

Open Access journals need to become first choice, in invasion ecology and beyond

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Open Science is a pivotal global movement to advance science and scholarship. It includes key elements such as Open Access to scientific publications, Open Data, Open Source, and Open Methodology (Kraker et al. 2011; McKiernan et al. 2016; Stodden et al. 2016), and therefore fosters reproducibility and verification of findings (Wilkinson et al. 2016). Scientific knowledge, the product of research, is a public good and should thus be made publicly available. The vast majority of researchers agree with the idea of Open Science (Dallmeier-Tiessen et al. 2011), yet many face challenges in implementing Open Science in practice.

Here we highlight one of these challenges, using invasion ecology as a case example. Consider a typical situation in many research projects: your collaborator, PhD student, or postdoc discovers new research results and approaches you to discuss where to publish the work. You both know that impact factors (IFs) are flawed (e.g. San Francisco Declaration on Research Assessment, DORA, <http://www.ascb.org/dora>). The IF of a journal does not allow one to assess the quality of an individual paper, and there seems to be an increasing commitment by the scientific community

not to use the IF when evaluating people or institutions. Indeed, the authors of this article strongly support the DORA declaration. At the moment, though, IFs are still frequently used by hiring and grant committees to evaluate researchers (McKiernan et al. 2016; Tregoning 2018). To be on the safe side, you'd like to publish your best work in high-impact journals. Given that you want to promote Open Science, and perhaps your research institution or the organization funding your work requires publication in Open Access (OA) journals, you look for a high-impact OA journal as first-choice outlet for the exciting results.

You may consider three options, (i) multidisciplinary, (ii) ecology, or (iii) invasion ecology journals, and use the latest Journal Citation Report by Clarivate Analytics to prepare a list of potential target journals, comparing OA with subscription journals (Table 1). You are not sure yet if you want to go for the classic multidisciplinary flagship journals “Nature” or “Science”, where rejection rates are very high, but you notice that both publishers of these journals, Springer Nature and AAAS, have launched OA journals with the same general scope as their flagship journals. These journals, “Nature Communications” and “Science Advances”, have high IFs, too, but they are markedly lower than those of “Nature” and “Science”. Clearly, “Nature Communications” and “Science Advances” are very good outlets, but from an IF perspective only second choice after “Nature” and “Science”. In addition, “Nature Communications” and “Science Advances” are the only OA journals in the top-10 of journals, based on IF, that sometimes publish papers related to biological invasions (Table 1A).

In the discipline of ecology, the 2018 Journal Citation Report (JCR) lists 164 journals, of which the subscription journal “Trends in Ecology & Evolution” has the highest IF (15.2; Table 1C). Only 23 OA journals (14.0%) are currently included for this discipline, with “Ecology and Society” having the highest IF (4.14; ranking 29 among all journals in ecology). Thus, there is currently no OA top-tier journal in ecology (Fig. 1; cf. Barbaro et al. 2015).

When focusing on specialist journals in the field of invasion ecology itself, the picture looks different. Here, four of the five journals that we consider as invasion ecology journals are OA (Table 1E). This is probably because these journals are rather young in the general field of ecology. Nonetheless, the single subscription journal focusing on invasion ecology, i.e. the journal “Biological Invasions”, currently has the highest IF in the field; “NeoBiota” follows on the second place.

Why are there only few top-tier OA journals?

Most of the prominent subscription journals have existed for a much longer time period than OA journals. This is one obvious explanation why high-impact OA journals are currently lacking in invasion ecology and most other disciplines: OA journals simply have not had the time to build a reputation (although counterexamples such as “eLife” exist, see Table 1B, primarily through major financial support and promotion by leading research organizations, such as the Howard Hughes Medical Institute, the

Table 1. Top 10-impact factor journals included in Clarivate Analytics' 2018 Journal Citations Report (JCR): (A) all journals that, at least sometimes, publish invasion ecology articles (these journals are relevant to invasion ecologists); (B) Open Access journals that, at least sometimes, publish invasion ecology articles; (C) journals in JCR's category "Ecology"; (D) Open Access journals in JCR's category "Ecology"; (E) journals specialized in invasion ecology; (F) Open Access journals specialized in invasion ecology. In A-F, Open Access journals are highlighted in bold.

A) All relevant journals		B) Relevant Open Access journals	
Nature	43.1	Sci. Adv.	12.8
Science	41.0	Nat. Commun.	11.9
Nat. Clim. Change	21.7	PLOS Biol.	8.39
Trends Ecol. Evol.	15.2	eLife	7.55
Sci. Adv.	12.8	Conserv. Lett.	7.40
Nat. Commun.	11.9	BMC Biol.	6.72
Nat. Ecol. Evol.	11.0	Sci. Data	5.93
Front. Ecol. Environ.	10.9	Ecol. Soc.	4.14
Annu. Rev. Ecol. Evol. Syst.	10.9	Sci. Rep.	4.01
Biol. Rev.	10.3	BMC Plant Biol.	3.95
C) Ecology journals		D) Open Access ecology journals	
Trends Ecol. Evol.	15.2	Ecol. Soc.	4.14
Nat. Ecol. Evol.	11.0	Biogeosciences	3.95
Front. Ecol. Environ.	10.9	Mov. Ecol.	3.75
Annu. Rev. Ecol. Evol. Syst.	10.9	Conserv. Physiol.	3.63
ISME Journal	9.49	Glob. Ecol. Conserv.	2.75
Global Change Biol.	8.88	Ecosphere	2.75
Ecol. Lett.	8.70	Front. Ecol. Evol.	2.69
Ecol. Monogr.	7.70	NeoBiota	2.49
Methods Ecol. Evol.	7.10	Ecol. Evol.	2.42
Mol. Ecol. Resour.	7.05	BMC Ecol.	2.38
E) Invasion ecology journals		F) Open Access invasion ecology journals	
Biol. Invasions	2.90	NeoBiota	2.49
NeoBiota	2.49	Aquat. Invasions	1.71
Aquat. Invasions	1.71	Manag. Biol. Invasion	1.52
Manag. Biol. Invasion	1.52	BioInvasions Rec.	1.20
BioInvasions Rec.	1.20		

Max Planck Society, and the Wellcome Trust). 42% of the respondents to the SOAP project survey (Dallmeier-Tiessen et al. 2011) who indicated to not have published OA articles wrote they had specific reasons for it. One of the two most recurring reasons was: "OA journals are perceived/assumed not to be of good quality or they do not have an impact factor" (Dallmeier-Tiessen et al. 2011). This or a similar response related to journal quality was given by 30% of the respondents.

We would like to highlight another reason for the lack of high-impact OA journals that is often overlooked: As shown above, OA journals are frequently implemented as a second-choice option by publishers. Although new OA journals can become high-impact journals (see e.g. "PLOS Biology" or "eLife"), such a trajectory is hampered by publishers that offer authors of manuscripts rejected in their first-choice journals the option to transfer the work to an in-house OA journal. This is, for example, done by Wiley: "A number of Wiley Open Access journals participate in a Manuscript Transfer

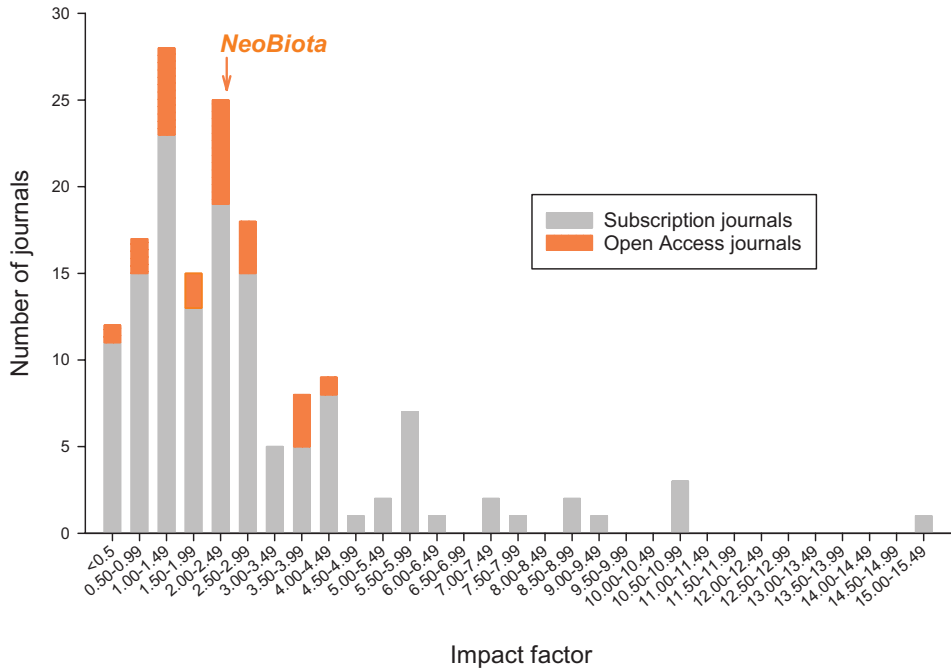


Figure 1. Distribution of 2018 journal impact factors in JCR's category "Ecology" (cf. Table 1C). "NeoBiota" is shown separately. The median and mean impact factor of Open Access journals in JCR's category "Ecology" is 2.08 and 2.12 ($n = 23$), respectively; for subscription journals, the median is 2.31 and mean 2.84 ($n = 141$). Thus, while the IF between Open Access and subscription journals does not strongly differ on average, there is a critical lack of Open Access journals with high impact factors—these are the journals where researchers aim to publish their best papers and that they highlight in their CVs.

Program. After review in a supporting journal, rejected articles of suitable quality can be identified by the Editor as candidates for publication in a Wiley Open Access journal" (<https://authorservices.wiley.com/open-science/open-access/about-wiley-open-access/manuscript-transfer-program.html>, accessed 29 August 2019). For example, manuscripts rejected by Wiley subscription journals such as "Global Change Biology", "Global Ecology and Biogeography", or the "Journal of Biogeography" can be transferred to the OA journals "Ecology and Evolution" or "Geo: Geography and Environment". Other publishers, e.g. Springer Nature (see above), and even some learned societies, e.g. AAAS (see above) and the Ecological Society of America, follow similar manuscript transfer policies, at least for some of their journals. These policies are considered a business model for publishers, taking benefit from efforts already spent on a submitted manuscript (e.g. internal and external review processes). They are also signalling authors that their subscription journals are first choice, whereas OA journals are second choice. They are nudging researchers to first submit to subscription journals and only later to OA journals.

Publishers might also be doing so to maximize profit via “double-dipping” (Barbaro et al. 2015). They receive money from libraries for subscribing to journals, and they receive additional money if publications are made OA in such subscription journals (Hybrid Open Access). Researchers who place their best work in high-impact journals (that are not OA) pay to make them OA, and publishers maximize their profit. Learned societies are in a bind right now (Brainard 2019). Their budgets typically depend on income generated through contracts with publishers, and these contracts are much more lucrative for subscription journals.

What are possible ways forward?

We identified five possible ways forward. First, publishers should make their classic flagship journals OA, rather than launching second-choice OA outlets. This could work if research foundations require their grant holders to openly publish their results. The Gates Foundation has such a requirement since 2017, and two prestigious subscription journals, “The New England Journal of Medicine” and “Proceedings of the National Academy of Sciences USA”, responded by offering Gates grant holders to publish their papers in these journals OA (Van Noorden 2018). European funding agencies that have formed the cOAlition S follow the Gates foundation in requiring OA publication by 2021; this initiative is called “Plan S” and has been pushed forward by the Open Access Envoy of the European Commission, the President of Science Europe, a group of heads of national funding organisations (including the senior author of this article) and the Scientific Council of the European Research Council (Schiltz 2018; <https://www.coalition-s.org/>). Further, given that journals are largely run by us researchers, we can directly ask publishers to switch a subscription journal to an OA journal without too expensive publication costs. If publishers decline to do so, an option would be to follow the former editors of the subscription journal “Lingua” who left the publisher Elsevier and re-established the journal under the new name “Glossa” as an OA outlet. As authors and reviewers, we can also boycott publishers by not submitting manuscripts to their journals or not reviewing for them (<http://thecostofknowledge.com>).

Second, publication costs in OA journals must become reasonable. Traditional scientific publishing has not only been criticized because of the paywall of subscription journals, but also because publishing houses have made a fortune with a product that is largely paid by taxpayers; these usually pay the scientists, including their equipment, to (i) do the research, (ii) write the manuscripts, and (iii) review and edit other manuscripts. Outrageous profit margins of publishers have been a key point in the critique against traditional publishing (e.g. Van Noorden 2013). If we now turn subscription journals into OA journals (point 1 above), but do not reduce the profit margins of the big publishers, we have not yet reached what we are aiming for. “Science Advances” and “Nature Communications”, i.e. the top-two OA multidisciplinary journals (cf. Table 1B), currently charge US\$ 4500 or even US\$ 5200 per article, respectively

(checked on 29 August 2019; cf. Van Noorden 2013). Even average charges for the three big publishers Springer Nature, Wiley, and Elsevier are between US\$ 2100 to 3000 (<https://treemaps.intact-project.org/apcdata/combined/#publisher/>, checked on 29 August 2019). An interesting example is the case of “Diversity and Distributions”, a Wiley journal that in 2019 switched from a subscription to an OA model (it is not counted as an OA journal in Table 1 and Fig. 1, as we followed the JCR’s classification where the journal is still included as a subscription journal because the switch happened so recently). The decision to switch to OA was apparently taken by the publisher without consulting the journal’s editorial board beforehand, and came along with a charge of US\$ 2200 to publish in this journal in the future. As a result, many editors protested and left the journal (Peterson et al. 2019). Journals from publishers such as Pensoft, which publishes “NeoBiota”, have considerably lower publication charges. In case of Platinum (also known as Diamond) Open Access, authors do not have to pay for their publications at all. Such a Platinum OA model is, for example, implemented for the Beilstein journals (financially supported by the Beilstein Institute) and “Web Ecology” (supported by the European Ecological Federation).

Third, those researchers who can afford to largely ignore impact factors (e.g. because they have a permanent position or a very high scientific standing) should submit their best work to OA journals even if these do not (yet) have a high reputation. If many colleagues do the same, the impact factor of such journals will rise, and so will their reputation.

Fourth, we must combat predatory journals which are typically OA and thus reduce the reputation of OA journals overall. The Directory of Open Access Journals (DOAJ; <https://doaj.org>) is a valuable source, as it lists high-quality OA journals and thus helps to discriminate those from purely profit-orientated predatory journals without any scientific quality control. The latter are reported at <https://predatoryjournals.com>, a follow-up of the well-known Beall’s list which discontinued in 2017.

Fifth, learned societies should change their business plans, so that they can afford converting their journals to OA. The European Group on Biological Invasions, NEOBIOTA, changed its publication model to OA in 2011—this is the reason why the journal you read right now is OA. Similarly, the latest journal of the International Association of Vegetation Science, “Vegetation Classification and Survey”, is OA as well. Learned societies could receive part of the OA publication fee (which is reduced for authors who cannot afford it and for society members). At the same time, learned societies bear particular responsibility and solidarity for scientists of the Global South, who lack the resources for many subscription journals. Indeed, we should not accept that they remain cut-off from the knowledge generated in wealthy countries. It is vital, however, that they are still able to publish their own work, that publication fees are not prohibitive (see above).

Eventually, subscription journals should disappear in science altogether. This is unrealistic in the very near future, but for example in Germany the project DEAL (<https://www.projekt-deal.de>) reached a three-year agreement with the publisher Wiley, allowing all members of project DEAL institutions to access Wiley publications back to 1997, and to publish OA articles in Wiley’s journals with no addi-

tional charge: the annual fee paid at the national level releases libraries at all project-DEAL institutions from paying additional subscription charges, and researchers in these institutions do not have to pay additional charges to publish OA papers in Wiley's journals (Sander et al. 2019). A major aim of the project DEAL is to make all publications submitted from German research institutions OA. Although negotiations with Elsevier are currently stuck (but see a recent agreement in Norway), a memorandum with Springer Nature was signed this August to make an agreement similarly to the one with Wiley (<https://www.projekt-deal.de>). If other countries follow, scientific journals will be effectively OA for all these countries. Indeed, the above-mentioned developments, e.g. "Plan S" that European research results should be exclusively published OA (Schiltz 2018; <https://www.coalition-s.org/principles-and-implementation/>), give hope that OA journals will become first choice—and that subscription journals will eventually disappear. As outlined above, though, we should keep in mind that a successful transition to OA publishing will crucially depend on fair pricing and quality control of OA journals.

