kreuz, 1999; Campbell-Culver,
226 2001). In their colonisation of Pacific islands, Polynesians introduced several crop and fibre
227 species to Hawaii and later New Zealand (Cox & Barnack, 1991; Roullier *et al.*, 2013). From
228 China, there is evidence of the early use of alien plants during the Han-Dynasty, where the
229 new long-distance trade network of the ‘silk road’ was used to introduce ornamental alien
230 plants for the extensive park created by Emperor Wu-Ti (140–89 BC; Hill, 1915; Keller,
231 1994). In pre-Columbian Mexico, there were already gardens, such as that of the Acolhua
232 king Netzahualcōyotl (1402–1472) and those of the Aztec kings Moctezuma I (1390–1469)
233 and Moctezuma II (1465–1520), with plants collected in Mexico and elsewhere in the
234 Americas (Hill, 1915; Sánchez, 1997). For other parts of the world, little or no information is
235 available on such historical plant introductions.

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

245 After the Middle Ages, global exploration by European nations expanded rapidly, the
246 intercontinental exchange of species gained momentum, and eventually a truly global

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

265 Similarly, many new ornamentals were introduced to North America from the 18th to
266 the 20th centuries from plant-collection expeditions in Eastern and Central Asia, North Africa
267 and the Middle East (Stoner & Hummer, 2007). During the first expedition of this kind
268 funded by the federal government of the USA, Robert Fortune (1812–1880) introduced
269 species of *Chrysanthemum*, *Paeonia* and *Rhododendron* (azaleas) as ornamentals into the
270 USA (Musgrave *et al.*, 1999). Another noteworthy plant hunter was Ernest Henry Wilson
271 (1876–1930), who introduced >2,000 plant species from Asia to Europe and North America.

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

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

289 Ornamental alien plants were not only introduced to the home countries of the
290 predominantly European plant hunters, but plants native to Europe were also introduced into,
291 and exchanged among the colonies. An important role in this exchange was played by the
292 acclimatisation societies, which arose in Europe and its colonies during the 19th century.
293 Initially, the acclimatisation societies were fuelled by interest in novel flora and fauna from
294 the colonies for introduction into European gardens and zoos (Dunlap, 1997). Later, the focus
295 changed to transplanting the biotic landscape from the mother country into the colonies and
296 the exchange of ornamental and crop species among colonies (di Castri, 1989; Osborne,

297 2001). Subsidies and free transport of explorers, plants and animals on cargo ships to and
298 from the colonies was offered by supporting governments (Grove, 1995). Many crops but
299 also ornamentals were transported this way, including bamboos and species of *Araucaria*,
300 *Acacia* and *Camellia* (Bennett, 1870). Soon after their foundation, popularity of the
301 acclimatisation societies waned due to growing concerns for the preservation of indigenous
302 biota (Dunlap, 1997). Twenty years after their rapid appearance, most acclimatisation
303 societies had been dissolved, and the few remaining ones started to focus on reintroduction of
304 threatened native species.

305 While botanical gardens were used as showcases by the acclimatisation societies in
306 the second half of the 19th century, their role in introducing and cultivating alien plants
307 started much earlier and continues today. Particularly, during the 17th and 18th century,
308 botanical gardens were part of the colonial infrastructure that facilitated the distribution of
309 useful plants around the world (Hulme, 2011). Between 1750 and 1850, the first botanical
310 gardens were founded in all non-European continents (with the exception of Antarctica):
311 Bartram's Garden (1728) in North America, the Calcutta Botanic Garden (1786) in Asia, the
312 Sydney Gardens (1788) in Australia, the Rio de Janeiro Botanical Garden (1808) in South
313 America, and Cape Town Botanic Garden (1848) in Africa (Hill, 1915). Botanical gardens
314 were also instrumental in the collation, evaluation and dissemination of new discoveries of
315 foods, agricultural products and ornamentals, generally sponsored by governments and
316 commercial enterprises (e.g. Diagre-Vanderpelen, 2011). Unsurprisingly, many of the
317 currently naturalised and invasive alien plant species were first planted in botanical gardens.
318 For example, in Europe, *Solidago canadensis* and *S. gigantea* were first planted in Paris and
319 London, respectively (Wagenitz, 1964; Weber, 1998), and *Agave americana* was first planted
320 in the Padua Botanical Garden (Italy; [http://www.ortobotanicopd.it/en/piante-introdotte-](http://www.ortobotanicopd.it/en/piante-introdotte-italia-dallorto-botanico)
321 [italia-dallorto-botanico](http://www.ortobotanicopd.it/en/piante-introdotte-italia-dallorto-botanico); accessed 23 March 2017). Many of the species introduced to

322 botanical gardens may first have been distributed to other gardens and public green spaces
323 before they escaped into the wild. However, some alien species escaped directly from
324 botanical gardens (Harris, 2002; Sukopp, 2006), including several listed among the worst
325 aliens worldwide (Hulme, 2011).

326 With the emergence and intensification of the global network of ornamental plant
327 species trade after the Middle Ages, it is not surprising that the rate at which new alien
328 species established in the wild increased dramatically (Seebens *et al.*, 2017). Some of these
329 species were not introduced intentionally for their economic and ornamental value, but were
330 accidentally transported with other cargo or in ballast soil (e.g. Brown, 1878; Hulme *et al.*,
331 2008). The exact role of ornamental horticulture in the temporal dynamics of naturalisation
332 events is therefore difficult to quantify. To gain some insights, we used the database of
333 Seebens *et al.* (2017) on first-record rates of established alien plants in combination with data
334 on their cultivation in domestic (data from Dave’s Garden PlantFiles and the Plant
335 Information Online database) and botanical (data from Botanic Gardens Conservation
336 International PlantSearch database) gardens. The first-record rate in the 19th century
337 increased faster for species that are now cultivated in gardens, particularly in botanical
338 gardens, than for species not known to be cultivated (Fig. 4). This suggests that species
339 introduced for horticultural purposes naturalised earlier than alien species introduced by other
340 pathways. However, while the first-record rates of species grown in domestic gardens only
341 and species not known to be cultivated are still increasing rapidly, the first-record rate
342 appears to slow down for species grown in botanical gardens (Fig. 4). Possibly, this is partly
343 a consequence of the increasing awareness about invasive plants among botanical gardens
344 and their stronger focus on native plants in recent times (Hulme, 2015).