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References

- Brainard J (2019) Scientific societies worry about threat from Plan S. *Science* 363: 332–333. <https://doi.org/10.1126/science.363.6425.332>
- Barbaro A, Zedda M, Gentili D, Greenblatt RL (2015) The presence of high-impact factor open access journals in science, technology, engineering and medicine (STEM) disciplines. *Italian Journal of Library, Archives and Information Science* 6: 57–75. <https://doi.org/10.4403/jlis.it-11257>
- Dallmeier-Tiessen S, Darby R, Goerner B, Hyppola J, Igo-Kemenes P, Kahn D, Lambert S, Lengenfelder A, Leonard C, Mele S, Nowicka M, Polydoratos P, Ross D, Ruiz-Perez S, Schimmer R, Swaisland M, van der Stelt W (2011) Highlights from the SOAP project survey. What scientists think about Open Access Publishing. arXiv 1101.5260.
- Kraker P, Leony D, Reinhardt W, Beham G (2011) The case for an open science in technology enhanced learning. *International Journal of Technology Enhanced Learning* 3: 643–654. <https://doi.org/10.1504/IJTEL.2011.045454>

- McKiernan EC, Bourne PE, Brown CT, Buck S, Kenall A, Lin J, McDougall D, Nosek BA, Ram K, Soderberg CK, Spies JR, Thaney K, Updegrove A, Woo KH, Yarkoni T (2016) How open science helps researchers succeed. *eLife* 5: e16800. <https://doi.org/10.7554/eLife.16800>
- Peterson AT, Anderson RP, Beger M, Bolliger J, Brotons L, Burridge CP, Cobos ME, Cervo-Robayo AP, Di Minin E, Diez J, Elith J, Embling CB, Escobar LE, Essl F, Feeley KJ, Hawkes L, Jiménez-García D, Jimenez L, Green DM, Knop E, Kühn I, Lahoz-Monfort JJ, Lira-Noriega A, Lobo JM, Loyola R, Mac Nally R, Machado-Stredel F, Martínez-Meyer E, McCarthy M, Merow C, Nori J, Nuñez-Penichet C, Osorio-Olvera L, Pyšek P, Rejmánek M, Ricciardi A, Robertson M, Rojas Soto O, Romero-Alvarez D, Roura-Pascual N, Santini L, Schoeman DS, Schröder B, Soberon J, Strubbe D, Thuiller W, Traveset A, Treml EA, Václavík T, Varela S, Watson JEM, Wiersma Y, Wintle B, Yanez-Arenas C, Zurell D (2019) Open access solutions for biodiversity journals: do not replace one problem with another. *Diversity and Distributions* 25: 5–8. <https://doi.org/10.1111/ddi.12885>
- Sander F, Herrmann G, Hippler H, Meijer G, Schimmer R (2019) Projekt DEAL – John Wiley & Son Publish and Read Agreement. <https://doi.org/10.17617/2.3027595>
- Schiltz M (2018) Science without publication paywalls: cOAlition S for the realisation of full and immediate Open Access. *PLoS Biology* 16: e3000031. <https://doi.org/10.1371/journal.pbio.3000031>
- Stodden V, McNutt M, Bailey DH, Deelman E, Gil Y, Hanson B, Heroux MA, Ioannidis JPA, Taufer M (2016) Enhancing reproducibility for computational methods. *Science* 354: 1240–1241. <https://doi.org/10.1126/science.aah6168>
- Tregoning J (2018) How will you judge me if not by impact factor? *Nature* 558: 345. <https://doi.org/10.1038/d41586-018-05467-5>
- Van Noorden R (2013) Open access: the true cost of science publishing. *Nature* 495: 426–429. <https://doi.org/10.1038/495426a>
- Van Noorden R (2018) Experimental open-access deal ends. *Nature* 559: 311–312. <https://doi.org/10.1038/d41586-018-05729-2>
- Wilkinson MD, Dumontier M, Aalbersberg IJ, Appleton G, Axton M, Baak A, Blomberg N, Boiten J-W, da Silva Santos LB, Bourne PE, Bouwman J, Brookes AJ, Clark T, Crosas M, Dillo I, Dumon O, Edmunds S, Evelo CT, Finkers R, Gonzalez-Beltran A, Gray AJG, Groth P, Goble C, Grethe JS, Heringa J, 't Hoen PAC, Hooft R, Kuhn T, Kok R, Kok J, Lusher SJ, Martone ME, Mons A, Packer AL, Persson B, Rocca-Serra P, Roos M, van Schaik R, Sansone S-A, Schultes E, Sengstag T, Slater T, Strawn G, Swertz MA, Thompson M, van der Lei J, van Mulligen E, Velterop J, Waagmeester A, Wittenburg P, Wolstencroft K, Zhao J, Mons B (2016) The FAIR Guiding Principles for scientific data management and stewardship. *Scientific Data* 3: 160018. <https://doi.org/10.1038/sdata.2016.18>

The effect of prey identity and substrate type on the functional response of a globally invasive crayfish

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Abstract

Biological invasions threaten biodiversity on a global scale, therefore, developing predictive methods to understand variation in ecological change conferred is essential. Trophic interaction strength underpins community dynamics, however, these interactions can be profoundly affected by abiotic context, such as substrate type. The red swamp crayfish (*Procambarus clarkii*) has successfully invaded a number of freshwater ecosystems. We experimentally derive the Functional Response (FR) (density dependent predation) of the red swamp crayfish preying upon both a benthic prey; chironomid larvae, and a pelagic prey; *Daphnia magna*, on a no substrate control, sand, and gravel substrates to determine whether (1) there is a higher impact on prey that are benthic, and (2) whether the presence of different substrate types can dampen the interaction strength. We apply and demonstrate the utility of the Functional Response Ratio (FRR) metric in unravelling differences in ecological impact not obvious from traditional FR curves. *Procambarus clarkii* is capable of constantly utilising high numbers of both benthic and pelagic prey items, showing a Type II functional response under all scenarios. The presence of gravel and sand substrate each independently decreased the magnitude FR upon *D. magna*. Though, with regards to chironomid larvae the FR curves showed no difference in magnitude FR, the FRR reveals that the highest impact is conferred when foraging on sand substrate. This reinforces the need for impact assessments to be contextually relevant.

Keywords

Aquatic invasions, functional response ratio, invader impact, macroinvertebrates, *Procambarus clarkii*, substrate

Introduction

Aquatic biological invasions are increasing at an alarming rate driven by increased connectivity due to new trade routes and ongoing climatic change (Davis and Darling 2017; Carlton and Fowler 2018; Seebens et al. 2017; Meyerson et al. 2019). Such invasions can result in substantial loss of biodiversity and homogenisation of communities (Bellard et al. 2016; Courchamp et al. 2017), which is often quantified and defined as “ecological impact” (Ricciardi et al. 2013; Blackburn et al. 2014; Dick et al. 2017a, b). The Aichi Biodiversity Targets (SCBD 2010) emphasise the importance of developing affirmative action to reduce biodiversity loss in order to increase resilience of ecosystem service production by reducing threats. Therefore, predicting and assessing the possible damage caused by invasive species is imperative to conserving biodiversity and valuable services derived from freshwater systems (Dickey et al. 2018; Cuthbert et al. 2019). Risk assessment and impact evaluation previously relied heavily upon invasion history (Ricciardi and Cohen 2007), which is of course of no use for emerging and new invasions. Recently, there has thus been an emphasis on quantifying and predicting invader impact before invasion occurs or in the initial stages of an emerging invasion (Dick et al. 2014, 2017a, b; Dickey et al. 2018). By determining impact under different environmental contexts, both mechanistically and phenomenologically, it is possible to identify the drivers of ecological impact exerted by a particular species on resources and incorporate preventative or mitigation measures into management policies (Wasserman et al. 2016; South et al. 2017; Dick et al. 2017a, b).

Invasive species are often characterised by their efficiency of resource consumption, whereby they generally show a higher *per capita* effect towards a focal resource in comparison to a native analogue (Dick et al. 2014, 2017a, b; Laverty et al. 2017). Comparative functional response analysis has thus been successfully employed to infer ecological impact upon resource populations across taxonomic and trophic groups (Alexander et al. 2014; Dick et al. 2017a, b; Kemp and Aldridge 2018). The functional response (FR) describes resource utilisation with respect to resource density, whereupon three categorical FR Types may be classified (Solomon 1949; Holling 1959). Type I FR, referring to a linear response is predominantly found in filter feeders as they are not limited by handling times (MacNeil et al. 1997; Jeschke et al. 2004). Type II FR describes high resource consumption at low resource density, and magnitude of the curve asymptote has been positively correlated with invader impact (Alexander et al. 2014; Dick et al. 2017b). Type III FR is a sigmoidal response that results in low consumption at low prey densities and which provides a low density refugia to prey species, and this FR type is often related to environmental stressors, as well as prey switching or learning (Holling 1959; Murdoch 1969; South et al. 2018). Upon determining FR type, it is possible to estimate parameter values for attack rate (a), handling time (h) and maximum feeding estimates ($1/h$). Consequently, this approach has been adopted as a standardised method to quantify and compare predator (and other consumer) impact upon recipient prey (and other resource) species (Dick et al. 2017a). Further,

due to ease of calculation through laboratory experiments and even field surveys, it is possible to factorially incorporate increased complexity such as habitat, temperature, and higher order predators in order to create more realistic environmental context (Barrios-O'Neill et al. 2015; South et al. 2018; Cuthbert et al. 2018). More recently, progress into developing the FR approach towards predictive capacity has resulted in the combination of the attack and handling parameters to derive a "Functional Response Ratio" (FRR), in order to elucidate potential intermediate impact where previously distinguishing differences between FR curves were problematic (Cuthbert et al. 2019). This is centred in the assertion that high attack rate values indicate high impact, while low handling time also implies high impact, and thus the parameters are combined to create a ratio of a/h , higher values of which are found in high-impact invaders (Cuthbert et al. 2019).

Species usually form habitat associations depending on their specific life history needs or due to optimal foraging theory, wherein the most productive habitat is selected (Schoener 1971). Due to the nature of biological invasions, the abiotic and biotic features of the new range may not be analogous to that of the native range, and therefore it is imperative to assess performance and ecological impact across a number of different contexts. Benthic substrate is highly variable depending on the system and is known to provide benefits and costs to both predator and prey depending on species specific traits and fractal dimensions (Tokeshi and Arakaki 2012; Barrios-O'Neill et al. 2015). Substrate has thus been shown to dampen interaction strength, but this may be a variable response depending on the type of substrate and the foraging behaviours of the predator (Barrios-O'Neill et al. 2015; Keyler et al. 2019; Gebauer et al. 2019). Determining whether abiotic context, such as substrate type, can affect the ability of an invasive species to consume resources is integral to informing management initiatives in order to deter and reduce spread and ecological impact of non-native species.

The red swamp crayfish, *Procambarus clarkii* (Girard, 1852), is a widespread invasive species due to its wide thermal tolerance, high trait plasticity, and popularity in aquaculture and the pet trade (Souty-Grosset et al. 2016). *Procambarus clarkii* is a polytrophic, omnivorous species which can be a destructive influence upon benthic invertebrate communities, which can result in trophic cascades and benthopelagic resource decoupling (Larson et al. 2017; Bucciarelli et al. 2019). *Procambarus clarkii* is spreading at an alarming rate through many countries, despite eradication and biocontrol attempts (Aquiloni et al. 2005; Nunes et al. 2017a, b; Loureiro et al. 2018). It is imperative to determine whether there is a differential ecological impact conferred by *P. clarkii* under different substrate conditions and whether this may lead to differential utilisation of prey species. Surprisingly, despite the damaging effect of *P. clarkii* on recipient systems, there is little empirical data quantifying and comparing resource consumption of important prey species. As such, we looked to address this by investigating whether there was a difference in the rate of resource utilisation over time by *P. clarkii* preying upon a benthic prey (chironomid larvae) and a pelagic prey (*Daphnia magna*) under three different substrate types (no substrate, sand, and gravel). As *P. clarkii* is a benthic species, we hypothesised that size of the prey and location in the water column

would affect the functional response magnitude and perception of the prey, wherein small pelagic prey items (i.e. *D. magna*) would be utilised less than larger benthic prey items, but that the interaction strength between *P. clarkii* and chironomid larvae would be dampened by the presence of substrate.

Methods

Specimens of sub-adult *P. clarkii* (mean \pm SD: 21.62 \pm 2.6 mm carapace length, $n = 25$) were supplied by Seahorse Aquariums (Republic of Ireland) and maintained at the Queen's University Marine Laboratory in a continuously aerated 600 L holding tank, with shelters made of drainpipe halves, supplied with dechlorinated tap water held at 23 \pm 1.0 °C using aquarium heaters and subject to natural light regime. During the experimental period there was no cannibalism. *Procambarus clarkii* were maintained on commercial sinking fish food (JBL, Germany) to avoid conditioning to experimental prey items. As this species breeds at small sizes and because they are controlled species within the United Kingdom and Northern Ireland non-reproductive sub-adult crayfish were used in this experiment. Two live prey species, chironomid larvae (3.0 \pm 0.6 SD mm total length) (Chironomidae) and *Daphnia magna* (0.3 \pm 0.01 SD mm) (*Daphnia magna*; Daphniidae), were supplied, also from Seahorse Aquariums. Appropriate ethical approval for the use of these animals in research was obtained from the QUB Ethics Committee (School of Biological Sciences) and National Research Foundation – South African Institute for Aquatic Biodiversity (NRF–SAIAB ethics boards (25/4/1/5_2018-06)).

Functional Response Experiment

A full factorial experimental design was employed to test differences in FR with regards to factors: “prey species” (2 levels), “density” (9 levels), and “substrate” (3 levels). Experimental arenas (W: 20 \times L: 30 \times H: 14 cm, 8 L) were held at 23 \pm 1.0 °C and experiments were completed in a fully randomised design. Three substrate treatments were supplied: no substrate, commercial aquarium sand supplied at a depth of 4 mm in the experimental arena, and gravel (grain size: 8 \times 4 mm) positioned using one 4 mm layer at the bottom of the experimental arena. Arenas were covered from the top and sides to avoid any synergistic or antagonistic conspecific effects. Individual predators were added per arena and allowed to acclimate for one hour before adding prey items. Each prey species was supplied at 9 densities (2, 7, 15, 40, 60, 90, 120, 200, 300 individuals per arena, $n = 5$ for each treatment), crayfish were allowed to feed for 1 h, after which the predators were removed, and number of prey items consumed were enumerated.

Control trials were carried out in experimental tanks at identical environmental conditions, wherein each prey species was supplied at the highest density in the ab-

sence of predators ($n = 3$ per substrate treatment) to determine potential background mortality. Each crayfish was re-used multiple times, but experienced each density of each prey type only once. Crayfish were given at least 3 days between use and were not fed for 24 h prior to experimental procedure to standardise hunger levels.

All analyses were undertaken using the R Statistical Software (v. 3.4.3). A generalised linear model (GLM) with a quasi-Poisson error distribution was used to determine differences in prey consumption with regards to factors “prey species”, “prey density”, and “substrate complexity”, using a Type 3 Anova and χ^2 to report the effect size of a factor on the dependent variable. Tukey’s HSD was used to generate pairwise estimates with Holm-Bonferroni adjustment of P values post-hoc.

The R package ‘*frair*’ (Pritchard 2014) was used to model the functional response type following methodology in Pritchard et al. (2017) (*frair::frair_fit*). Therein, a logistic regression was initially used to ascertain whether the proportion of prey consumed decreases with increasing prey density and consequently produces a significantly negative first order term, indicating a Type II FR. If a significantly positive first order term is obtained this indicates a Type III FR (Juliano 2001). Functional responses were modelled using maximum likelihood estimation (MLE; Bolker 2010) and Rogers’ (1972) Random Predator Equation to account for prey depletion over time:

$$N_e = N_o \left(1 - \exp(a(N_e h - T)) \right) \quad (1)$$

wherein, N_e represents the number of prey eaten, N_o is the initial density of prey, a is the attack parameter, h is the handling parameter, and T is the total time available. The Lambert W function was implemented to fit the model to the data (Bolker 2008). The data were non-parametrically bootstrapped (*frair::frair_boot*; $n = 2000$) to produce 95% BCa confidence intervals around the mean functional response curve for each treatment, wherein any overlap of BCa curves indicates a lack of statistical difference in FR. This method allows visual assessment of differences between FR curves and allows inferences to be made at a population level. Maximum feeding estimates ($1/h$) were calculated from the handling time estimates.

The FRR (Cuthbert et al. 2019) was calculated for each prey species and substrate type using the parameter estimates of a and h from the maximum likelihood estimate results of **eqn (1)**:

$$\text{FRR} = a / h \quad (2)$$

where a is the attack parameter and h is the handling parameter derived from the FR curve. In this case the FRR is used as a diagnostic tool to determine whether there were differences that can not be observed from the usual FR outputs. Therefore, the higher the FRR value the higher the inferred impact (Cuthbert et al. 2019). As FRR results are derived from the FR values of one set of experiments and the relatively small sample size, they are, in this instance, not bootstrapped for comparison as the FR model already incorporates $n = 2000$ bootstrapping of parameters.

Results

Prey survival was >99% under all control treatments and thus any mortality was due to predation by *P. clarkii*, which was also frequently observed. *Procambarus clarkii* were observed in pilot experiments to feed upon chironomid larvae by searching with their antennae and maxillipeds, contrastingly they fed upon *D. magna* in a filter feeding fashion by generating a flow via tail flicking behaviours.

All model terms significantly affected prey consumption by *P. clarkii* (Table 1). There was a significant three way interaction between ‘prey × prey density × substrate’ (Table 1) where at higher densities (above 120) *P. clarkii* consumed more chironomids than *D. magna* on gravel than on sand and no substrate (both $p < 0.001$) but there was no difference in prey consumption between prey species consumption on no substrate and sand ($p = 0.47$). At prey densities of 200 and above *P. clarkii* consumed more chironomids than *D. magna* on gravel compared to no substrate and sand (both $p < 0.001$), however, when on no substrate and sand *P. clarkii* consumed more *D. magna* than chironomid larvae ($p < 0.001$). Prey density and substrate significantly interacted on number of prey eaten (Table 1), whereby at higher prey densities (above 120) there were less prey consumed on gravel than on no substrate and sand (all $p < 0.001$), however, there was no difference between no substrate and sand at densities of 120 ($p = 0.93$). Although at densities of 200 and 300 there were less prey consumed on sand than on no substrate (all $p < 0.001$). Substrate type significantly interacted with prey species to affect number of prey consumed (Table 1) where there was no difference in number of chironomid larvae consumed between substrate type (all $p > 0.05$), but there were more *D. magna* consumed on no substrate and sand compared to on gravel (both $p < 0.001$) and more consumed on no substrate compared to sand ($p < 0.001$). Prey density significantly interacted with prey species (Table 1) causing more chironomids to be consumed than *D. magna* at densities of 120 ($p < 0.001$) but at densities of 200 and 300 *P. clarkii* consumed more *D. magna* than chironomid larvae. At densities below 120 there were no differences in prey consumption (all $p > 0.005$). Overall substrate type affected number of prey consumed by *P. clarkii* (Table 1) as more prey were consumed when no substrate was present compared to gravel and sand (both $p < 0.001$) and the presence of gravel substrate reduced prey consumption compared to sand ($p < 0.001$). Increasing prey density significantly affected prey consumption (Table 1) between all densities apart from between 200 and 300. Prey species significantly affected the number of prey individuals consumed (Table 1) as *P. clarkii* consumed significantly more *D. magna* than chironomid larvae ($p < 0.001$).