345

346 **(2) Historical garden-fashion trends**

347 Changing garden and landscaping fashions impact on plant introductions and subsequent
348 invasions through floral design, style elements and layouts of gardens, parks and other green
349 spaces, as well as through the choice of plants they promote (e.g. Müller & Sukopp, 2016).
350 Historic fashion trends were not only driven by demand but also by the chronological order in
351 which plants from different parts of the world became available. For example, with the
352 discovery of the New World, novel ornamental plants were introduced into European
353 horticulture as early as the 16th century, many of which are still common in today's gardens –
354 e.g. *Helianthus* spp., *Amaranthus caudatus* and *Mirabilis jalapa*. Increased trade with the
355 Orient also opened the door to plants from Asia (e.g. *Hemerocallis* spp.) into Europe. While
356 most of these species are herbaceous, the development of landscape gardens and arboreta in
357 the 18th and 19th centuries marked the start of the widespread introduction of ornamental trees
358 to Europe (see e.g. Goeze, 1916). Landscape gardens were characterised by the opening up of
359 gardens into a wider landscape accompanied by careful positioning of artificial lakes, trees
360 and hedges. Many alien trees introduced to create such gardens still characterise urban parks
361 today, and some of them – such as the North American species *Acer negundo*, *Robinia*
362 *pseudoacacia*, *Pinus strobus*, *Prunus serotina* and *Quercus rubra* – have also become
363 naturalised in Europe and elsewhere (Brundu & Richardson, 2016; Richardson & Rejmánek,
364 2011; Campagnaro, Brundu & Sitzia, 2017).

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

371 Plant recommendations for these habitats in Britain were provided by William Robinson with
372 his influential book *The wild garden or, our groves and shrubberies made beautiful by the*
373 *naturalization of hardy alien plants* (Robinson, 1870). The trend of using hardy perennial
374 plants continued into the 20th century, first driven by the desire to create *Colour in the flower*
375 *garden* as Gertrude Jekyll (1908) titled her influential book. It was also influenced by the
376 ornamental plant breeder Karl Foerster (1874–1970), one of the first to promote the use of
377 grasses as ornamentals in Germany (Hottenträger, 1992). These are just a few of the
378 individuals that influenced garden fashions in Europe. Examples of influential people in the
379 Americas are Andrew Jackson Downing (1815–1852) and Frederick Law Olmsted (1822–
380 1903), who both preached the English or natural style of landscape gardening, and more
381 recently Thomas Church (1902–1978), who designed the ‘California Style’ of garden
382 landscapes (<https://www.gardenvisit.com>, accessed 28 November 2017). The consequences
383 of these different ‘garden fashions’ initiated by these people on plant invasions in different
384 regions of the world still need more research.

385

386 **IV. THE RECENT ROLE OF HORTICULTURE IN PLANT INVASIONS**

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

388 Horticulture continues to play a prominent role in alien plant introductions (Reichard &
389 White, 2001; Bradley *et al.*, 2011; Humair *et al.*, 2015). This is confirmed by analyses of the
390 monetary value of live-plant imports in different parts of the world, which show a steady
391 increase in live-plant imports in Europe and North America (Fig. 5). This may, however, not
392 necessarily translate into a higher diversity of species traded, as such trade statistics do not
393 specify the number of species traded, and include non-ornamental plants. Live-plant imports
394 in South and Central Asia are rising at an increasing rate, and, while imports to East Asia
395 appear to have undergone a rise and fall at the end of the 1990s, imports are increasing once

396 again (Fig. 5). Understanding who is involved in horticulture in these regions would help
397 invasive-plant management plans to be targeted to the appropriate audience.

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

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

421 Nevertheless, North American botanical gardens play a leading role in using their living
422 collections of alien ornamentals as a basis for commercial breeding and marketing (Pooler,
423 2001; Kintgen, Krishnan & Hayward, 2013; Ault & Thomas, 2014).

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

436 With already a significant proportion of the global flora in cultivation (Fig. 2) and
437 increased availability of plant propagules through other sources, wild collection has probably
438 decreased in the last decades. It is likely to decrease further due to global restrictions on
439 collecting wild plants imposed by the Nagoya Protocol on access and benefit-sharing of the
440 Convention of Biological Diversity (2011; <https://www.cbd.int/abs/>). This means that home
441 gardens and plantings in public green spaces will rely on nurseries, but also that botanical
442 gardens will have to maintain or expand their collections using commercially bought plant
443 material or through exchange with other botanical gardens. To obtain an impression of the
444 importance of different plant sources for current botanical garden collections, we sent a
445 questionnaire to botanical gardens around the globe (Appendix 1). Of the 161 respondents,

446 37%, 29% and 27% indicated that their major sources of plants are commercial nurseries,
447 other botanical gardens and collections from the wild, respectively (Fig. 7). Commercial
448 nurseries were particularly important sources for North American botanical gardens, whereas
449 other botanical gardens were particularly important sources for European botanical gardens
450 (Fig. 7). The latter might reflect that many European botanical gardens produce an Index
451 Seminum (i.e. seed catalogue) of the species available for exchange.

452

453 **(2) Modern garden-fashion trends**

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

471 native species (e.g. Kruckeberg, 2001; Shaw, Miller & Wescott, 2017). This is likely due to
472 awareness of biological invasions but also because people want to have gardens that promote
473 diversity and wildlife, and are less labour intensive.

474

475 **(3) Horticultural selection favours traits related to invasiveness**

476 The horticultural industry identifies particularly prized species, varieties or cultivars through
477 specific accolades, e.g. Awards of Garden Merit (Great Britain), Mérites de Courson
478 (France), All-America Selection Winners (USA), Gold Medal Plant (Pennsylvania). Such
479 accolades are an important marketing strategy to promote specific plants, and are an
480 important aspiration for many ornamental plant breeders. While the criteria differ for
481 individual accolades, in general the plants must be excellent for garden use, exhibit
482 consistently good performance in different garden environments and climates, should be easy
483 to grow, and should not be particularly susceptible to insect pests or pathogens (Hulme,
484 2011). Such characteristics, together with the higher market frequency of these species may
485 have contributed to the high propensity of award-winning plants to become invasive (Hulme,
486 2015).

487 There are several plant characteristics that might promote both horticultural use and
488 invasion. Environmental matching is an obvious criterion when considering a species for
489 horticulture (Reichard, 2011), and at the same time is also important for naturalisation and
490 invasiveness (Richardson & Pyšek, 2012). For example, in Germany – a temperate region
491 with winter frost – hardier species are planted more frequently (Maurel *et al.*, 2016) and have
492 a higher probability of naturalisation (Hanspach *et al.*, 2008; Maurel *et al.*, 2016) than less
493 hardy species. Horticultural usage should also be favoured by ease of propagation (Mack,
494 2005; Reichard, 2011), and alien species with rapid and profuse seedling emergence are also
495 more likely to naturalise (van Kleunen & Johnson, 2007). Similarly, fast vegetative growth is

496 promoted by the horticultural industry (Reichard, 2011), and also promotes invasiveness of
497 plants (Dawson, Fischer & van Kleunen, 2011; Grotkopp, Erskine-Ogden, & Rejmánek,
498 2010). Furthermore, early-flowering species and genotypes often have a long flowering
499 period or have repeated bouts of flowering (Mack, 2005) and can be sold sooner or for a
500 longer time, thus increasing profit (Reichard, 2011). At the same time, a longer flowering
501 period has also been found to be associated with invasiveness (Lloret *et al.*, 2005; Gallagher,
502 Randall & Leishman, 2015). So, horticulture may facilitate plant invasions by screening
503 species and genotypes of ornamental value based on traits that inadvertently promote spread
504 (Drew *et al.*, 2010; Knapp *et al.*, 2012).

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

517 To date there has been very limited involvement of plant breeders in reducing
518 invasion risk of ornamental plants (e.g. Burt *et al.*, 2007; Novoa *et al.*, 2015a). Anderson,
519 Gomez & Galatowitsch (2006) proposed 10 traits to reduce invasiveness while retaining
520 commercial value of ornamentals: reduced genetic variation in propagules, slowed growth

521 rates, non-flowering, elimination of asexual propagules, lack of pollinator rewards, non-
522 dehiscing fruits (to prevent seed dispersal), lack of edible fruit flesh, lack of seed
523 germination, sterility and programmed death prior to seed production. So far, most effort in
524 producing non-invasive cultivars has focussed on reduced fecundity (e.g. Freyre *et al.*, 2016).
525 Unfortunately, for perennial species, even relatively low levels of seed production may be
526 sufficient for plant invasions (Knight, Havens & Vitt, 2011). Furthermore, traits such as seed
527 sterility and dwarfism, bred into cultivars to reduce invasion potential, may revert back to
528 their original states (Brand, Lehrer & Lubell, 2012). Perhaps the way forward is for
529 horticultural accolades to recognise the risk of invasiveness more formally and at least
530 account for this in field trials and subsequent selection of award-winning taxa.

531

532 **V. THE NEXT GENERATION OF INVADING ALIEN HORTICULTURAL PLANTS**

533 **(1) New pathways and horticultural practices**

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

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

553

554 **(2) Climate change**

555 Environmental changes, such as atmospheric nitrogen deposition, habitat fragmentation and
556 disturbance due to land-use change, have contributed to plant invasions and are likely to do
557 so in the future (Bradley *et al.*, 2010; Sheppard, Burns & Stanley, 2014; Dullinger *et al.*,
558 2017; Liu *et al.*, 2017). In addition, it is commonly expected that climate change will increase
559 plant invasions globally, although its impacts may vary considerably among geographic areas
560 and species (Lambdon *et al.*, 2008; Hulme, 2009; Bradley *et al.*, 2010; Seebens *et al.*, 2015;
561 Early *et al.*, 2016; Dullinger *et al.*, 2017). This expectation is mainly based on the anticipated
562 destabilisation of resident native plant communities caused by an emerging disequilibrium
563 with climatic conditions (Svenning & Sandel, 2013) and by increased frequencies of extreme
564 events, such as droughts, hurricanes and heat waves (Diez *et al.*, 2012). Both will likely
565 decrease the biotic resistance of resident vegetation against the establishment and spread of
566 alien species (e.g. Eschtruth & Battles, 2009; Early *et al.*, 2016; Haeuser, Dawson & van
567 Kleunen, 2017).

568 Although climatic suitability is an important criterion in horticulture, many
569 ornamental species are grown beyond the climatic conditions they would be able to tolerate in
570 the wild (Van der Veken *et al.*, 2008). A warming climate potentially increases the match
571 between current cultivation areas and suitable climatic conditions, especially in temperate

572 regions where many garden plants have been introduced from warmer parts of the world
573 (Niinimets & Peñuelas, 2008; Bradley *et al.*, 2011; Dullinger *et al.*, 2017). Cultivated
574 ornamental plants will have a ‘head start’ (Van der Veken *et al.*, 2008) allowing them to
575 colonise newly suitable areas long before other range-shifting species arrive. This head-start
576 advantage may become even more important in the coming decades. First, adaptation of
577 gardeners’ demands to anticipate changes in regional climates could improve the climatic
578 match of newly planted species. Demand for drought-tolerant ornamental species is already
579 growing in the USA in response to forecasted drier conditions (Bradley *et al.*, 2011). Second,
580 rising urbanisation all around the world will lead to an increased concentration of demand for
581 ornamental plants in metropolitan areas. These areas usually have higher temperatures than
582 the surrounding rural areas (i.e. the urban heat-island effect). Consequently, warm-adapted
583 garden plants will have the chance to establish naturalised populations in cities, which may
584 facilitate their spread into the surrounding landscapes (e.g. Essl, 2007; but see Botham *et al.*,
585 2009).