All prey species and substrate treatments resulted in a significant Type II FR by *P. clarkii* (Table 2, Fig. 1). The FR of *P. clarkii* towards chironomid larvae was not affected by substrate type (Table 2; Fig. 1), whereas the magnitude FR towards *D. magna* was significantly reduced by both sand and gravel substrates (Table 2; Fig. 1). The attack parameter of *P. clarkii* upon *D. magna* (i.e. initial slope of the FR curve) confidence intervals overlap indicating that the attack efficiency is not driving the difference in FR

Table 1. Model terms for all factors from GLM with a quasi-Poisson error distribution used to determine differences in prey consumption with regards to factors “prey species”, “density”, and “substrate”, using a Type 3 Anova and χ^2 to report the effect size of a factor on the dependent variable.

Model term	Chisq	df	p-value
Prey species	14	1	<0.001
Density	207713	8	<0.001
Substrate	78	2	<0.001
Prey species * Density	607	8	<0.001
Prey species* Substrate	112	2	<0.001
Density * Substrate	1556	16	<0.001
Prey species * Density * Substrate	1681	16	<0.001

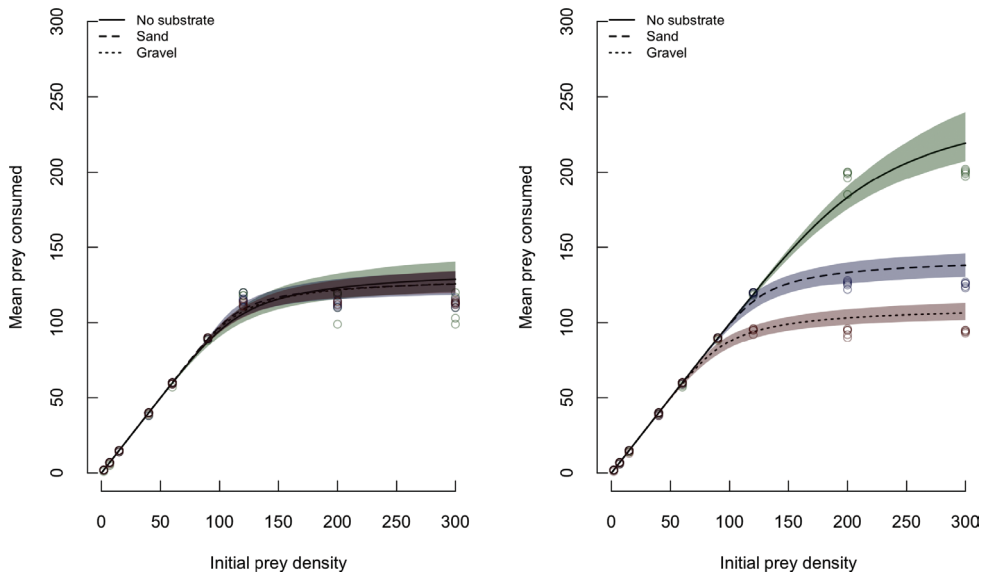


Figure 1. Functional responses of *Procambarus clarkii* preying on chironomid larvae and *Daphnia magna* under different substrate treatments; no substrate (solid line), sand (dashed line), gravel (dotted line). Points indicate raw data distributions; no substrate (green), sand (blue), gravel (brown). Shaded areas are bootstrapped ($n = 2000$) 95% confidence intervals.

(Table 2; Fig. 1). However, there are significant differences in the handling and maximum feeding parameters between the three substrate types, whereupon no substrate elicited the highest maximum feeding estimate, with sand intermediate and gravel producing the longest handling time and thus lowest maximum feeding estimate (Table 2; Fig. 1).

The FRR shows that when preying on chironomid larvae the impact of *P. clarkii* is highest on sand substrate compared to gravel or no substrate (Fig. 2). Whereas, when preying on *D. magna*, *P. clarkii* were almost as effective on sand and no substrate, while gravel elicited the lowest FRR for *D. magna* (Fig. 2).

Table 2. First order terms and significance levels from logistic regression of the proportion of prey consumed against initial prey density, with FR Type, functional parameters (a , b , and $1/h$), associated significance levels from Rogers' random predator equation, bias accelerated and corrected 95% confidence intervals for a and b , and the functional response ratio (a/b) with regards to *Procambarus clarkii* preying upon chironomid larvae and *Daphnia magna* under different substrate types. a = attack rate; b = handling time; $1/h$ = maximum feeding estimate.

Prey	Substrate	First order term (p -value)	FR type	a (p -value)	a 95% BCa CI	b (p -value)	b 95% BCa CI	Maximum Feeding Estimate ($1/h$)	Functional Response Ratio (a/b)
Chironomid larvae	None	-0.016, <0.001	II	9.51, <0.001	6.79 – 3.53	0.007, <0.001	0.007–0.008	136.9	3102.7
	Sand	-0.016, <0.001	II	14.54, <0.001	9.30 – 28.8	0.007, <0.001	0.007–0.008	129.8	1888.3
	Gravel	-0.016, <0.001	II	12.40, <0.001	8.79 – 19.08	0.007, <0.001	0.007–0.008	131.5	1631.5
<i>D. magna</i>	None	-0.022, <0.001	II	8.37, <0.001	6.43 – 12.09	0.003, <0.001	0.003–0.004	263.1	2202.6
	Sand	-0.017, <0.001	II	14.50, <0.001	8.60 – 28.58	0.006, <0.001	0.006–0.007	144.9	2101.4
	Gravel	-0.014, <0.001	II	9.63, <0.001	6.58 – 15.31	0.009, <0.001	0.008–0.009	111.1	1070.9

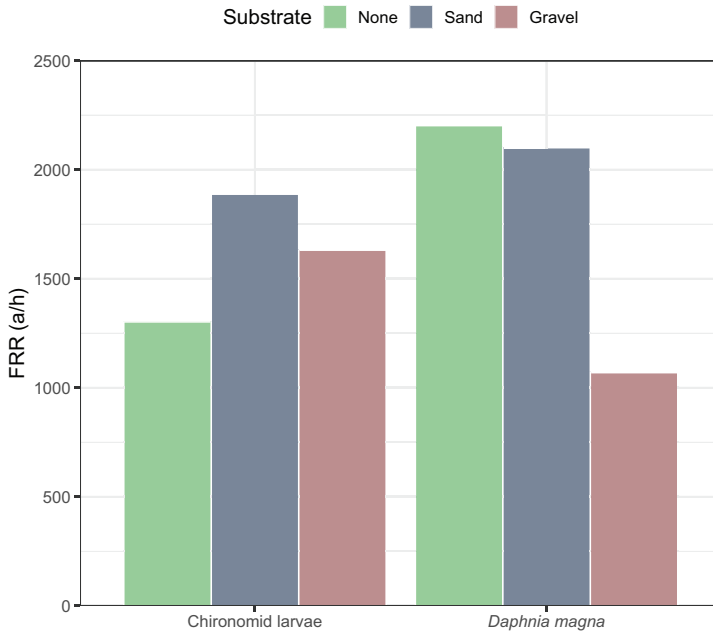


Figure 2. Functional response ratio (FRR) (a/h) of *Procambarus clarkii* preying on chironomid larvae and *Daphnia magna* under different substrate treatments; no substrate (green), sand (blue), gravel (brown).

Discussion

Management of invasive species depends upon generating contextually relevant and accurate estimates of potential impact conveyed upon a recipient ecosystem (Dick et al. 2017a, b; Evangelista et al. 2019). *Procambarus clarkii* has established as an invasive species around the globe due to human mediated transportation revolving around the aquaculture and the pet trade (Chucholl 2013; Patoka et al. 2014; Oficialdegui et al. 2019). *Procambarus clarkii* is known to alter aquatic communities through both con-

sumptive and non-consumptive effects (Carreira et al. 2017; Bucciarelli et al. 2019) but there are few quantitative estimates of their ecological impact upon macroinvertebrate communities (but see Klose and Cooper 2012).

Through the comparison of FR curves, it was possible to parameterise attack rate and handling time of a consumer upon a resource. Further, by comparing the FR curves for each prey species, we were able to distinguish whether one species may have higher pressures exerted upon it by an invasive species. Our results corroborate that *P. clarkii* indeed utilises both benthic and pelagic resources (Brown et al. 1992, 1998; Geiger et al. 2004; Lodge et al. 2005), but that the extent can be altered by substrate type but also effects prey morphology or behaviour increasing handling time. *Procambarus clarkii* has the capacity to exert substantial predatory pressure on macroinvertebrate populations as they are able to consume over 100 prey items per hour irrespective of substrate or prey identity. When taking into account possible differences in predator abundance on different benthic substrates, there could be the potential for a large per capital offtake rate of zooplankton; however, this would be very system dependent as water depth and flow dynamics affect encounter rate (Ruokonen et al. 2012). Therefore, as our experimental setup was rather shallow and devoid of natural hydrological characteristics, the results should be interpreted relative to each other rather than as a direct estimation of consumption in a system such as a large lake or stream. We recommend that habitat associations and abundance data for *P. clarkii* in invaded systems is reported on in the future in order to improve impact prediction. We also show the utility of the FRR method in determining subtle differences between impact predictions where comparison of standard FR curves become inconclusive.

The presence of different substrata affects the predation efficiency of crayfish towards each prey type. Compared to the control treatment of no substrate, both sand, and gravel substrate caused a slight reduction in the attack parameter (or search efficiency) of *P. clarkii* upon the benthic chironomid prey rather than altering the handling time. This suggests that the presence of both sand and gravel can offer a refuge for benthic prey species as the crayfish is not able to access the meiofauna as readily. Similar trends are seen in benthic invasive gobiids, where gravel substrate reduces magnitude FR compared to sand substrates (Gebauer et al. 2019). When only presented with the standard FR curve it is practically impossible to differentiate between them due to large overlap of confidence intervals. However, when the FRR is considered, it becomes apparent that due to the higher attack rate the impact exerted on chironomids when foraging on sand is higher than both no substrate and gravel substrates, despite the identical handling estimates. With regards to in situ evidence towards our results, Klose and Cooper (2012) found that *P. clarkii* abundance was negatively associated with larval chironomid abundance in two streams, one with sand and one with gravel and cobble substrate. In a similar fashion to the present results, the stream with cobble and gravel substrate showed a weaker negative relationship between predator and chironomid abundance (Klose and Cooper 2012).

Daphnia magna is an important prey species for larval and adult crayfish (Brown et al. 1992; Meakin et al. 2009; Kozák et al. 2015). Our results substantiate this, but data on field effects of crayfish species on daphniid populations is limited. Although, it is established that crayfish are polytrophic consumers, wherein invasion can lead to the

creation of new energy pathways between benthic and pelagic resources, but that this is system and species specific (Ruokonen et al. 2012; Lipták et al. 2019). While *D. magna* is generally found in the water column and exhibits diel vertical migration, this species also forages at the sediment-water interface. This behaviour thus makes this species more accessible to predation by benthic suspension feeders such as crayfish (Horton et al. 1979). This is where the FR and FRR approaches to impact prediction shows their value by elucidating the subtle differences in strengths of behaviours controlling foraging success (Cuthbert et al. 2019). The presence and type of substrate reduced the maximum feeding rate of *P. clarkii* on *D. magna* where gravel had the lowest maximum feeding rate due to a high handling time, despite having a higher attack parameter under no substrate. It is possible that there are substantial field effects of crayfish invasions upon daphniid populations; however, further realistic context and in situ data needs to be incorporated to address the actual extent as *D. magna* can alter anti-predator behaviour in response to cues (Langer et al. 2019). Differences in impact between substrata are likely due to foraging mode in crayfish being generally benthic rather than the filter feeding behaviour observed within these experiments. Further, while *P. clarkii* is a behaviourally plastic species they may exhibit substrate preferences, especially as they are non-obligate burrowers (Hobbs and Barr 1960; Kouba et al. 2016), which could lead to differences in abundance. Further information is necessary on habitat associations and abundances of crayfish in novel environments in order to determine relative impact potential (Dick et al. 2017b)

Crayfish were able to generate a flow wherein the prey items were drawn closer, perhaps facilitating the low handling time demonstrated and indicating that filter feeding efficiency by adults is comparable to benthic foraging and thus warrants further investigation. Plasticity in feeding mode and flexible omnivory have been identified in other crustacean invaders (Platvoet et al. 2009; Kestrup et al. 2011) and could contribute to broad invasive impact. Some austral native crayfish species do not show flexible omnivory in the same manner (Johnston et al. 2011), which supports the idea that a flexible diet is a driver of invasion success and impact in invasive crustaceans (Hänfling et al. 2011). Due to a focus on agonistic behaviours, descriptions or ethograms of crayfish feeding behaviours are rare in the literature (but see Panksepp and Huber 2004) and none explicitly describe the mechanism of capturing prey in a filter feeding behaviour. Filter feeding is however documented in marine crustaceans and larval crayfish (Gerlach et al. 1976; Budd et al. 1978; Brown et al. 1992; Kim et al. 2015), indicating that this may be an opportunistic behaviour facilitated by morphological similarities.

Procambarus clarkii is a global polytrophic keystone consumer which has facilitated its spread and pervasion into numerous systems (Momot 1995; Jackson et al. 2017). Due to the nature of polytrophy and generalist foraging strategies it is essential to consider multiple resources when attempting to quantify utilisation as well as context. There is substantial field and experimental data that points towards the idea that much of *P. clarkii* predation is frequency dependent (Correia 2002; Klose and Cooper 2012; Nishijima et al. 2017). Therefore, future work should focus on quantifying the frequency dependence of predation upon a variety of food resources under different contexts, especially as Nishijima et al. (2017) found that macrophyte availability also contributes to dampening *P. clarkii* impacts on invertebrate communities.

In the context of furthering approaches to impact prediction in invasion science, we establish here how the application of FR and FRR methods can be used to powerfully predict impact where traditional assessment methods would not have identified a difference between contexts. Furthermore, we discern that there is high potential for crayfish to differentially consume both benthic and pelagic macroinvertebrate species which has implications for nutrient cycling and resource provisioning for native species. In a destructive and spreading species like *P. clarkii* it is imperative to continue to determine scenarios wherein its predatory effect can be dampened in order to implement mitigation strategies as removal of crayfish once established is unfeasible.

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References

- Alexander ME, Dick JTA, Weyl OLF, Robinson TB, Richardson DM (2014) Existing and emerging high impact invasive species are characterized by higher functional responses than natives. *Biology Letters* 10: e20130946. <https://doi.org/10.1098/rsbl.2013.0946>
- Aquiloni L, Ilhéu M, Gherardi F (2005) Habitat use and dispersal of the invasive crayfish *Procambarus clarkii* in ephemeral water bodies of Portugal. *Marine and Freshwater Behaviour and Physiology* 38: 225–236. <https://doi.org/10.1080/10236240500310195>
- Barrios-O'Neill D, Dick JTA, Emmerson MC, Ricciardi A, MacIsaac HJ (2015) Predator-free space, functional responses and biological invasions. *Functional Ecology* 29: 377–384. <https://doi.org/10.1111/1365-2435.12347>
- Bellard C, Cassey P, Blackburn TM (2016) Alien species as a driver of recent extinctions. *Biology Letters* 12: 20150623. <https://doi.org/10.1098/rsbl.2015.0623>
- Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, Kumschick S, Marková Z, Mrugała A, Nentwig W, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM, Sendek A, Vilà M, Wilson JRU, Winter M, Genovesi P, Bacher S (2014) A unified classification of alien species based on the magnitude of their environmental impacts. *PLOS Biology* 12: e1001850. <https://doi.org/10.1371/journal.pbio.1001850>
- Bolker BM (2008) *emdbok: ecological models and data in R*. Princeton University Press, Princeton.
- Bolker BM (2010) *bbml: Tools for General Maximum Likelihood Estimation*. R Package. <http://www.cran.rproject.org>

- Brown KM (1998) The role of shell strength in selective foraging by crayfish for gastropod prey. *Freshwater Biology* 40: 255–260. <https://doi.org/10.1046/j.1365-2427.1998.00350.x>
- Brown PB, Wetzel JE, Spacie A, Konopka A (1992) Evaluation of naturally-occurring organisms as food for juvenile crayfish *Procambarus clarkii*. *Journal of the World Aquaculture Society* 23: 211–216. <https://doi.org/10.1111/j.1749-7345.1992.tb00771.x>
- Bucciarelli GM, Suh D, Lamb AD, Roberts D, Sharpton D, Shaffer HB, Fisher RN, Kats LB (2019) Assessing effects of non-native crayfish on mosquito survival. *Conservation Biology* 33: 122–131. <https://doi.org/10.1111/cobi.13198>
- Budd TW, Lewis JC, Tracey ML (1978) The filter-feeding apparatus in crayfish. *Canadian Journal of Zoology* 56: 695–707. <https://doi.org/10.1139/z78-097>
- Carlton J, Fowler A (2018) Ocean rafting and marine debris: a broader vector menu requires a greater appetite for invasion biology research support. *Aquatic Invasions* 13: 11–15. <https://doi.org/10.3391/ai.2018.13.1.02>
- Carreira BM, Segurado P, Laurila A, Rebelo R (2017) Can heat waves change the trophic role of the world's most invasive crayfish? Diet shifts in *Procambarus clarkii*. *PLOS ONE* 12: e0183108. <https://doi.org/10.1371/journal.pone.0183108>
- Chucholl C (2013) Invaders for sale: trade and determinants of introduction of ornamental freshwater crayfish. *Biological Invasions* 15: 125–141. <https://doi.org/10.1007/s10530-012-0273-2>
- Correia AM (2002) Niche breadth and trophic diversity: feeding behaviour of the red swamp crayfish (*Procambarus clarkii*) towards environmental availability of aquatic macroinvertebrates in a rice field (Portugal). *Acta Oecologica* 23: 421–429. [https://doi.org/10.1016/S1146-609X\(02\)01166-9](https://doi.org/10.1016/S1146-609X(02)01166-9)
- Courchamp F, Fournier A, Bellard C, Bertelsmeier C, Bonnaud E, Jeschke JM, Russell JC (2017) Invasion biology: specific problems and possible solutions. *Trends in Ecology and Evolution* 32: 13–22. <https://doi.org/10.1016/j.tree.2016.11.001>
- Cuthbert RN, Dalu T, Wasserman RJ, Dick JTA, Mofu L, Callaghan A, Weyl OLF (2018) Intermediate predator naïveté and sex-skewed vulnerability predict the impact of an invasive higher predator. *Scientific Reports* 8: 14282. <https://doi.org/10.1038/s41598-018-32728-0>
- Cuthbert RN, Dickey JWE, Coughlan NE, Joyce PWS, Dick JTA (2019) The Functional Response Ratio (FRR): advancing comparative metrics for predicting the ecological impacts of invasive alien species. *Biological Invasions* 21: 2543–2547. <https://doi.org/10.1007/s10530-019-02002-z>
- Davis AJS, Darling JA (2017) Recreational freshwater fishing drives non-native aquatic species richness patterns at a continental scale. *Diversity and Distributions* 23: 692–702. <https://doi.org/10.1111/ddi.12557>
- Dick JTA, Alexander ME, Jeschke JM, Ricciardi A, MacIsaac HJ, Robinson TB, Kumschick S, Weyl OLF, Dunn AM, Hatcher MJ, Paterson RA, Farnsworth KD, Richardson DM (2014) Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. *Biological Invasions* 16: 735–753. <https://doi.org/10.1007/s10530-013-0550-8>
- Dick JTA, Alexander ME, Ricciardi A, Laverty C, Downey PO, Xu M, Jeschke JM, Saul W-C, Hill MP, Wasserman R, Barrios-O'Neill D, Weyl OLF, Shaw RH (2017a) Functional responses can unify invasion ecology. *Biological Invasions* 19: 1667–1672. <https://doi.org/10.1007/s10530-016-1355-3>

- Dick JTA, Lavery C, Lennon JJ, Barrios-O'Neill D, Mensink PJ, Britton JR, Médoc V, Boets P, Alexander ME, Taylor NG, Dunn AM, Hatcher MJ, Rosewarne PJ, Crookes S, MacIsaac HJ, Xu M, Ricciardi A, Wasserman RJ, Ellender BR, Weyl OLF, Lucy FE, Banks PB, Dodd JA, MacNeil C, Penk MR, Aldridge DC, Caffrey JM (2017b) Invader Relative Impact Potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. *Journal of Applied Ecology* 54: 1259–1267. <https://doi.org/10.1111/1365-2664.12849>
- Dickey JWE, Cuthbert RN, Rea M, Lavery C, Crane K, South J, Briski E, Chang X, Coughlan NE, MacIsaac HJ, Ricciardi A, Riddell GE, Xu M, Dick JTA (2018) Assessing the relative potential ecological impacts and invasion risks of emerging and future invasive alien species. *NeoBiota* 40: 1–24. <https://doi.org/10.3897/neobiota.40.28519>
- Evangelista C, Olden JD, Lecerf A, Cucherousset J (2019) Scale-dependent patterns of intraspecific trait variations in two globally invasive species. *Oecologia* 189: 1083–1094. <https://doi.org/10.1007/s00442-019-04374-4>
- Gebauer R, Veselý L, Vanina T, Buřič M, Kouba A, Drozd B (2019) Prediction of ecological impact of two alien gobiids in habitat structures of differing complexity. *Canadian Journal of Fisheries and Aquatic Sciences* 76(11): 1954–1961. <https://doi.org/10.1139/cjfas-2018-0346>
- Geiger W, Otero M, Alcorlo P (2004) Feeding preferences and food selection of the red swamp crayfish, *Procambarus clarkii*, in habitats differing in food item diversity. *Crustaceana* 77: 435–453. <https://doi.org/10.1163/1568540041643283>
- Gerlach SA, Ekstrøm DK, Eckardt PB (1976) Filter feeding in the hermit crab. *Oecologia* 24: 257–264. <https://doi.org/10.1007/BF00345477>
- Hänfling B, Edwards F, Gherardi F (2011) Invasive alien Crustacea: dispersal, establishment, impact and control. *BioControl* 56: 573–595. <https://doi.org/10.1007/s10526-011-9380-8>
- Hobbs HH, Barr TC (1960) The origins and affinities of the troglobitic crayfishes of North America (Decapoda, Astacidae). I. The genus *Cambarus*. *The American Midland Naturalist* 64: 12–33. <https://doi.org/10.2307/2422890>
- Holling CS (1959) Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist* 91: 385–398. <https://doi.org/10.4039/Ent91385-7>
- Horton PA, Rowan M, Webster KE, Peters RH (1979) Browsing and grazing by cladoceran filter feeders. *Canadian Journal of Zoology* 57: 206–212. <https://doi.org/10.1139/z79-019>
- Jackson MC, Evangelista C, Zhao T, Lecerf A, Britton JR, Cucherousset J (2017) Between-lake variation in the trophic ecology of an invasive crayfish. *Freshwater Biology* 62: 1501–1510. <https://doi.org/10.1111/fwb.12957>
- Jeschke JM, Kopp M, Tollrian R (2004) Consumer-food systems: why type I functional responses are exclusive to filter feeders. *Biological Reviews Cambridge Philosophical Society* 79: 337–349. <https://doi.org/10.1017/S1464793103006286>
- Johnston K, Robson BJ, Fairweather PG (2011) Trophic positions of omnivores are not always flexible: evidence from four species of freshwater crayfish. *Austral Ecology* 36: 269–279. <https://doi.org/10.1111/j.1442-9993.2010.02147.x>
- Juliano SA (2001) Nonlinear curve fitting: predation and functional response curves. In: Scheiner SM, Gurevitch J (Eds) *Design and Analysis of Ecological Experiments*. Oxford University Press, Oxford, 178–196.

- Kemp JS, Aldridge DC (2018) Comparative functional responses to explain the impact of sympatric invasive bivalves (*Dreissena* spp.) under different thermal regimes. *Journal of Molluscan Studies* 84: 175–181. <https://doi.org/10.1093/mollus/eyy006>
- Kestrup ÅM, Dick JTA, Ricciardi A (2011) Interactions between invasive and native crustaceans: differential functional responses of intraguild predators towards juvenile heterospecifics. *Biological Invasions* 13: 731–737. <https://doi.org/10.1007/s10530-010-9863-z>
- Keyler TD, Hrabik TR, Mensinger AF, Rogers LS, Gorman OT (2019) Effect of light intensity and substrate type on siscowet lake trout (*Salvelinus namaycush siscowet*) predation on deepwater sculpin (*Myoxocephalus thompsonii*). *Hydrobiologia* 840: 77–88. <https://doi.org/10.1007/s10750-019-3944-5>
- Kim S-K, Guo Q, Jang I-K (2015) Effect of Biofloc on the survival and growth of the post-larvae of three penaeids (*Litopenaeus vannamei*, *Fenneropenaeus chinensis*, and *Marsupenaeus japonicus*) and their Biofloc feeding efficiencies, as related to the morphological structure of the third maxilliped. *Journal of Crustacean Biology* 35: 41–50. <https://doi.org/10.1163/1937240X-00002304>
- Klose K, Cooper SD (2012) Contrasting effects of an invasive crayfish (*Procambarus clarkii*) on two temperate stream communities. *Freshwater Biology* 57: 526–540. <https://doi.org/10.1111/j.1365-2427.2011.02721.x>
- Kouba A, Tíkal J, Císař P, Veselý L, Fořt M, Příborský J, Patoka J, Buřič M (2016) The significance of droughts for hyporheic dwellers: evidence from freshwater crayfish. *Scientific Reports* 6: 26569. <https://doi.org/10.1038/srep26569>
- Kozák P, Ďuriš Z, Petrušek A, Buřič M, Horká I, Kouba A, Kozubíková-Balcarová E, Polícar T, Němečková K (2015) Crayfish Biology and Culture. University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, Vodňany, 201–249.
- Langer SM, Weiss LC, Ekvall MT, Bianco G, Hansson L-A, Tollrian R (2019) A three-dimensional perspective of *Daphnia*'s swimming behavior with and without predator cues. *Limnology and Oceanography* 64: 1515–1525. <https://doi.org/10.1002/lno.11132>
- Larson ER, Twardochleb LA, Olden JD (2017) Comparison of trophic function between the globally invasive crayfishes *Pacifastacus leniusculus* and *Procambarus clarkii*. *Limnology* 18: 275–286. <https://doi.org/10.1007/s10201-016-0505-8>
- Laverty C, Green KD, Dick JTA, Barrios-O'Neill D, Mensink PJ, Médoc V, Spataro T, Cafrey JM, Lucy FE, Boets P, Britton JR, Pegg J, Gallagher C (2017) Assessing the ecological impacts of invasive species based on their functional responses and abundances. *Biological Invasions* 19: 1653–1665. <https://doi.org/10.1007/s10530-017-1378-4>
- Lipták B, Veselý L, Ercoli F, Bláha M, Buřič M, Ruokonen T, Kouba A (2019) Trophic role of marbled crayfish in a lentic freshwater ecosystem. *Aquatic Invasions*: 14: 299–309. <https://doi.org/10.3391/ai.2019.14.2.09>
- Lodge DM, Rosenthal SK, Mavuti KM, Muohi W, Ochieng P, Stevens SS, Mungai BN, Mkoji GM (2005) Louisiana crayfish (*Procambarus clarkii*) (Crustacea: Cambaridae) in Kenyan ponds: non-target effects of a potential biological control agent for schistosomiasis. *African Journal of Aquatic Science* 30: 119–124. <https://doi.org/10.2989/16085910509503845>
- MacNeil C, Dick JTA, Elwood RW (1997) The trophic ecology of freshwater *Gammarus* spp. (Crustacea: Amphipoda): Problems and perspectives concerning the functional feeding

- group concept. *Biological Reviews of the Cambridge Philosophical Society* 72: 349–364. <https://doi.org/10.1017/S0006323196005038>
- Meakin CA, Qin JG, Mair GC (2009) Zooplankton predation and consumption by freshwater crayfish, *Cherax tenuimanus*, at different sizes and light conditions. *Journal of Freshwater Ecology* 24: 159–167. <https://doi.org/10.1080/02705060.2009.9664276>
- Meyerson LA, Carlton JT, Simberloff D, Lodge DM (2019) The growing peril of biological invasions. *Frontiers in Ecology and the Environment* 17: 191–191. <https://doi.org/10.1002/fee.2036>
- Momot WT (1995) Redefining the role of crayfish in aquatic ecosystems. *Reviews in Fisheries Science* 3: 33–63. <https://doi.org/10.1080/10641269509388566>
- Murdoch WW (1969) Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs* 39: 335–354. <https://doi.org/10.2307/1942352>
- Nishijima S, Nishikawa C, Miyashita T (2017) Habitat modification by invasive crayfish can facilitate its growth through enhanced food accessibility. *BMC Ecology* 17: 37. <https://doi.org/10.1186/s12898-017-0147-7>
- Nunes AL, Hoffman AC, Zengeya TA, Measey GJ, Weyl OLF (2017a) Red swamp crayfish, *Procambarus clarkii*, found in South Africa 22 years after attempted eradication. *Aquatic Conservation: Marine and Freshwater Ecosystems* 27: 1334–1340. <https://doi.org/10.1002/aqc.2741>
- Nunes AL, Zengeya TA, Measey GJ, Weyl OLF (2017b) Freshwater crayfish invasions in South Africa: past, present and potential future. *African Journal of Aquatic Science* 42: 309–323. <https://doi.org/10.2989/16085914.2017.1405788>
- Oficialdegui FJ, Clavero M, Sánchez MI, Green AJ, Boyero L, Michot TC, Klose K, Kawai T, Lejeune C (2019) Unravelling the global invasion routes of a worldwide invader, the red swamp crayfish (*Procambarus clarkii*). *Freshwater Biology* 64: 1382–1400. <https://doi.org/10.1111/fwb.13312>
- Panksepp JB, Huber R (2004) Ethological analyses of crayfish behavior: a new invertebrate system for measuring the rewarding properties of psychostimulants. *Behavioural Brain Research* 153: 171–180. <https://doi.org/10.1016/j.bbr.2003.11.014>
- Patoka J, Kalous L, Kopecký O (2014) Risk assessment of the crayfish pet trade based on data from the Czech Republic. *Biological Invasions* 16: 2489–2494. <https://doi.org/10.1007/s10530-014-0682-5>
- Platvoet D, Van Der Velde G, Dick JTA, Li S (2009) Flexible omnivory in *Dikerogammarus villosus* (Sowinsky, 1894) (Amphipoda) – Amphipod Pilot Species Project (AMPIS) Report 5. *Crustaceana* 82: 703–720. <https://doi.org/10.1163/156854009X423201>
- Pritchard DW (2014) frair: a package for functional response analysis in R. GitHub. <https://github.com/dpritchard/frair>
- Pritchard DW, Paterson RA, Bovy HC, Barrios-O'Neill D (2017) Frair: an R package for fitting and comparing consumer functional responses. *Methods in Ecology and Evolution* 8: 1528–1534. <https://doi.org/10.1111/2041-210X.12784>
- R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>

- Ricciardi A, Cohen J (2007) The invasiveness of an introduced species does not predict its impact. *Biological Invasions* 9: 309–315. <https://doi.org/10.1007/s10530-006-9034-4>
- Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs* 83: 263–282. <https://doi.org/10.1890/13-0183.1>
- Rogers D (1972) Random search and insect population models. *Journal of Animal Ecology* 41: 369–383. <https://doi.org/10.2307/3474>
- SCBD (2010) COP-10 Decision X / 2: Strategic Plan for Biological Diversity 2011–2020. Secretariat of the Convention on Biological Diversity, Nagoya.
- Schoener TW (1971) Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2: 369–404. <https://doi.org/10.1146/annurev.es.02.110171.002101>
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications* 8: 14435. <https://doi.org/10.1038/ncomms14435>
- Solomon ME (1949) The natural control of animal populations. *Journal of Animal Ecology* 18: 1–35. <https://doi.org/10.2307/1578>
- South J, Dick JTA, McCard M, Barrios-O’Neill D, Anton A (2017) Predicting predatory impact of juvenile invasive lionfish (*Pterois volitans*) on a crustacean prey using functional response analysis: effects of temperature, habitat complexity and light regimes. *Environmental Biology of Fishes* 100: 1155–1165. <https://doi.org/10.1007/s10641-017-0633-y>
- South J, Welsh D, Anton A, Sigwart JD, Dick JTA (2018) Increasing temperature decreases the predatory effect of the intertidal shanny *Lipophrys pholis* on an amphipod prey. *Journal of Fish Biology* 92: 150–164. <https://doi.org/10.1111/jfb.13500>
- Souty-Grosset C, Anastácio PM, Aquiloni L, Banha F, Choquer J, Chucholl C, Tricarico E (2016) The red swamp crayfish *Procambarus clarkii* in Europe: impacts on aquatic ecosystems and human well-being. *Limnologica* 58: 78–93. <https://doi.org/10.1016/j.limno.2016.03.003>
- Tokeshi M, Arakaki S (2012) Habitat complexity in aquatic systems: fractals and beyond. *Hydrobiologia* 685: 27–47. <https://doi.org/10.1007/s10750-011-0832-z>
- Wasserman RJ, Alexander ME, Dalu T, Ellender BR, Kaiser H, Weyl OLF (2016) Using functional responses to quantify interaction effects among predators. *Functional Ecology* 30: 1988–1998. <https://doi.org/10.1111/1365-2435.12682>

Urban trees facilitate the establishment of non-native forest insects

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Abstract

Cities, due to the presence of ports and airports and the high diversity of trees in streets, parks, and gardens, may play an important role for the introduction of invasive forest pests. We hypothesize that areas of urban forest facilitate the establishment of non-native forest pests. Based on scientific literature and a pan-European database on non-native species feeding on woody plants, we analysed where the first detections occurred in European countries. We collected site data for 137 first detections in Europe and 508 first European country-specific records. We also estimated the percentage of tree cover and suitable habitat (green areas with trees) in buffers around detection points. The large majority of first records (89% for first record in Europe and 88% for first records in a European country) were found in cities or suburban areas. Only 7% of the cases were in forests far from cities. The probability of occurrence decreased sharply with distance from the city. The probability to be detected in urban areas was higher for sap feeders, gall makers, and seed or fruit feeders (>90%) than for bark and wood borers (81%). Detection sites in cities were highly diverse, including public parks, street trees, university campus, arboreta, zoos, and botanical gardens. The average proportion of suitable habitat was less than 10% in urban areas where the species were detected. Further, more than 72% of the cases occurred in sites with less than 20% of tree cover. Hotspots of first detection were identified along the coastal regions of the Mediterranean and Atlantic, and near industrial areas of central Europe. We conclude that urban trees are main facilitators for the establishment of non-native forest pests, and that cities should thus be intensely surveyed. Moreover, as urban areas are highly populated, the involvement of citizens is highly recommended.