586 A warming climate may also foster the establishment of ornamental plants in those
587 ecosystems that have so far been less affected by biological invasions. Mountains, for
588 example, have few invasive species so far due to climatic constraints and low human
589 population densities, and hence low propagule pressure (Pauchard *et al.*, 2016). Indeed, the
590 few alien species currently found in mountains are mostly lowland generalists able to cope
591 with the cold climate (Alexander *et al.*, 2011). However, climate warming, in combination
592 with changing land use and increased tourism, will potentially relax these constraints and
593 increase invasion risks at higher elevations (Pyšek *et al.*, 2011; Petitpierre *et al.*, 2016;
594 Dainese *et al.*, 2017). Specifically, ornamental plants currently cultivated in mountain
595 villages and resorts will have a head start under a warming climate and profit from greater
596 propagule availability with increasing human population (Pauchard *et al.*, 2009). Further, in

597 order to satisfy the growing demands of tourism, nurseries selling into mountainous regions
598 are also likely to increase the supply of garden plants pre-adapted to mountain conditions, i.e.
599 originating from other alpine environments around the world (Kueffer *et al.*, 2013; Alexander
600 *et al.*, 2017). The threat posed to mountains by escaping ornamental plants will thus probably
601 increase in the future because of globalisation and climate change.

602

603 **VI. RESEARCH OPPORTUNITIES AND NEEDS**

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

616 **Topic 1: an improved understanding of the origins of ornamental alien species**
617 **and the means by which they arrive and are distributed.** Here, it is important to go
618 beyond analyses on where from and by which pathway the most successful (most frequent)
619 species, or those with the highest impacts arrived. It is crucial to take into account the species
620 pool in the area of their origin and the trade pattern and volume to disentangle the effect of
621 propagule pressure ('transport mass effect') from other factors related to invasion success or

622 impact. In this light, it is also important to know how species are distributed through new
623 ways of trading or social networks. For example, how important is garden-plant exchange
624 among relatives and friends (Verbrugge *et al.*, 2014)? In addition, there might be certain plant
625 traits associated with specific origins and pathways.

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

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

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

646 2005). However, it is not known whether these corridors provide appropriate dispersal habitat
647 for many ornamental alien species.

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

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

658 **Topic 7: legal regulations that permit a thriving industry with a low risk of plant**
659 **invasions.** First, one would need to review the existing regulatory frameworks (Hulme *et al.*,
660 2018), identify gaps, address the demands of nature conservation to prevent the spread of
661 ornamental species, and investigate how to promote the success of novel schemes (e.g.
662 assurance schemes) in the industry that can incentivise behavioural changes. Given the
663 diversity of stakeholders, this needs to be done sensitively to gain support from a diverse
664 community. Importantly, sufficient long-term funding should be made available for
665 monitoring by regulatory agents and land managers.

666 **Topic 8: public awareness and building partnerships with stakeholders.** Finally,
667 we need to inform, educate and convince the public to promote native or benign alien plants
668 as ornamentals rather than detrimental ones. Public awareness campaigns need to be
669 underpinned by research on the role of cultural and social values in processes leading to new
670 introductions. In addition to raising awareness, we need to build long-term, enduring

671 partnerships with stakeholders, such as the plant industry, gardeners and the public (Humair,
672 Siegrist & Kueffer, 2014*b*). They harness important knowledge about how to regulate trade
673 and inform the involved actors. Moreover, they are also interested in avoiding unregulated
674 trade that leads to the introduction of new plant diseases and pests.

675

676 **VII. CONCLUSIONS**

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

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

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

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

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

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

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

706 (8) There are still many open questions on the role of horticulture in plant invasions (Table
707 1). Therefore, more intensive research efforts on the role of horticulture are urgently needed
708 to develop science-based regulatory frameworks that help to prevent further plant invasions.
709

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721

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1153 X. SUPPORTING INFORMATION

1154 Additional supporting information may be found in the online version of this article.

1155 **Appendix S1.** The questionnaire sent to botanical gardens.

1156 Table 1. Eight key research topics proposed for studying horticulture and plant invasions,
 1157 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

1158

1159

1160 **Fig. 1.** The main pools (boxes) and flows (arrows) of species introduced for ornamental
1161 purposes, and the actors and processes involved. The width of the different species pools
1162 illustrate differences in their sizes: the cultivated species pool represents a subset of the wild
1163 species pool, and the escaped species pool is a subset of the cultivated species pool. Note that
1164 although we do not include arrows from breeders and propagators, and from wholesalers and
1165 retailers to the escaped species pool, alien plants may also escape at those stages of the
1166 supply chain. The dashed arrow indicates that the escaped alien species become part of the
1167 wild species pool, and thus that in certain regions alien species might subsequently be
1168 collected again for ornamental purposes. Across the different horticultural and ornamental
1169 trade stages, the size of the cultivated species pool changes; some of the species collected by
1170 plant hunters will not be used by breeders and propagators, but the latter will through
1171 breeding and hybridisation create new taxa, and some of the species offered by the nursery
1172 trade network of wholesalers and retailers will not be sold and planted. The thin arrows from
1173 plant hunters to botanical gardens and domestic gardens, indicate that some species planted in
1174 these gardens were collected in the wild, and by-passed the commercial ornamental plant
1175 industry. The looped arrow for botanical gardens indicates the exchange of seeds/plants
1176 among botanical gardens and the looped arrow for domestic gardens indicates the exchange
1177 of seeds/plants among hobby gardeners. Public spaces include both public green spaces (e.g.
1178 city parks) and infrastructure (e.g. road-side plantings). For similar diagrams, see Drew *et al.*
1179 (2010) and Hulme *et al.* (2018).