Keywords

Cities, forest pests, invasive species, surveillance, urban trees

Introduction

Forests, like other terrestrial ecosystems, are increasingly threatened by the establishment and spread of non-native pests worldwide (Brockhoff and Liebhold 2017). Some examples of forest invasive species with large distribution range are the Pine wood nematode, *Bursaphelenchus xylophilus*, causing the pine wilt disease in Asia (Kishi 1995; Robinet et al. 2009) and Europe (Sousa et al. 2001); the Emerald ash borer, *Agrilus planipennis*, in North America (Herms and McCullough 2014); *Anoplophora glabripennis* which was introduced into North America and Europe (Carter et al. 2010; Roques et al. 2010); the invasion of the USA by the gypsy moth, *Lymantria dispar* (Liebhold et al. 1992); or the increasing numbers of *Eucalyptus* pests established in all continents where eucalypts are grown in intensive plantations (Hurley et al. 2016).

The increase of forest pest invasions in recent years is mostly the consequence of increasing global trade and international travel (Brockhoff et al. 2006a; Roques 2010). International trade has remarkably increased during the 20th century, with a rate of 7.1 percent per year between 1987 and 2007, and is still increasing (Constantinescu et al. 2015). As a result, the invasion rate continues to rise, with no sign of saturation (Seebens et al. 2017).

The main pathways for the accidental introduction of non-native forest insects are the trade of live trees for planting, hitchhiking with containers, imports of timber, and use of wood packaging material (Brockhoff and Liebhold 2017), all of which are much more frequent than in the past. A common feature of these pathways is that they often converge to urban areas. Cities, in particular large cities, are close to international airports and seaports and thus are expected to be main gateways for the entry of new, non-native insect species. Cities are also more populated, attracting more and more goods every day. It is expected that by 2050, almost 70% of humanity will be living in urban areas. In Europe, where urbanization occurred earlier, 82% of people are already living in cities (United Nations 2018).

There is little doubt that urbanization and population concentration in large cities are of critical importance for the arrival rate of invasive species (Paap et al. 2017). However, whether the convergence of main invasion pathways towards cities will ultimately result in more introductions, and most importantly in the establishment of non-native forest insects, remains an open question. Indeed, the establishment of non-native forest insects in urban areas depends not only on the probability of arrival, but also on the presence and abundance of suitable host trees. If the introduced pest species needs only a small number of trees or small tree patches to become established, then urban trees, even if isolated in parks, gardens, or streets might provide a suitable

environment for their establishment. In addition, trees are more likely to be stressed in warmer (urban heat island effect) (Debbage and Shepherd 2015) and drier urban areas, making trees then more susceptible to non-native secondary pests like bark or longhorn beetles (Meineke et al. 2013; Chakraborty et al. 2014). Species originating from warm regions, e.g. the Neotropical region, could particularly benefit from these microclimatic conditions to invade cities in temperate, cooler regions.

Most cities usually harbor a relatively high diversity of tree species, dispersed in many urban parks and gardens. These could provide a larger number of putative hosts and, thus, increase the risk of non-native pest establishment (Liebhold et al. 2018). According to these assumptions, the higher diversity of host tree species observed in cities than on countryside would aid the establishment of forest insects of different functional traits, like voltinism and diet breadth (Brockerhoff and Liebhold 2017).

To test these hypotheses, we compared the rate of first detection in urban vs non-urban areas of invasive pests feeding on woody plants in Europe. We focused on this continent because it is among the most affected by forest pest invasions in the world, and we have very good records of non-native species detection in European countries (Roques et al. 2010). We also estimated the distance of detection locations to small and large cities. We further investigated the habitat requirements in urban areas for the establishment of non-native tree pests, particularly in relation to their feeding requirements. By identifying areas of higher risk of establishment, we provide relevant knowledge to improve the methods for early detection of non-native forest pests. This is crucial as the success of eradication mainly depends on the speed and accuracy of first detection (Liebhold et al. 2016).

Methods

Data gathering

Data sources. We first used the pan-European database for non-native organisms, **DAISIE** (Delivering Non-native Invasive Species Inventories for Europe) (Hulme and Roy 2010), which provides historical invasion data at the country level for the species introduced to Europe after 1700. Since the data from the DAISIE database were recently updated in the **EASIN** catalogue (European Alien Species Information Network), which additionally provided year and country of first records of species in Europe (Katsanevakis et al. 2015; Roques et al. 2016; <http://easin.jrc.ec.europa.eu>), we finally used EASIN to select the non-native insect species affecting woody plants, i.e. trees and palms. The EPPO Global Database (<https://gd.eppo.int/>) was also used to search for new non-native insects recently arrived in Europe. The bibliographic databases Google Scholar and Science Direct were additionally used. We searched for literature using specific keywords to detect papers reporting first records of new species

feeding on trees in Europe. The combination of keywords was the following: (First record or Introduction) and (Pest or Insect or Emerging or Non-native or Invasive or Non-native) and (Forest or Tree) and (Europe or Austria, Belgium, Bulgaria, Croatia, Republic of Cyprus, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Ireland, Italy, Latvia, Lithuania, Luxembourg, Malta, Netherlands, Poland, Portugal, Romania, Slovakia, Slovenia, Spain, Sweden, UK).

Criteria for data selection. Only insect species introduced in Europe since 1950 were considered because most of the forest non-native species in Europe were introduced in the last five decades (Roques 2011). Previous introductions were disregarded to avoid inaccuracies from ancient reports.

For each country, a unique first record was retrieved with the exception of a particular species detected in geographically well separated regions of a given country (e.g. mainland and distant islands). A case study was thus defined as a new species detected in a new country for the first time. The same introduced species could be reported several times in Europe as long as it was successively recorded for the first time in different European countries. We further distinguished between first record in Europe and first records in any of the European regions as a given species could use the first introduction as bridgehead for spreading through Europe, or be introduced several times in different European regions. Rare cases where two different European countries reported the first detection in the same year were both accounted as first records in Europe.

Complementary data. For each case study (one species \times one country \times one date of first detection) we documented information regarding the insect species, and the time and location of first record. For each species we retrieved from the literature the order, family, feeding guild (Bark & wood borers, Defoliators, Sap suckers, Gall makers, Root feeders, Seed and fruit feeders), host range (Broadleaves, Conifers, Palms, Polyphagous), and body length (mm). For each first detection we recorded the year of detection, the geographical coordinates of the site, the type of habitat (Urban if reported in a city or suburban urbanized areas, Forests, Rural areas, or Nurseries), and the distance in km to the border of the nearest city (with at least 10 000 inhabitants) or large city (at least 100 000 inhabitants or with an international transport system, e.g. airport, seaport, railway station).

The site coordinates were retrieved from the reporting articles. In several cases, exact site coordinates were not available. When the description of the location was reliable and narrow enough to delimitate a location area (e.g. Lisbon Zoo, Nepliget Park in Budapest), its central point was used to recalculate site coordinates. For records that had inaccurate location but with some useful geographical information, e.g. “in the town of Rome” (Migliaccio and Zampetti 1989), we used their central point to estimate distance to the nearest city but we did not use them to estimate habitat and tree cover in their surroundings. Lastly, records that did not have a location precise enough to deduce any specific geographic information, e.g. “the Italian region of Lombardy”, were discarded.

The Euclidean (straight-line) distance between the detection location and the external limit of the nearest city and nearest large city were calculated using ArcGIS 10.5 (ESRI, Redlands, CA, USA). Cities were visually identified using ArcGIS Online World Imagery map (Copyright ESRI). The distances were then reclassified in distance classes ($\times 10$ km).

Hotspot analysis was performed with Getis-Ord GI^* spatial statistics (Ord and Getis 1995) using the Spatial Statistics Tools of ArcGIS 10.5. Hotspot analysis is frequently used in biological invasion studies (Liang et al. 2014; Shaker et al. 2017), as it enables the detection of spatial clustering patterns using a landscape-scale approach. Getis-Ord GI is an index used to evaluate spatial autocorrelation. Z-scores and P-values indicate whether features, like detection points, are significantly spatially clustered. For statistically significant positive z-scores, the larger the z-score, the greater the clustering of high values (hotspot); for significantly negative z-scores, the smaller the z-score, the greater the clustering of low values (coldspot). For this analysis, we used only the first records in Europe. We used the false discovery rate (FDR) method of Benjamini and Hochberg (1995) to determine the confidence levels of 80%, 90%, 95%, and 99% of their respective GI z-score. This method allows controlling for false discoveries, i.e., the Type I errors.

Population size of cities near detection points was retrieved from the online Wikipedia encyclopedia. For each detection point the population density, i.e. inhabitants per square kilometer, by NUTS 2 region (Nomenclature of Territorial Units for Statistics, level 2) was obtained from Eurostat (<https://ec.europa.eu/eurostat/web/products-datasets/product?code=tgs00024>, assessed on 2019-8-22). The year 2015 was used as reference. We then estimated the ratio between the average population density in the NUTS 2 region where the detection point was located and the population density of the respective country. For the analysis, we considered countries with two or more NUTS 2 regions.

Forest cover and suitable habitat around the point of detection. The percentage of forest cover was estimated using the Tree Cover Density (TCD) of the Copernicus Land Monitoring Service – High Resolution Layer Forest (<https://land.copernicus.eu/pan-european/high-resolution-layers/forests/view>, 2012). TCD provides continuous-scale information on the proportional crown coverage (0–100%) detected per pixel (20 m of spatial resolution) at the European scale, including the following Land Use – Land Cover (LULC) classes: evergreen and deciduous broadleaved, sclerophyllous and coniferous trees, orchards, olive groves, fruit and other tree plantations, agro-forestry areas, transitional woodlands, forests in regeneration, groups of trees within urban areas. The percentage of forest cover was calculated in four buffers (100, 500, 1000, and 5000 m of radius) around the detection points with precise geographical coordinates. The Set Null function was used to remove the no-data values from the databases.

Complementarily, to test the hypothesis that the percentage of tree cover within 100 m around the detection point was similar to that of any other 100 m radius buffer in the surrounding area, we randomly created three additional 100 m radius sampling areas within the 5000 m buffer area. These sampling areas were generated with the con-

straints of its central point being at least 200 m far from the central detection point and 200 m far from the other two random sampled areas. Additionally, any randomly created central point that was located in the ocean or inland water surface was manually removed and replaced. The tree cover around each of the three random central points was calculated in the same manner as around the central detection point.

To estimate the percentage cover of suitable habitats in large cities we used the Urban Atlas database from 2012, from the Copernicus Land Monitoring Service (<https://land.copernicus.eu/local/urban-atlas>). Urban Atlas delivers pan-European comparable LULC data for Functional Urban Areas, i.e. city and its commuting zone (OECD 2012) including 17 urban classes with a Minimum Mapping Unit (MMU) of 0.25 ha. For the selection of suitable habitats, we used as criterion the probable occurrence of trees and retained the following five LULC classes: Green Urban Areas, Sports and Leisure Facilities, Orchards, Forests, and Herbaceous vegetation associations. The percentage of suitable habitats was calculated in three buffers (radius of 500 m, 1000 m, and 5000 m) around the detection points.

Statistical analyses

To estimate the probability of detection in function of the classes of distance to the nearest city we used generalized linear models (GLM) with Binomial distribution and log link function. A model was applied to each feeding guild separately. A Gaussian GLM with log link function was further used to test the effect of body size on the distance to the nearest small city and large city. We also used Gaussian GLM to test temporal trends in detection years and distance of the detection points to the nearest city and nearest large city.

Paired *t*-test statistic was used to compare the percentage tree cover in the 100, 500, 1000, and 5000 m radius buffer. Paired *t*-test statistic was also used to compare the percentage of tree cover in the buffer area (100 m radius) around the detection point and the mean percentage of tree cover in the three buffer areas (100 m radius) sampled at random within the same 5000 m buffer area. One-way ANOVA was used to compare the percentage of tree cover in the buffer area (100 m radius) per feeding guilds. The relationship between the average population density per NUTS 2 and the country population density was tested by paired *t*-test statistics.

Results

Number of first detection, and distribution in Europe, of non-native forest insects

We retrieved data from 133 non-native insect species, belonging to six feeding guilds. Sap feeders (order Hemiptera) were the most represented guild (40% of the cases), followed by bark beetles and woodborers (29%). Defoliators, gall makers, and seed and fruit feeders represented 14%, 10%, and 7% respectively. Only

one species was a root feeder, which was not used for comparisons between feeding guilds due to its low representativeness.

In total 508 first country-specific records were retrieved, from 38 regions (including mainland and separated islands) and 25 countries (Suppl. material 1: Table S1). The top 10 non-native species most frequently detected were reported from 12 or more different countries: *Belonochilus numenius*, *Cameraria ohridella*, *Corythucha ciliata*, *Cydalima perspectalis*, *Dasineura gleditchiae*, *Dryocosmus kuriphilus*, *Halyomorpha halys*, *Leptoglossus occidentalis*, *Metcalfa pruinosa*, and *Obolodiplosis robiniae*. On the other hand, 57 non-native species were reported in just one country. More than 87% of first detections resulted from occasional visual observations, mainly made by scientists, naturalists, or forest technicians. Only a few first reports (11%) mentioned that observations were due to planned survey or trapping. Three cases were interceptions in ports. They were excluded from spatial analysis.

From our data, 137 cases were first records for Europe (mainland and islands). Italy registered the highest number of first records in Europe (36), followed by Spain (19), France (18), and Portugal (10). Eight first detections were made in islands of the Mediterranean Sea (Sicily, Corsica, and Balearics) or the Atlantic Ocean (the Canaries, Madeira, and the Azores). UK and Germany had intermediate values of 8 and 7, respectively. All other cases were distributed among 19 other countries.

The hotspot analysis of first records in Europe revealed an uneven distribution at the European scale. Several hotspot areas with a Getis-Ord G_i^* Z-score greater than 3.80 (p -value < 0.01) were identified in continental Europe (Fig. 1). The largest concentration of hotspot clusters was located in coastal areas of the Mediterranean near large cities of Italy, southern France, Catalonia and Andalucía in Spain, and along the Atlantic coast, e.g. in Lisbon, Vigo in Galicia, Amsterdam, and London. Hotspots of first detection were also found around Switzerland (Zurich, Strasbourg, and Stuttgart) and in Hungary around Budapest. Hotspots also appeared in the islands of Corsica, Sicily, Cyprus, Madeira, the Azores, and the Canaries (Fig. 1).

Distance to nearest cities

About 64% of first records in Europe occurred in large cities and 89% in cities or their suburban areas. Similarly, 62% of country specific detections were reported in large cities and 88% in cities or their suburban areas (i.e. within 10 km distance from their limit). The probability of first detection decreased sharply with distance from the nearest city or large city (Fig. 2). When fitting an exponential decline, the rate of decrease was on average (\pm SE) higher around small cities (-0.08 ± 0.016) compared with large cities (-0.02 ± 0.003). The probability of occurrence within the first two classes distances, i.e. within city (class 0) and up to 10 km distance (class 1), was $92 \pm 2\%$ for sap suckers and seed and fruit seeders, $88 \pm 4.1\%$ for gall makers, $85 \pm 4.1\%$ for defoliators and $82 \pm 3.8\%$ for bark & wood borers. However, differences between guilds were not significant (Wald $\chi^2 = 7.461$, $p = 0.113$). Body size was not a significant predictor of the distance of first detection either

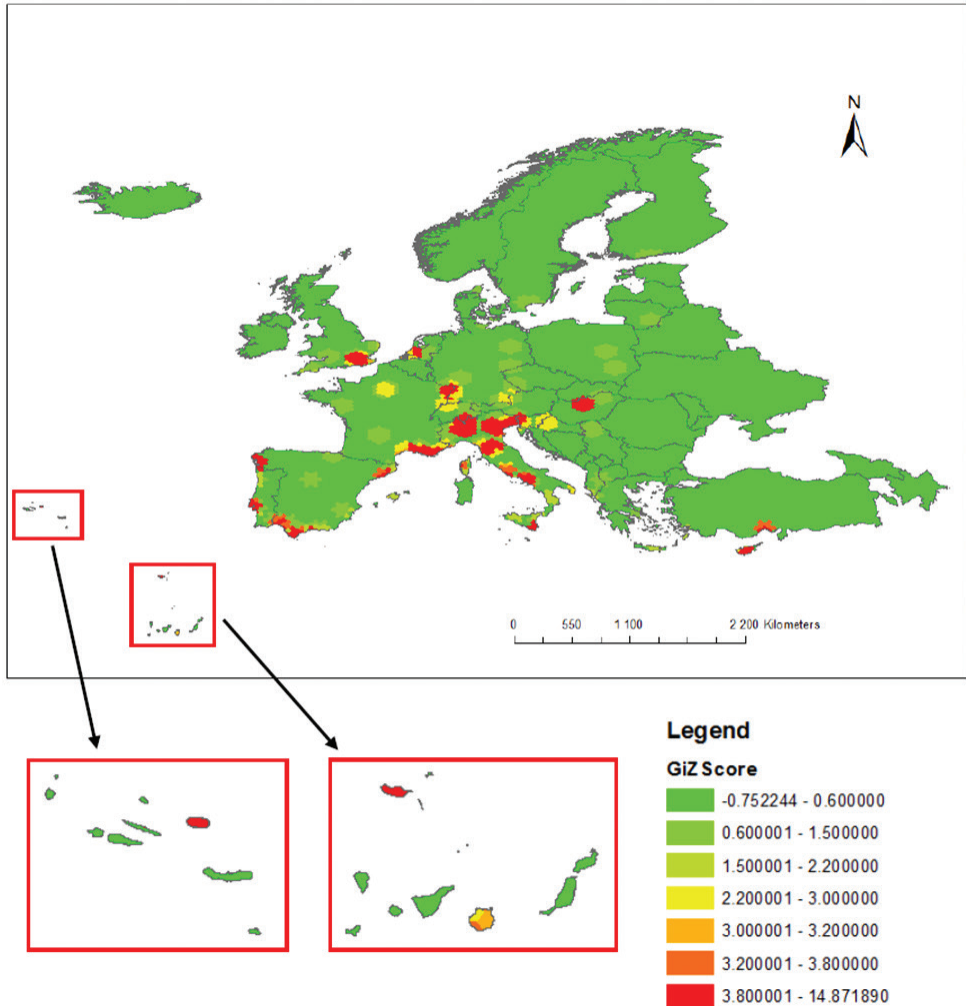


Figure 1. Hotspots map of first detection points in Europe of non-native insects feeding on woody plants, recorded since 1950. The Getis-Ord GI^* (GiZ Scores) are provided to indicate different levels of clustering of either high values (Z-score positive, hotspot) or low values (Z-score negative, coldspot). The respective p -values are: Z Score > 3.8 , p -value < 0.01 ; ZScore $[3.2, 3.8]$, p -value < 0.05 ; ZScore $[3.0, 3.2]$, p -value < 0.1).

from small city (Wald $\chi^2 = 0.128$, $df = 1$, $p = 0.720$) or large city (Wald $\chi^2 = 0.559$, $df = 1$, $p = 0.455$).