1180

1181 **Fig. 2.** Venn diagram illustrating that most of the species that have become naturalised
1182 somewhere in the world are grown in private gardens and in botanical gardens. A circle
1183 illustrating the size of the global vascular plant flora has been added for comparison. Data on
1184 the global naturalised flora were extracted from the Global Naturalized Alien Flora database

1185 (GloNAF version 1.1; van Kleunen *et al.*, 2015). Data on species grown in private gardens
1186 were extracted from Dave’s Garden PlantFiles (<http://davesgarden.com/guides/pf/>) and the
1187 Plant Information Online database (<https://plantinfo.umn.edu/>). Data on species grown in
1188 botanical gardens were extracted from the PlantSearch database of Botanic Gardens
1189 Conservation International (BGCI; http://www.bgci.org/plant_search.php). All species names
1190 were standardised according to The Plant List (<http://www.theplantlist.org/>), which also
1191 provided the number for the size of the global vascular plant flora.

1192

1193 **Fig. 3.** Among naturalised species, those grown in domestic or botanical gardens have
1194 become naturalised in more regions around the globe than species not known to be grown
1195 (labelled ‘No’ on figure) in gardens (Kruskal-Wallis $\chi^2 = 1379.8$, $df = 3$, $P < 0.001$). Data
1196 were taken from the Global Naturalized Alien Flora database (version 1.1; van Kleunen *et al.*,
1197 2015), Dave’s Garden PlantFiles (<http://davesgarden.com/guides/pf/>), the Plant Information
1198 Online database (<https://plantinfo.umn.edu/>) and PlantSearch of Botanic Gardens
1199 Conservation International (http://www.bgci.org/plant_search.php).

1200

1201 **Fig. 4.** (A) Absolute and (B) normalised first-record rates for naturalised species that are not
1202 known to be planted in gardens, and that are planted in domestic gardens (Dave’s Garden
1203 PlantFiles, <http://davesgarden.com/guides/pf/>; the Plant Information Online database,
1204 <https://plantinfo.umn.edu/>), botanical gardens (PlantSearch of Botanic Gardens Conservation
1205 International, http://www.bgci.org/plant_search.php) or both. The data on first-record rates
1206 were taken from Seebens *et al.* (2017). First-record rates are defined as the number of first
1207 records of alien species per ten-year period. As the first-record rates for naturalised species
1208 that are only known to occur in domestic gardens or in no garden at all were very low, the
1209 inset of A zooms in on those species. In B, the data were normalised by setting the highest

1210 first-record rate of each group equal to 1, and changing the other values proportionally. The
1211 trends in B are indicated by running medians (lines).

1212

1213 **Fig. 5.** (A) The import value (US\$) of live plants to each country averaged for the period
1214 2001–2010, and expressed per person. Plant import data were extracted from the United
1215 Nations Commodity Trade Statistics database (Comtrade; <http://comtrade.un.org>), and
1216 included commodity codes 0601 (bulbs and seeds) and 0602 (other live plants). Human
1217 population data were taken from CIESIN *et al.* (2011). Values are presented as 20%
1218 quantiles. (B) The increase in the imports of live plants expressed relative to the region with
1219 the greatest increase, Europe. Rates of increase were calculated as the area under the trend
1220 curve, and for East Asia was calculated from 2005 to 2015 due to the decrease in plant
1221 imports that occurred prior to that. (C, D) Change in import value (US\$) of live plants (from
1222 1995 to 2015, reliable plant import data were not available before 1995), for the highest four
1223 (C) and lowest five (D) importing regions shown in B. Colours correspond to the legend in B.
1224 As the rates of increase for Africa and Western Asia were identical, we distinguish Africa
1225 with white stippling on the map in panel B, and a dashed line on the graph in panel D. Import
1226 values were summed across all countries in a region, and regions were defined according to
1227 sub-continent and similarity among import trends. Import values and trends were very similar
1228 for some geographically disjunct regions, and so values were aggregated to reduce the
1229 number of lines and maximise colour differences: for Central-South America and Africa
1230 Pearson's $r=0.81$, $P<0.00001$, $df=19$; the combined import values for Central-north Asia,
1231 south and south-east Asia, and Oceania were grouped as they were relatively low.

1232

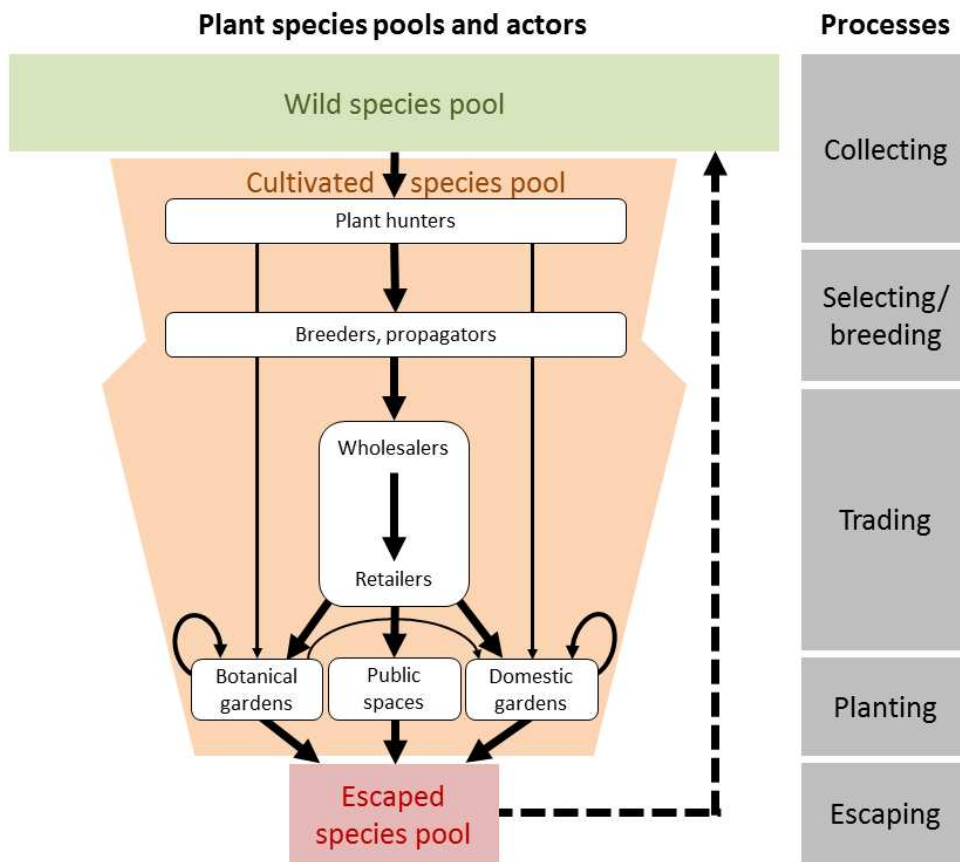
1233 **Fig. 6.** Proportion of 947 botanical gardens across six continents that participate in retail plant
1234 sales, horticulture or plant breeding research, or undertake plant explorations. Data from