In 69% of the cases the population of the nearest city to the detection point, i.e. located within a 20 km distance, was over 100 000 people, and in 35% of the cases above 500 000 people (Fig. 3). Average population density was 128 ± 18 people/km² at the country level and 697 ± 172 people/km² in the NUTS2 region with first occurrence (paired t -test mean difference = -570 ± 163 , $p = 0.002$, $N = 28$). The average

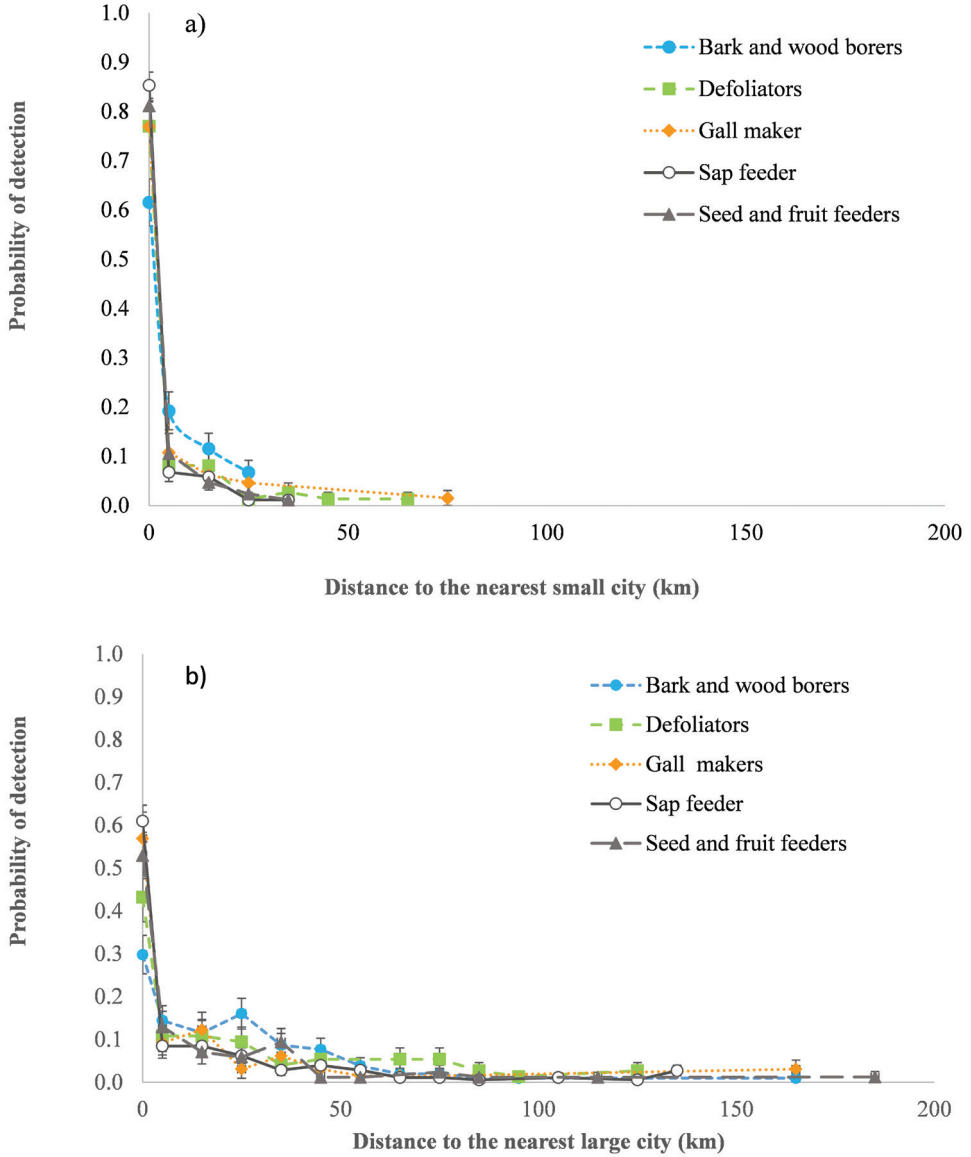


Figure 2. Probability (mean \pm SE) of first detection of non-native insect feeding on woody plants in Europe (estimated by GLM) in function of distance class (in 10 km) to **a)** the nearest city and **b)** the nearest large city.

population density in NUTS2 region of the detection point was on average 6.2 ± 1.0 times higher than the population density of the respective country (Fig. 4). Highest invaded NUTS 2 to country ratios (above tenfold) were observed for Hungary (21.6), Austria (19.5), Bosnia and Herzegovina (12.5), UK (11.5), Finland (11.1), Belgium (10.7), and Norway (10.3) (Fig. 4).

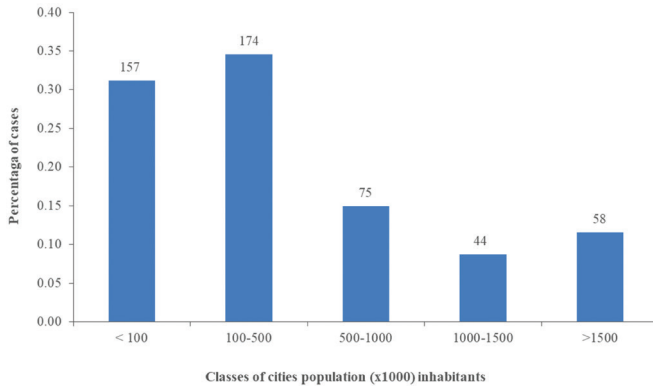


Figure 3. Percentage and number of first detections of non-native forest insect species by class of city population (up to 20 km distance).

Type of recipient habitat for non-native species

Urban habitat was the most frequently observed land cover type around first detection points, accounting for 74% of the cases. Urban habitats reported were highly diverse, including schoolyards, university campuses and experimental stations, trees in airport and port areas, railway stations, industrial areas, urban arboreta, botanical gardens, public parks, zoos, and street trees. Arboreta, botanical gardens, gardens, and urban parks were the most often reported cases in cities (60% of the cases with site information). Only 11% of the cases were found in forest habitats. In 4% of the cases these forests were close to cities (i.e. at less than 10 km), while the other 7% were in forests far from cities. Other cases were reported in nurseries (4%) and rural landscapes (11%).

The percentage of first detection in the urban habitat significantly varied with the insect feeding guild ($\chi^2 = 19.519$; $p < 0.001$). Sap suckers, gall makers, and seed and fruit seeders were more frequently found in urban habitats, 80%, 78%, and 81%, respectively, than defoliators (69%) and bark & wood borers (58%) (Fig. 5). Only a few detections were found in nurseries (Fig. 5).

Insects feeding on broadleaves were more frequently found for the first time in urban habitat (76%) than species feeding on conifers (59%). Still, the difference was not significant ($\chi^2 = 1.130$, $p = 0.288$). Polyphagous species, feeding on both conifers and broadleaves, were reported in nine cases only, but six of these cases (67%) were also in urban areas.

Temporal trend of detection

Temporal trend shows an exponential increase in the number of first records with decade, with a steep increment since the 1990s (Fig. 6). However, overall mean distances

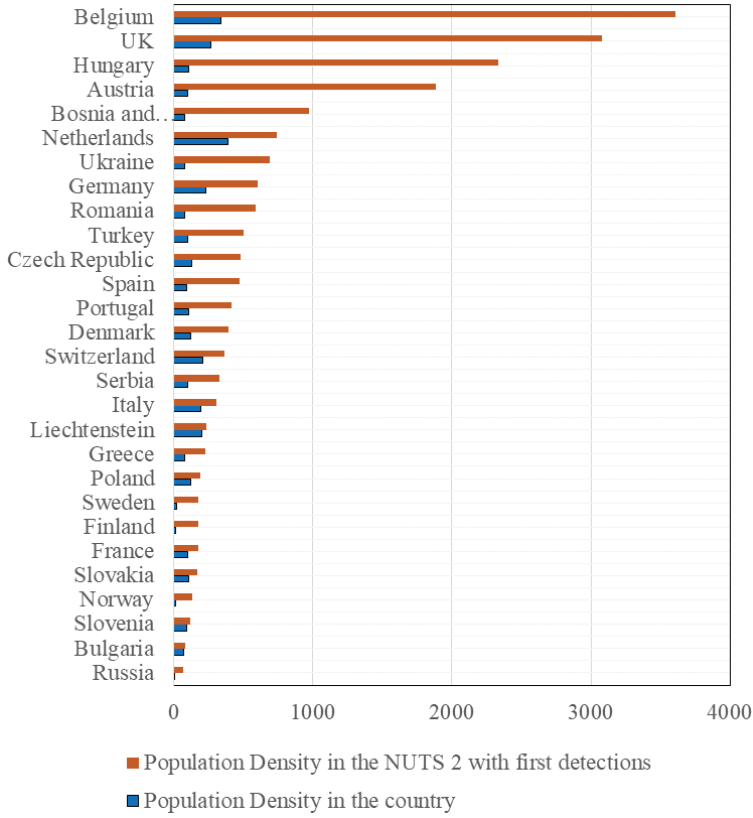


Figure 4. Average population density of the NUTS 2 regions where the non-native forest insect species were first detected and of the corresponding country (inhabitants per km²).

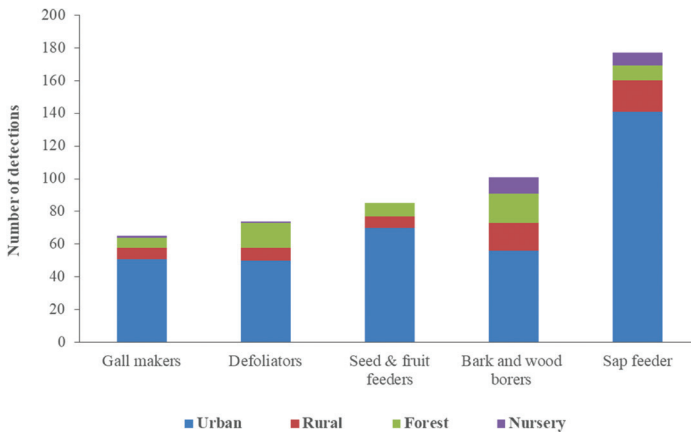


Figure 5. Distribution of first detections in Europe of non-native insects feeding on woody plants per feeding guild and habitat type.

to the nearest small city (Wald $\text{Chi}^2 = 0.291$, $\text{df} = 1$, $p = 0.589$), or large city (Wald $\text{Chi}^2 = 0.479$, $\text{df} = 1$, $p = 0.489$) did not vary with time (Fig. 6).

Land cover composition of recipient areas

The mean percentage of tree cover at 100 and 500 m around the detection point was $17.1\% \pm 1.3$ and $17.2\% \pm 1.1$, respectively, ranging from 1 to 85%, with no differences between these two buffer sizes (t -test = 0.158, $\text{df} = 307$, $p = 0.875$). Considering these buffer radii, 55% of the detection points were in sites with only 10% or less of tree cover, and in 73% of the cases in sites with less than 20% of tree cover. However, within a buffer of 1000 m radius around the detection point, the mean proportion of tree cover was significantly higher ($31.8\% \pm 1.9$) than at 100 m (t -test = 14.6, $\text{df} = 307$, $p < 0.001$). Again, at 5000 m radius buffer size, the proportion of tree cover was higher ($35.4\% \pm 1.0$) than at 100 m (t -test = 14.5, $\text{df} = 307$, $p < 0.001$). Within the largest buffer radii, i.e. 1000 m and 5000 m around the detection point, there were no difference among feeding guilds for the percentage of tree cover ($F_{4,300} = 2.179$, $p = 0.071$, and $F_{4,300} = 1.928$, $p = 0.106$, respectively for 1 km and 5 km). However, at 100 and 500 m radius, we found differences among feeding guilds for the proportion of tree cover around the detection point ($F_{4,300} = 3.065$, $p = 0.017$ and $F_{4,300} = 3.132$, $p = 0.015$, respectively for 100 and 500 m). In both cases, defoliators tend to occur in sites with higher percentage of tree cover (which was 27% and 25%, respectively for 100 and 500) than for other feeding guilds.

A complementary analysis concerning the estimation of the percentage cover of suitable habitats (following five LULC classes: Green Urban Areas, Sports and Leisure

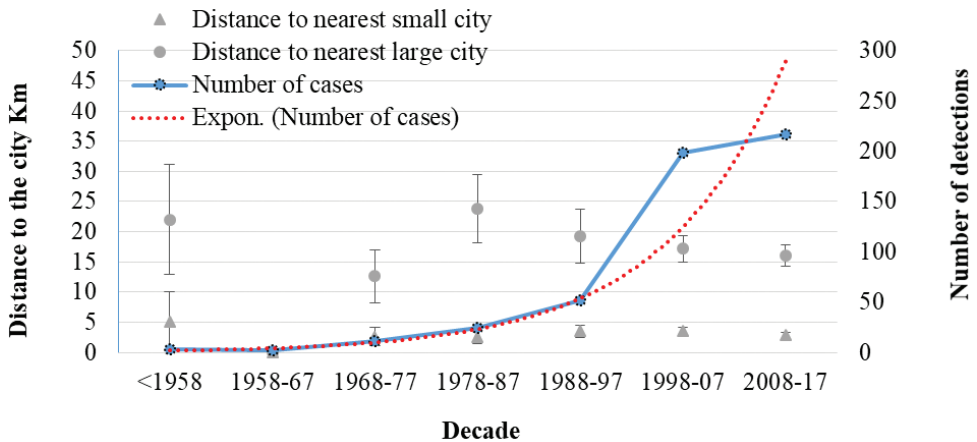


Figure 6. Temporal trend of first detection in Europe of non-native insects feeding on woody plants and mean distance to the nearest small and large cities.

Facilities, Orchards, Forests, and Herbaceous vegetation associations) in urban areas of large cities was conducted in 94 cases. The proportion of suitable habitat was on average $9.7\% \pm 1.1$, $9.0\% \pm 0.6$, and $9.0\% \pm 0.6$, for 500 m, 1000 m and 5000 m buffer radius, respectively. There were no significant differences between buffer sizes.

The comparison with surrounding landscape showed that the percentage of tree cover within a 100 m buffer radius around the detection point (focal point) was slightly, but significantly (t -test mean difference = -4.937 ± 1.471 , $p = 0.001$), lower than tree cover in three buffer areas of the same radius randomly sampled within a distance of 5000 m ($17\% \pm 1.3$ vs $22\% \pm 1.2$).

Discussion

Using European data on first detection records of non-native insect species feeding on woody plants since 1950, we could confirm the trend for an exponential increase with time. However, the most striking outcome of the survey is that 88% of first detections were made in cities and, for the majority, in large cities (62% in total, 70% of urban records). Moreover, the number of detections decreased dramatically in the first 10 km outside the city (Fig. 2). Although trees were always present in the urban area around the detection point, the percentage of tree cover was moderate, being less than 20% in general.

Higher amount of non-native forest pests arriving in cities

The proximity of main transport facilities (e.g. airports and ports) and the high density of people make cities under high propagule pressure, i.e. high frequencies of introductions of non-native organisms, plants or animals (Gaertner et al. 2016; Rassati et al. 2016). As arrivals are expected to occur in ports and airports, trees near these international transport facilities are particularly sensitive. Similar human-assisted introductions of non-native forest pests have been reported in other studies (Yemshanov et al. 2013), and analogous trends have been found in other continents. For example, the emerald ash borer, native to Asia, was first introduced and became established in North America in the highly urbanized Detroit area (Poland and McCullough 2006).

Several records specifically documented first occurrences in urban areas near transport facilities and could identify the pathways. For example, the first infestation of *A. glabripennis* in the Netherlands, in 2010, was found on native host plants, in an industrial area in the city of Almere, and was related to pallets used for transport of industrial machinery (Loomans et al. 2013). The long horn beetle *Callidiellum rufipenne* (Coleoptera, Cerambycidae), attacking cypress trees was first reported on a European host species, *Juniperus communis*, in Italy in an experimental station, next to the harbor of Porto de Ravenna in which large amounts of transported wood accumulated (Cam-

padelli and Sama 1988). The leaf miner, *Parectopa robinella*, was first found close to the Milan airport in Italy (Whitebread 1989).

We may argue that first occurrences occurred mostly in urban areas because more researchers are living in these areas and are, thus, more likely to detect recently introduced forest pests. In some cases, researchers found new records within their own faculty campus (e.g. Del Estal et al. 1998; Garcia et al. 2013). This pattern could be also explained by the higher visibility of insect pests on single trees, along streets or in urban parks, than on nearby stands of forests. In fact, we found that more than 87% of first detections resulted from occasional observations with no planned survey or trapping methods targeting specific species.