1235 Botanic Garden Conservation International Garden Search
1236 (www.bgci.org/garden_search.php; accessed on 1 November 2016).

1237

1238 **Fig. 7.** Main sources of plants in botanical gardens, based on a questionnaire to which 161
1239 botanical gardens responded. Six of the botanical gardens indicated two sources as the main
1240 ones; these were assigned to both sources. The botanical gardens were grouped according to
1241 continent (TDWG continent; Brummitt, 2001).

1242 **FIGURE 1**

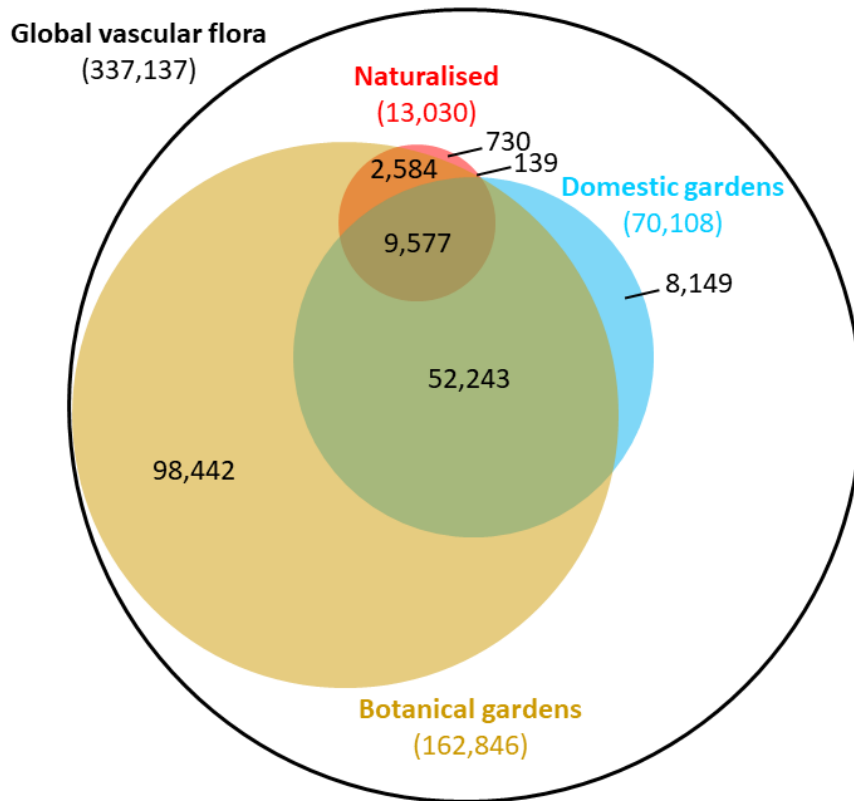


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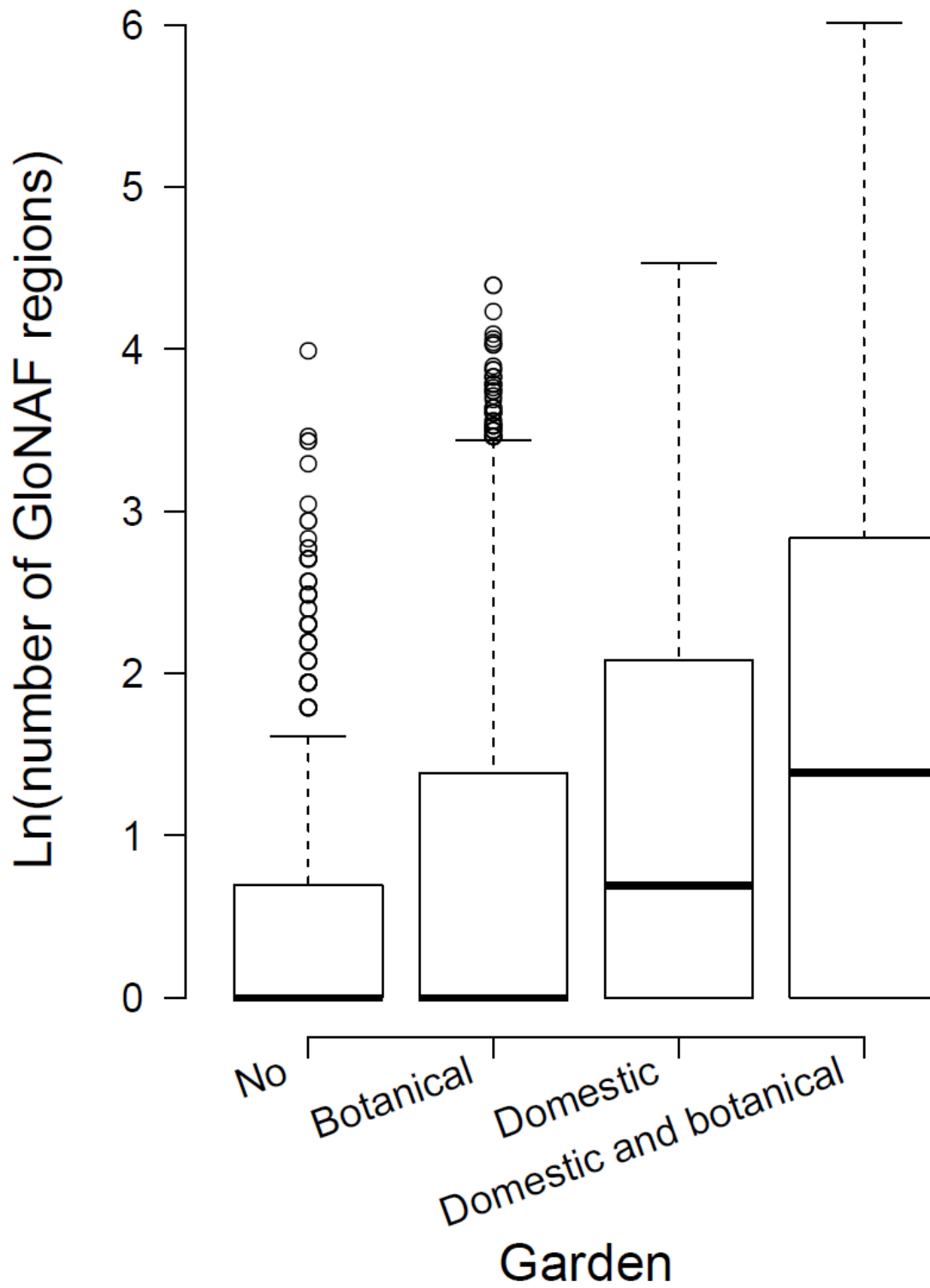
1246 **FIGURE 2**



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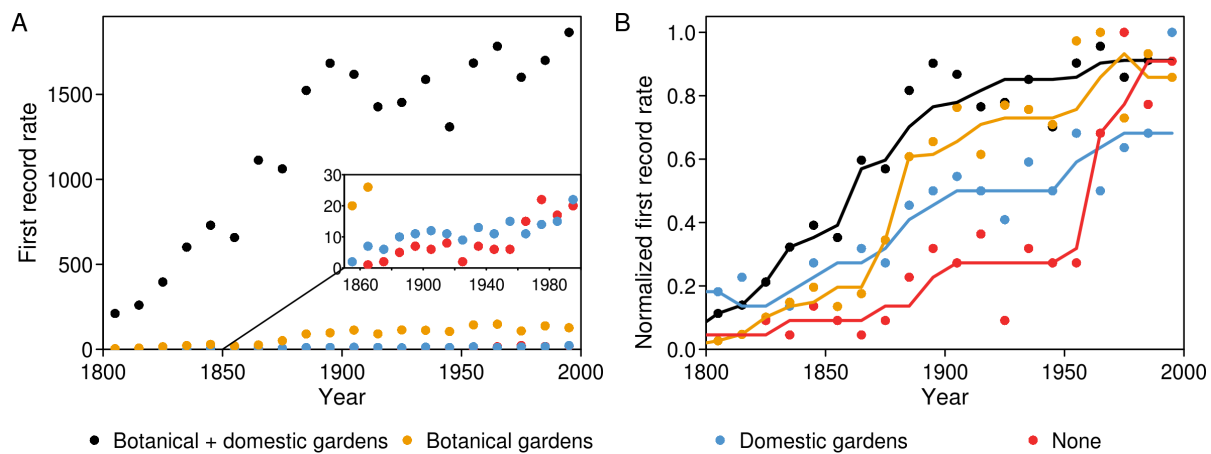
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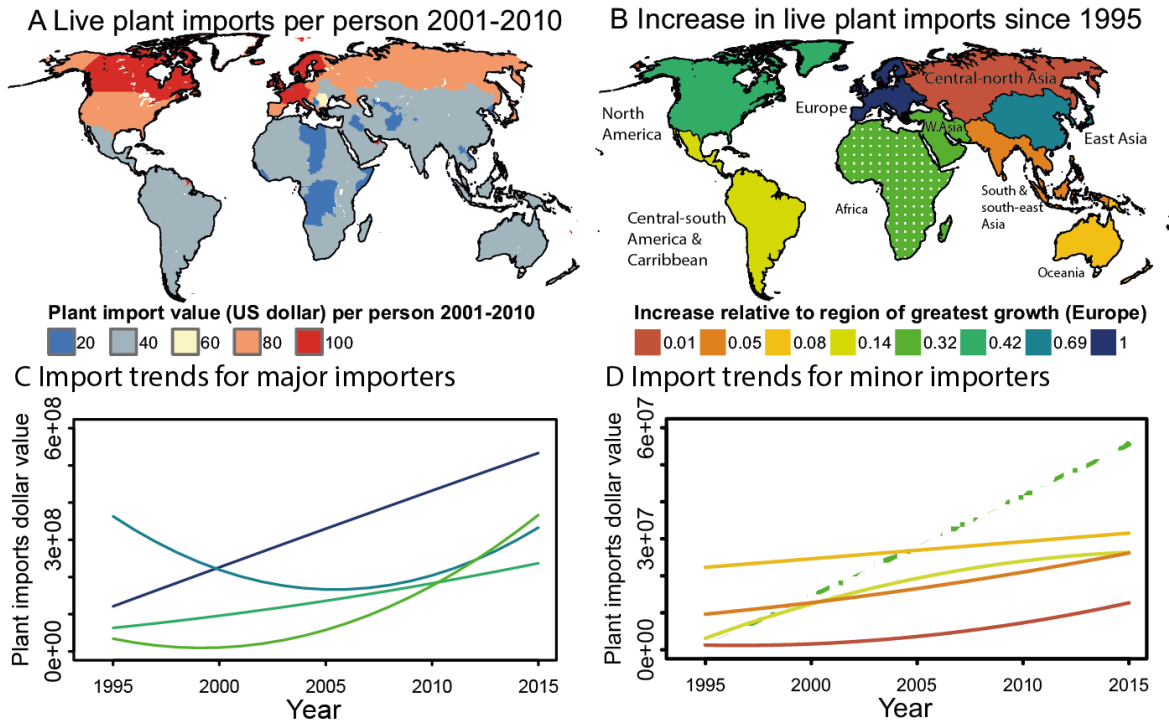
1253 **FIGURE 4**