Presence of suitable habitats for non-native forest pests to establish in cities

Arrival does not necessarily imply successful establishment of introduced species. The establishment of a species in a new area further needs suitable habitat and resources, depending on its ecological niche. In fact, it is estimated that only a minor proportion of new arrivals results in successful establishment in a new region (Mack et al. 2000). This is evident when the frequencies of interceptions are compared with the number of species established (Brockerhoff et al. 2006b, 2014; Eschen et al. 2015). The presence of suitable host trees is an essential prerequisite for new forest pest species to become established in a given area. Reports in urban areas are rather diverse. Examples from the studied reports include schoolyards, public gardens (EPPO 2019); zoological parks, (e.g. Franco et al. 2017), urban parks, botanical gardens (e.g. *Penestrangia apicalis* in France; Nickel et al. 2013), arboreta inside university campuses (e.g. Del Estal et al. 1998), trees along avenues and squares, or trees near airports or seaports (e.g. Campadelli and Sama 1988). However, a striking finding of the present study is that tree cover could be very limited in the exact site where species are found. Detection points were located in areas with little proportion tree cover, on average 17% but in more than 30% of the cases, the proportion of tree cover was less than 5%. Further, for sites located in large cities, the proportion of suitable habitat likely to contain trees (using Urban Atlas habitat categories) represented on average less than 10%. This suggests that a small size of suitable habitat, or even a few street trees, can be enough for forest pest species to establish in urban areas and that they do not need large natural or rural forests. For example, *Macrohormotoma gladiata*, a tropical Asian psyllid, was first found in Italy on *Ficus* trees along avenues of Naples (Pedata et al. 2012). More generally, the large presence of non-native trees planted as ornamentals in cities is likely to allow the establishment of non-native insects associated to these woody plants in the native range. Actually, about half of the exotic insect species of woody plants that have been introduced to Europe are still confined to the original, exotic host tree and have not switched to another host plant (Roques 2010).

However, we did find some differences in habitat requirements according to feeding guild. Defoliators seemed to be more demanding in terms of the presence of a cer-

tain density of tree cover. Bark and wood borers were more frequently detected outside urban areas than other guilds. On the other extreme, gall makers, sap suckers, and seed and fruit feeders were mostly found (more than 90% of the cases) in urban areas. In some cases, these species occurred in circumstances in which only a small number of trees of a specific host was present. For example, the invasive gall wasp *Epicbrysocharis burwelli*, which is known to form galls only on the lemon-scented gum, *Corymbia citriodora* (Myrtaceae), was found in an urban park and the Zoo in Lisbon, where only a few host trees of that particular host species were present (Franco et al. 2016). Furthermore, within hundreds of kilometers around the central point of detection, there were no plantations of lemon-scented gum, and only isolated or small clusters of trees in urban gardens or arboreta, could be found. Therefore, as seen in *E. burwelli*, the presence of a small number of host trees may be sufficient for a new insect species to establish itself. This may be particularly true when the microhabitat used by the insect on the host tree is small, as normally occurs for gall makers, sap suckers, and seed and fruit seeder. For these insect species, the entire tree or a few trees may provide sufficient habitat for a population to develop. A number of these species can reproduce parthenogenetically, e.g. hemipteran sap suckers or seed chalcids (Auger-Rozenberg and Roques 2012), or are inbreeders, e.g. seed beetles, which may limit Allee effects arising from mate-finding failure (Liebhold et al. 2016), thus explaining their establishment success on a few isolated urban trees (Brockerhoff and Liebhold 2017).

Cities may facilitate the establishment of tree pests because of their large diversity of tree genera and species, giving non-native pests a better chance of finding a suitable host tree (Liebhold et al. 2018). Most cities in North America and Europe have street tree diversity concentrated in few tree genera and species, mostly broadleaves, like *Platanus*, *Acer*, *Tilia*, and *Fraxinus*, but also a number of non-native woody ornamentals. Still, a large diversity of tree species and shrubs is found in cities when urban parks and gardens are considered (Raupp et al. 2006; Sjöman et al. 2012). An archetype of such diversity is found in botanical gardens, where a large collection of species is present, which are mostly non-native tree species. In fact, urban gardens and arboreta may accumulate hundreds of tree species in only a few hectares. Examples from the records that we retrieved in this study, are Tapada da Ajuda in Lisbon that harbors more than 300 tree species (Vasconcelos et al. 2013) where *T. peregrinus* was found for the first time in Portugal (Garcia et al. 2013), or the Gibraltar Botanic Gardens, with an area of only 6 ha which holds a collection of over 1700 species of plants, largely non-native, where the cycadellid *Sophonia orientalis* was first found in Europe (Wilson et al. 2011). The bark beetle *Ambrosiodmus rubricollis* (Coleoptera, Curculionidae), was found in *Aesculus hippocastanum* in a botanical garden of Padova, Italy (Faccoli et al. 2009). Interestingly, broadleaves are more abundant and diverse in cities than conifers (Raupp et al. 2006), which possibly explains the result from our study where the probability of a non-native insect being detected for the first time in a city was higher for insect species feeding on broadleaves than on conifers.

In several cases, species were found near cities, i.e. in suburban areas. These areas are often characterized by heterogeneous landscapes, where gardens, orchards, forest

fragments, and many rural habitats are present and tree abundance and diversity is greatly increased. In fact, the proportion of tree cover increased from 17% in urban areas around detection points to 32% and 35% in buffers of 1000 m and 5000 m radius, respectively. Thus, suburban areas could further facilitate the establishment of non-native forest pests. In only 4% of the cases (20 out of 508), non-native species were detected in nurseries. For these particular cases, detections occurred probably before establishment, which would also facilitate eradication attempts.

Cities may also offer better conditions for non-native species establishment due to their more suitable climate, in particular warmer temperatures resulting from the heat island effect (Debbage and Shepherd 2015). For example, increasing temperature caused by impervious surface was observed to significantly increase insect fecundity and contribute to higher population growth (Dale and Frank 2014). This would be particularly relevant for cities in temperate regions receiving non-native species that originate from subtropical countries. In addition, urban trees are frequently exposed to environmental stress factors, such as water stress, poor soil conditions and pollution (Sjöman and Nielsen 2010). In such conditions, trees can be more vulnerable to some non-native insect species, in particular the secondary pests feeding on declining trees. Contrarily, irrigation and fertilization may render urban trees vulnerable to other guilds such as defoliators, sap suckers, and gall makers. An example of better suitability of cities is the distribution of the gall midge *Obolodiplosis robiniae* affecting *Robinia pseudoacacia* in Slovakia, for which greater infestations were found within cities than in the countryside (Tóth et al. 2009). Observations that invasive species are more prevalent in cities than in rural areas because of environmental stress were also reported for other groups of organisms like plants (Gaertner et al. 2016)

Where are first detections in Europe occurring?

At a larger spatial scale, hotspot analyses clearly showed a clustered pattern of first detection records in Europe. Most hotspots for the first detection of non-native forest pests were found along the coastal regions of Europe, from the Mediterranean coast of Italy, France, and Spain to the Atlantic coast, from Portugal to the Netherlands (Fig. 1). They clearly match with the location of major cargo seaports, close to large cities (e.g. Genova, Napoli, Venice, Ravenna, Marseille, Barcelona, Lisbon, Vigo, London, and Amsterdam), where the intense flow of imported goods provides more opportunities for non-native forest insect introduction. The majority of the busiest cargo seaports in Europe (excluding Russia) by total cargo volume (Kiprof 2018) were located in the hotspot clusters or their vicinity (Rotterdam in the Netherlands, Antwerp in Belgium, Marseilles/Fos, La Rochelle, and Le Havre in France, Botas in Turkey, Valencia in Spain, and Trieste and Genova in Italy).

Still, two other hotspots of first detections were identified, one in Central Europe, from southern Germany, to northern Italy, and the other in Eastern Europe. These

areas coincide with intense industrial regions and a number of river ports. Their proximity to Middle East and Asia, from where more than 40% of the non-native species from our study originate, may further suggest a pathway of progression from eastern regions. Some particular areas may also reflect a concentration of forest entomologists, but this is difficult to verify.

Conclusions

The economic impact of invasive forest insect pests is huge on both forest and urban environments (Poland and McCullough 2006; Boyd et al. 2013). Early detection is the main prerequisite for successful eradication. From the present study, we conclude that surveillance and monitoring for invasive forests pests should be focused on trees in urban and suburban areas. More especially, we recommend that surveys give priority to urban parks with high tree diversity, such as botanical gardens, arboreta, and woodlots near airports and seaports. These areas should concentrate the attention of forest protection authorities and be dedicated to structured surveys and trapping networks. Recently, trapping methods using multiple lures have been shown effective for early detection of non-native forest moths and beetles (Brockerhoff et al. 2013; Rassati et al. 2015; Fan et al. 2019) and, thus, should be used more systematically. Another way forward is to promote the use of urban trees as sentinels for monitoring the introduction of non-native forest pests and diseases (Paap et al. 2017), with the increasing awareness and involvement of citizens, who could use smartphone applications for day-to-day surveillance of urban tree health (Marzano et al. 2015). Several factors can contribute to urban areas becoming hotspots for the establishment of non-native forest pests. The high population density and vicinity to main international transport facilities (seaports and airports) likely enable the arrival of new species. However, it is the diversity of host tree species, scattered over multiple urban green spaces, and favorable microclimatic conditions (warmer, drier) that can ultimately favor the establishment of non-native insect species in cities. Still, other studies are needed for an accurate assessment of the relative importance of these factors.

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References

- Auger-Rozenberg MA, Roques A (2012) Seed wasp invasions promoted by unregulated seed trade affect vegetal and animal biodiversity. *Integrative Zoology* 7: 228–246. <https://doi.org/10.1111/j.1749-4877.2012.00308.x>
- Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society, Series B (Methodological)* 57(1): 289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>
- Boyd IL, Freer-Smith PH, Gilligan CA, Godfray HC (2013) The consequence of tree pests and diseases for ecosystem services. *Science* 342: 1235773. <https://doi.org/10.1126/science.1235773>
- Brockhoff EG, Liebhold AM (2017) Ecology of forest insect invasions. *Biological Invasions* 19(11): 3141–3159. <https://doi.org/10.1007/s10530-017-1514-1>
- Brockhoff EG, Liebhold AM, Jactel H (2006a) The ecology of forest insect invasions and advances in their management. *Canadian Journal of Forest Research* 36(2): 263–268. <https://doi.org/10.1139/x06-013>
- Brockhoff EG, Bain J, Kimberley M, Knížek M (2006b) Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. *Canadian Journal of Forest Research* 36(2): 289–298. <https://doi.org/10.1139/x05-250>
- Brockhoff EG, Kimberley M, Liebhold AM, Haack RA, Cavey JF (2014) Predicting how altering propagule pressure changes establishment rates of biological invaders across species pools. *Ecology* 95: 594–601. <https://doi.org/10.1890/13-0465.1>
- Brockhoff EG, Suckling DM, Roques A, Jactel H, Branco M, Twidle AM, Mastro VC, Kimberley MO (2013) Improving the efficiency of lepidopteran pest detection and surveillance: constraints and opportunities for multiple-species trapping. *Journal of Chemical Ecology* 39(1): 50–58. <https://doi.org/10.1007/s10886-012-0223-6>
- Campadelli G, Sama G (1988) Prima segnalazione per l'Italia di un cerambicide giapponese: *Callidiellum rufipenne* Motschulsky. *Bollettino dell'Istituto di Entomologia "Guido Grandi" dell'Università di Bologna* 43: 69–73.
- Carter M, Smith M, Harrison R (2010) Genetic analyses of the Asian longhorned beetle (Coleoptera, Cerambycidae, *Anoplophora glabripennis*), in North America, Europe and Asia. *Biological Invasions* 12(5): 1165–1182. <https://doi.org/10.1007/s10530-009-9538-9>
- Chakraborty S, Whitehill JG, Hill AL, Opiyo SO, Cipollini D, Herms DA, Bonello P (2014) Effects of water availability on emerald ash borer larval performance and phloem phenolics of Manchurian and black ash. *Plant, Cell & Environment* 37(4): 1009–1021. <https://doi.org/10.1111/pce.12215>
- Constantinescu C, Mattoo A, Ruta M (2015) The Global Trade Slowdown: Cyclical or Structural? IMF Working Paper No. 15/6. 2015. <https://doi.org/10.5089/9781498399135.001>
- Dale AG, Frank SD (2014) Urban warming trumps natural enemy regulation of herbivorous pests. *Ecological Applications* 24(7): 1596–1607. <https://doi.org/10.1890/13-1961.1>
- Debbage N, Shepherd JM (2015) The urban heat island effect and city contiguity. *Computers, Environment and Urban Systems* 54: 181–194. <https://doi.org/10.1016/j.compenurb-sys.2015.08.002>

- Del Estal P, Soria S, Viñuela E (1998) Nota de la presencia en España de *Dasineura leditchiae* (Osten Sacken), sobre acacia de tres espinas. *Boletín de Sanidad Vegetal Plagas* 24: 225–230.
- EPPO (2019) EPPO Global Database. <https://gd.eppo.int/reporting/article-6064>
- Eschen R, Roques A, Santini A (2015) Taxonomic dissimilarity in patterns of interception and establishment of alien arthropods, nematodes and pathogens affecting woody plants in Europe. *Diversity and Distributions* 21(1): 36–45. <https://doi.org/10.1111/ddi.12267>
- Faccoli M, Frigimelica G, Mori N, Petrucco Toffolo E, Vettorazzo M, Simonato M (2009) First record of *Ambrosiodmus* (Hopkins, 1915) (Coleoptera: Curculionidae, Scolytinae) in Europe. *Zootaxa* 2303: 57–60. <https://doi.org/10.11646/zootaxa.2303.1.4>
- Fan JT, Denux O, Courtin C, Bernard A, Javal M, Millar JG, Hanks LM, Roques A (2019) Multicomponent blends for trapping native and exotic longhorn beetles at potential points-of-entry and in forests. *Journal of Pest Science* 92: 281–297. <https://doi.org/10.1007/s10340-018-0997-6>
- Franco JC, Garcia A, Branco M (2016) First report of *Epichrysocharis burwelli* in Europe, a new invasive gall wasp attacking eucalypts. *Phytoparasitica* 44(4): 443–446. <https://doi.org/10.1007/s12600-016-0539-9>
- Garcia A, Figueiredo E, Valente C, Monserrat VJ, Branco M (2013) First record of *Thaumastocoris peregrinus* in Portugal and of the neotropical predator *Hemerobius bolivari* in Europe. *Bulletin of Insectology* 66(2): 251–256.
- Gaertner M, Larson BM, Irlich UM, Holmes PM, Stafford L, van Wilgen BW, Richardson DM (2016) Managing invasive species in cities: a framework from Cape Town, South Africa. *Landscape and Urban Planning* 151: 1–9. <https://doi.org/10.1016/j.landurbplan.2016.03.010>
- Hermes DA, McCullough DG (2014) Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. *Annual Review of Entomology* 59: 13–30. <https://doi.org/10.1146/annurev-ento-011613-162051>
- Hulme P, Roy D (2010) DAISIE and arthropod invasions in Europe. *BioRisk* 4(1): 1–3. <https://doi.org/10.3897/biorisk.4.41>
- Hurley BP, Garnas J, Wingfield MJ, Branco M, Richardson DM, Slippers B (2016) Increasing numbers and intercontinental spread of invasive insects on eucalypts. *Biological Invasions* 18(4): 921–933.
- Katsanevakis S, Deriu I, D'amico F, Nunes AN, Pelaez Sanchez S, Crocetta F, Arianoutsou M, Bazos I, Christopoulou A, Curto G, Delipetrou P, Kokkoris Y, Panov VE, Rabitsch W, Roques A, Scalera R, Shirley SM, Tricarico E, Vannini A, Zenetos A, Zervou S, Zikos A, Cardoso AC (2015) European Alien Species Information Network (EASIN): supporting European policies and scientific research. *Management of Biological Invasions* 6: 147–157. <https://doi.org/10.3391/mbi.2015.6.2.05>
- Kiprop V (2018) The busiest cargo ports in Europe. *WorldAtlas*. [Mar. 1, 2018] <http://worldatlas.com/articles/the-busiest-cargo-ports-in-europe.html>
- Kishi Y (1995) The Pine Wood Nematode and the Japanese Pine Sawyer. *Forests Pests in Japan*, No. 1. Thomas Co., Tokyo, 302 pp.
- Liang L, Clark JT, Kong N, Rieske LK, Fei S (2014) Spatial analysis facilitates invasive species risk assessment. *Forest Ecology and Management* 315(1): 22–29. <https://doi.org/10.1016/j.foreco.2013.12.019>

- Liebhold AM, Berec L, Brockerhoff E G, Epanchin-Niell RS, Hastings A, Herms DA, Kean JM, McCullough DG, Suckling DM, Tobin PC, Yamanaka T (2016) Eradication of invading insect populations: from concepts to applications. *Annual Review of Entomology* 61: 335–352. <https://doi.org/10.1146/annurev-ento-010715-023809>
- Liebhold AM, Halverson JA, Elmes GA (1992) Gypsy moth invasion in North America: a quantitative analysis. *Journal of Biogeography* 1992: 513–520. <https://doi.org/10.2307/2845770>
- Liebhold AM, Yamanaka T, Roques A, Augustin S, Chown SL, Brockerhoff EG, Pyšek P (2018) Plant diversity drives global patterns of insect invasions. *Scientific Reports* 8(1): 12095. <https://doi.org/10.1038/s41598-018-30605-4>
- Loomans AJM, Wessels-Berk B, Copini P, Mentink NJB, de Hoop MB, den Hartog WGSA (2013) Import-inspections, surveys, detection and eradication of the longhorn beetles *Anoplophora chinensis* and *A. glabripennis* in the Netherlands. *Journal of Entomological and Acarological Research* 45 (no. s1): 1–8.
- Mack RN, Simberloff D, Mark Lonsdale W, Evans H, Clout M, Bazzaz, FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10(3): 689–710. [https://doi.org/10.1890/1051-0761\(2000\)010\[0689:BICEGC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2)
- Marzano M, Dandy N, Bayliss HR, Porth E, Potter C (2015) Part of the solution? Stakeholder awareness, information and engagement in tree health issues. *Biological Invasions* 17(7): 1961–1977. <https://doi.org/10.1007/s10530-015-0850-2>
- Meineke EK, Dunn RR, Sexton JO, Frank SD (2013) Urban warming drives insect pest abundance on street trees. *PloS ONE* 8(3): e59687. <https://doi.org/10.1371/journal.pone.0059687>
- Migliaccio E, Zampetti MF (1989) *Megabruchidius dorsalis* e *Acanthoscelides pallidipennis*, specie nuove per la fauna Italiana. *Bollettino dell'Associazione Romana di Entomologia* 43: 63–69.
- Nickel H, Callot H, Knop E, Kunz G, Schrameyer K, Sprick P, Walter S (2013) *Penestragania apicalis* (Osborn & Ball, 1898), another invasive Nearctic leafhopper found in Europe (Hemiptera: Cicadellidae, Iassinae). *Cicadina* 13: 5–15.
- OECD (2012) Redefining urban: a new way to measure metropolitan areas: Functional Urban Areas in OECD countries: 148. <http://www.oecd.org/regional/redefiningurbananewway-tomeasuremetropolitanareas.htm>
- Ord JK, Getis A (1995) Local spatial autocorrelation statistics: distributional issues and an application. *Geographical Analysis* 27(4): 286–306. <https://doi.org/10.1111/j.1538-4632.1995.tb00912.x>
- Paap T, Burgess TI, Wingfield MJ (2017) Urban trees: bridge-heads for forest pest invasions and sentinels for early detection. *Biological Invasions* 19(12): 3515–3526. <https://doi.org/10.1007/s10530-017-1595-x>
- Pedata PA, Burckhardt D, Mancini D (2012) Severe infestations of the jumping plant-louse *Macrohomonotoma gladiata*, a new species for Italy in urban *Ficus* plantations. *Bulletin of Insectology* 65(1): 95–98.
- Poland TM, McCullough DG (2006) Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. *Journal of Forestry* 104(3): 118–124.