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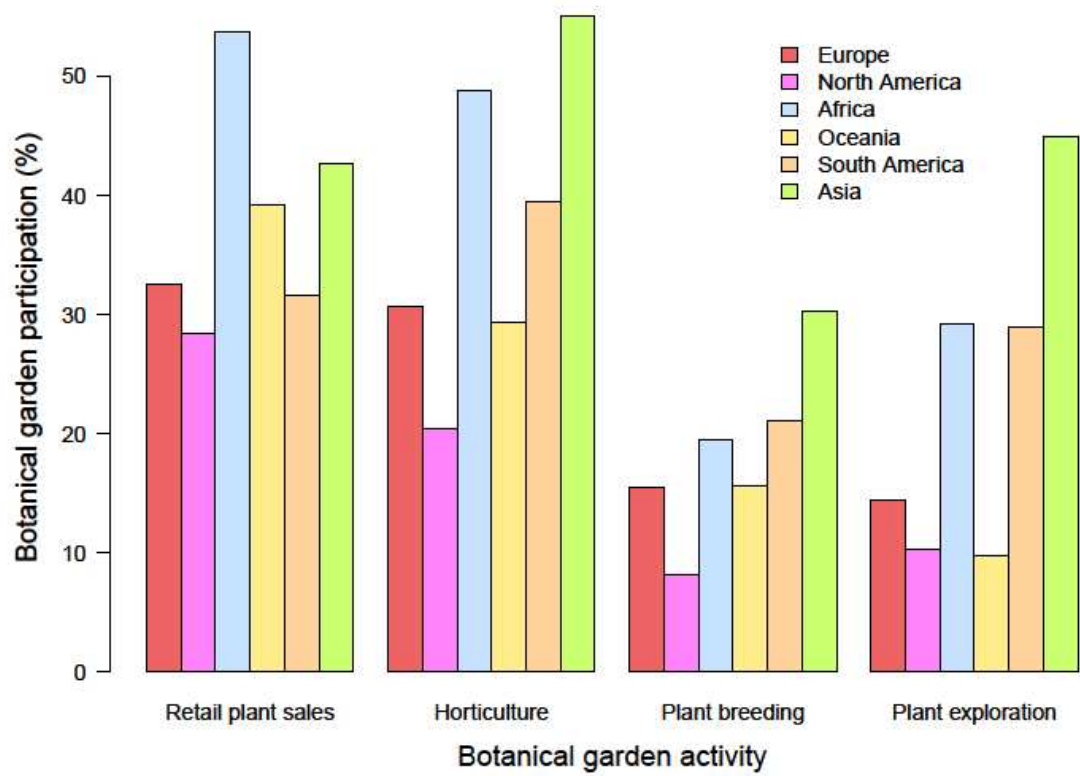
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1261 **FIGURE 6**

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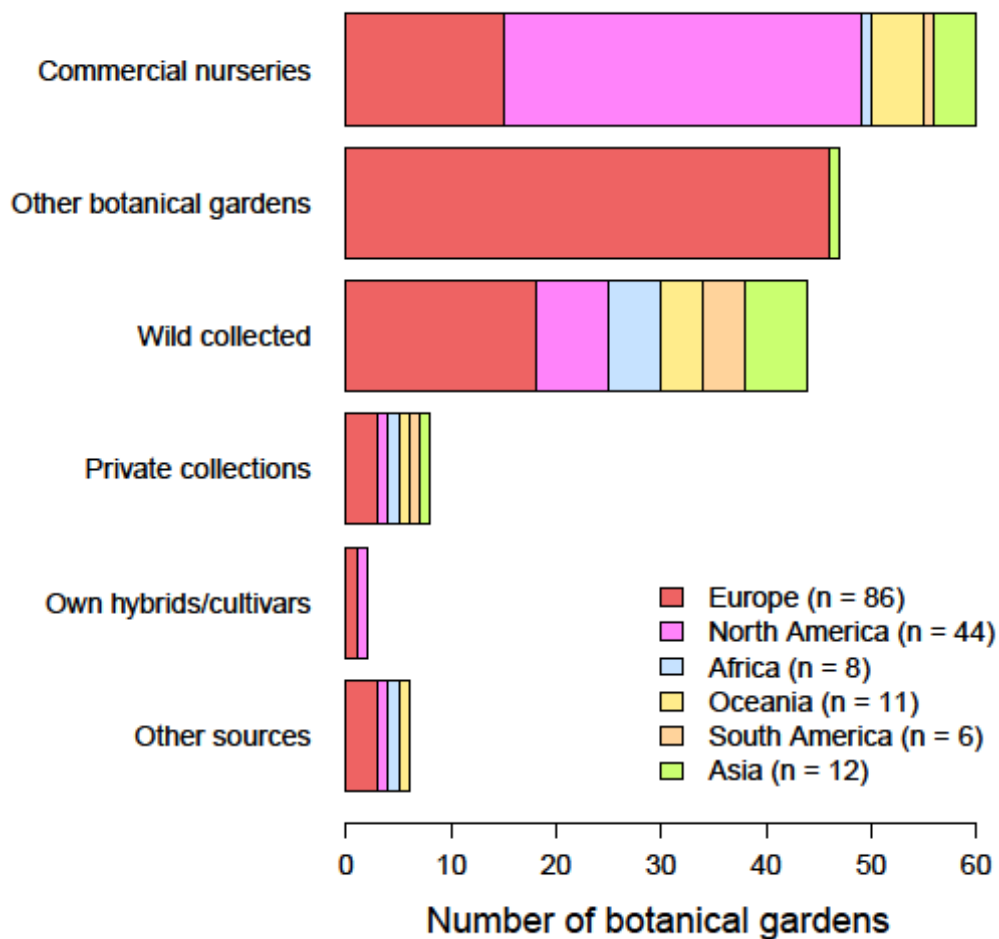


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1265 **FIGURE 7**

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