- Rassati D, Faccoli M, Petrucco Toffolo E, Battisti A, Marini L (2015) Improving the early detection of alien wood-boring beetles in ports and surrounding forests. *Journal of Applied Ecology* 52(1): 50–58. <https://doi.org/10.1111/1365-2664.12347>
- Rassati D, Faccoli M, Haack RA, Rabaglia RJ, Petrucco Toffolo E, Battisti A, Marini L (2016) Bark and ambrosia beetles show different invasion patterns in the USA. *PLoS ONE* 11(7): e015851. <https://doi.org/10.1371/journal.pone.0158519>
- Raupp MJ, Cumming AB, Raupp EC (2006) Street tree diversity in eastern North America and its potential for tree loss to exotic borers. *Arbiculture and Urban Forestry* 32(6): 297–304.
- Robinet C, Roques A, Pan H, Fang G, Ye J, Zhang Y, Sun J (2009) Role of human-mediated dispersal in the spread of the pinewood nematode in China. *PLoS ONE* 4(2): e4646. <https://doi.org/10.1371/journal.pone.0004646>
- Roques A (2010) Alien forest insects in a warmer world and a globalized economy: impacts of changes in trade, tourism and climate on forest biosecurity. *New Zealand Journal of Forestry* 40: 77–94. [Supplement]
- Roques A (2011) Invasive patterns of alien terrestrial invertebrates in Europe. In: Pimentel D (Ed.) *Biological Invasions – Economic and Environmental Costs of Alien Plant, Animal and Microbe Species* (2nd edn). CRC Press, Boca Raton, New York and London, 199–226. <https://doi.org/10.1201/b10938-13>
- Roques A, Kenis M, Lees D, Lopez-Vaamonde C, Rabitsch W, Rasplus JY, Roy DB (2010) Alien terrestrial arthropods of Europe. *BioRisk* 4: 1–1028. <https://doi.org/10.3897/biorisk.4.42>
- Roques A, Auger-Rozenberg M-A, Blackburn TM, Garnas JR, Pyšek P, Rabitsch W, Richardson DM, Wingfield MJ, Liebhold AM, Duncan RP (2016) Temporal and interspecific variation in rates of spread for insect species invading Europe during the last 200 years. *Biological Invasions* 18(4): 907–920. <https://doi.org/10.1007/s10530-016-1080-y>
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications* 8: 14435. <https://doi.org/10.1038/ncomms14435>
- Shaker RR, Yakubov AD, Nick SM, Vennie-Vollrath E, Ehlinger TJ, Forsythe KW (2017) Predicting aquatic invasion in Adirondack lakes: a spatial analysis of lake and landscape characteristics *Ecosphere* 8(3): 1–25. <https://doi.org/10.1002/ecs2.1723>
- Sjöman H, Nielsen AB (2010) Selecting trees for urban paved sites in Scandinavia—a review of information on stress tolerance and its relation to the requirements of tree planners. *Urban Forestry & Urban Greening* 9(4): 281–293. <https://doi.org/10.1016/j.ufug.2010.04.001>
- Sjöman H, Östberg J, Bühler O (2012) Diversity and distribution of the urban tree population in ten major Nordic cities. *Urban Forestry & Urban Greening* 11(1): 31–39. <https://doi.org/10.1016/j.ufug.2011.09.004>

- Sousa E, Bravo MA, Pires J, Naves P, Penas AC, Bonifacio L, Mota MM (2001) *Bursaphelenchus xylophilus* (Nematoda; aphelenchoididae) associated with *Monochamus galloprovincialis* (Coleoptera; Cerambycidae) in Portugal. *Nematology* 3(1): 89–91. <https://doi.org/10.1163/156854101300106937>
- Tóth P, Váňová M, Lukáš J (2009) The distribution of *Obolodiplosis robiniae* on black locust in Slovakia. *Journal of Pest Science* 82(1): 61–66. <https://doi.org/10.1007/s10340-008-0220-2>
- United Nations (2018) World Urbanization Prospects: The 2018 Revision United Nations. Department of Economic and Social Affairs, Population Division, New York, 1–103. <https://www.un.org/development/desa/publications/2018-revision-of-world-urbanization-prospects.html>
- Vasconcelos T, Forte P, Arsénio P, Soares AL (2013) Diversidade arbórea no Parque Botânico da Tapada da Ajuda. *O Botânico* 7: 7–10.
- Whitebread SE (1989) *Phyllonorycter robiniella* (Clemens, 1859) in Europe (Lepidoptera, Gracillariidae). *Nota Lepidopterologica* 12(4): 344–353.
- Wilson M, Bensusan K, Perez C, Torres JL (2011) First records of the exotic leafhopper *Sophonia orientalis* (Matsumura, 1912) (Hemiptera: Auchenorrhyncha: Cicadellidae) for the Iberian Peninsula and mainland Europe. *Annals of the Entomological Society of America* 94(5): 664–669.
- Yemshanov D, Koch FH, Siltanen M, Wilson K, Koehler K (2013) Exploring critical uncertainties in pathway assessments of human-assisted introductions of alien forest species in Canada. *Journal of Environmental Management* 129: 173–182. <https://doi.org/10.1016/j.jenvman.2013.07.013>

Supplementary material I

Table S1. Data on first records by species and countries

Authors: Manuela Branco, Pedro Nunes, Alain Roques, Maria Rosário Fernandes, Christophe Orazio, Hervé Jactel

Data type: species data

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Horizon scanning to identify invasion risk of ornamental plants marketed in Spain

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Abstract

Horticulture is one of the main pathways of deliberate introduction of non-native plants, some of which might become invasive. Of the 914 commercial ornamental outdoor plant species sold in Spain, 700 (77%) are non-native (archaeophytes excluded) marketed species. We classified these into six different lists based on their invasion status in Spain and elsewhere, their climatic suitability in Spain and their potential environmental and socioeconomic impacts. We found sufficient information for 270 species. We provide a Priority List of eight regulated invasive species that were still available on the market. We also established an Attention List with 68 non-regulated invasive and potentially invasive species that might cause various impacts. To prioritise the species within the Attention List, we further assessed the risk of invasion of these species by using an adaptation of the Australian WRA protocol and the level of societal interest estimated from values of the Google Trends tool. We also propose a Green List of seven species with probably no potential to become invasive, a Watch List with 27 potentially invasive species with few potential impacts and an Uncertainty List with 161 species of known status but with insufficient information to include them in any of the previous lists. We did not find sufficient information for 430 (61%) of the marketed non-native plant species, which were compiled into a Data Deficient List. Our findings of prohibited species for sale highlight the need for stronger enforcement of the regulations on invasive plant species in Spain. In addition, our results highlight the need for additional information on potential impacts and climate suitability of horticultural plants being sold in Spain, as insufficient information could be found to assess the invasion risk for most species.

Keywords

e-commerce, Google trends, horizon-scanning, impact assessment, non-native plants, nursery, priority list, risk assessment

Introduction

The introduction of invasive non-native species by humans may be accidental – for example seed crops as contaminants amongst cargo – or deliberate (Mack et al. 2000), such as the introduction of species used in forestry, aquaculture and horticulture. In particular, the sale of ornamental plants, including sale by nurseries, is the main deliberate pathway for plant invasions (Van Kleunen et al. 2018) which includes some of the most harmful invasive plant species in the wild (Hulme 2007).

There is a close relationship between domestic market-based propagule pressure and invasion success (Dehnen-Schmutz et al. 2007a; Johnston et al. 2009; Blackburn et al. 2013; García-Díaz et al. 2015). Horticulture activities reduce biotic and abiotic stresses on plants, bring species of different geographic origin together and increase the likelihood that plants escape into the wild (Niinemets and Peñuelas 2008). Moreover, introduction biases, or preferences for non-native species that perform better than natives (Chrobock et al. 2011), include plants that have increased germination rates, faster and larger growth and higher fecundity than native plants (Chrobock et al. 2011; Parker et al. 2013; Maurel et al. 2016). Therefore, the commercial use of non-native ornamental plant species is not only important as the main pathway of introduction (Hulme 2007), but it also favours the invasion potential of these plants and their impacts. In fact, in less than 20 years on the market, some non-native species can become invasive (Pemberton and Liu 2009).

The most effective way to manage the impacts of non-native species is through prevention (Convention on Biological Diversity 2010). In the last two decades, there has been great progress in developing risk assessment protocols as an essential management component to identify potentially invasive species (Pheloung et al. 1999; Leung et al. 2012; Roy et al. 2014, 2015). Most of these risk assessments are used to rank non-native species according to their probability of becoming established and causing harm. Horizon-scanning of invasive species is a particular type of rapid screening risk analysis based on the systematic examination of future potential threats, leading to the prioritisation of non-native species for further investigation (Roy et al. 2014). Horizon-scanning has been applied when prioritisation identifies a small fraction of species selected from a large list of scanned species, for which a thorough risk analysis is not feasible in a short period of time (Andreu and Vilà 2010; Roy et al. 2015; Roy et al. 2019). This is the case, for example, for testing the invasion risk of all ornamental plants commercialised within a country because the number of non-native plant taxa sold is very high.

A parsimonious way to perform a horizon-scanning analysis for ornamental plants is to use four of the most widely used criteria to identify potentially invasive species: climate matching, being invasive elsewhere, their potential impacts on the environment and their impacts on socioeconomic activities (Weber and Gut 2004; Otfinowski et al. 2007, Gassó et al. 2010; Blackburn et al. 2014; Roy et al. 2014).

As the number of non-native species being used as ornamentals is very high, but resources are limited to manage them all in the same way, it is necessary to create prioritisation lists of plant species identifying those that are (1) regulated invasive but still

commercialised, (2) potentially invasive with the risk of causing numerous impacts, (3) potentially invasive with few potential impacts, (4) probably safe because there is no potential to establish in the wild and (5) those for which there is insufficient information to classify them by their risk of invasion and impact (Dehnen-Schmutz 2011). This coarse screening is the basis for prioritising the potentially most invasive species and to later perform a more detailed risk assessment (Pheloung et al. 1999; Weber and Gut 2004; Andreu and Vilà 2010; Gassó et al. 2010), as well as for proposing a list of the least harmful species (Gederaş et al. 2012).

Since many regulations expressly prohibit the commercialisation of listed species, it is expected that none of them is sold. However, regulation is not always effective, especially for the online plant trade (Humair et al. 2015). In fact, many nurseries continue to stock and supply invasive regulated species (Wirth et al. 2004; Cronin et al. 2017). In addition, nowadays most of the nurseries offer internet purchasing. This model of commerce is currently one of the most important sources of gardening plants (Humair et al. 2015). The online plant trade significantly increases transportation distance and propagule pressure of non-native species (Walters et al. 2006; Lenda et al. 2014; Humair et al. 2015). As an innovative approach, the Google Trends tool can be used to forecast consumption and commerce, which is a valuable source of information (Vosen and Schmidt 2011). Therefore, the level of interest in each ornamental species measured by Google Trends can provide information on the interest for a particular species by society in general. Google Trends provides information on how frequently a keyword or group of keywords has been searched for on the Internet. Resulting data are not necessarily composed of only people interested in buying the plant. In fact, it is possible that some of these searches are performed because they are looking for ways to control or manage already invasive species. In our study, we used Google Trends data to assess “popularity” or “interest”, defined in a broad sense, as the data do not allow distinguishing whether plant name searches were motivated by Internet users’ positive or negative views of a plant.

To our knowledge, this tool has not yet been used for the prevention of biological invasions.

In this paper, we perform a horizon-scanning analysis of the 914 commercial ornamental outdoor plant species in Spain from a total of 1063 taxa to facilitate policy implementation. The main aim is to generate six species lists based on their regulation and invasive status in Spain and elsewhere, climate matching between their native region and Spain, the magnitude of the environmental and socioeconomic impacts they might cause and their societal interest (Fig. 1):

- A Priority List that includes regulated (by Spain or the EU) invasive non-native species that were still commercially available in the Spanish peninsular territory (Spain, hereafter).
- An Attention List that includes climatically suitable non-regulated invasive in Spain and potentially invasive species (i.e. invasive elsewhere) with many potential impacts.
- A Watch List that includes climatically suitable non-regulated invasive in Spain and potentially invasive species (i.e. invasive elsewhere) with few potential impacts.

- A Green List that includes species with no climatic suitability and probably no potential to be invasive in Spain.
- An Uncertainty List that includes non-invasive species with probably no potential to be invasive that do not meet the requirements to be included in the Green List. It also includes species with known invasion status but with insufficient information available on impacts and non-native species with known invasion status but with insufficient information on climatic suitability or invasiveness elsewhere.
- A Data Deficient List with all the non-native species with no information about their invasion status and not enough data to classify them in any other list.

To rank the species of the Attention List, we conducted an in-depth analysis based on their risk of invasion and societal interest. The risk of invasion was scored according to the Australian weed risk assessment performed by Pheloung et al. (WRA 1999). This WRA protocol has been tested successfully for its consistent accuracy in different geographic regions (Gordon et al. 2008) including Spain (Gassó et al. 2010). Societal interest in non-native species was measured using Google Trends. We wanted to answer the following questions: Does the risk of invasion and interest to society grow across the different invasion status groups of species currently in Spain (i.e. not in the wild, casual, naturalised and invasive)? Does the number of potential environmental and socioeconomic impacts rise with increasing invasion status. Moreover, for each non-native species, we calculated a Priority Index based on the impacts, WRA score and interest of the species. We tested if the Priority Index increased with increasing invasion status of the species.

Material and methods

We compiled a database including the vast majority of ornamental outdoor plants with commercial use in gardening in the Spanish peninsular territory excluding the Canary and Balearic Islands (Spain, hereafter). We also included indoor plants that can survive and/or reproduce outdoors. However, we excluded strictly indoor plants because their ecological requirements might prevent survival outdoors. We included fruit trees as they are of ornamental use in public and private gardens and green areas, but we excluded vegetables used in horticulture. The list of taxa was compiled through the systematic consultation of catalogues from the 21 main Spanish nurseries (Appendix 1) between December 2015 and October 2016, which provide plants for sale across the country. The number of new taxa added to the database (Appendix 1) did not increase at all after the 15th nursery catalogue was consulted. The total number of taxa compiled was 1036, of which 914 were actual species. Hybrids or genus level taxa were not included in the analysis and infraspecific taxa were pooled into species.

According to their origin, we first discriminated between native species and non-native species in Spain. We then identified archaeophytes (i.e. species introduced be-

fore 1500 A.D.), following Pyšek et al. (2004). Archaeophytes were not included in the analysis because they are poorly recorded and, for many species, their non-native status is under discussion.

Species were further classified according to their invasion status in Spain, following the definitions recommended by Richardson et al. (2000): not in the wild, casual, established or naturalised (hereafter “naturalised”), invasive non-regulated in Spain or Europe (hereafter “invasive”) or invasive regulated in Spain or Europe (hereafter “regulated”). Invasion status in Spain, as not in the wild, casual, naturalised or invasive, was based on the information provided in the Spanish Atlas of Invasive Non-native Plants (Sanz Elorza et al. 2004). The regulation status of the species, that in Spain involves the ban of possession, transport and commerce of living beings and propagules, was based on the Spanish Catalogue of Non-native Invasive Species (BOE 2013) and the List of Invasive Alien Species of Union Concern (European Commission 2016, 2017).

Once the non-native species were classified into these five invasion status groups (i.e. regulated invasive, invasive, naturalised, casual, not in the wild), we proceeded to perform the horizon-scanning to classify the species into the respective lists based on the flow diagram illustrated in Fig. 1 as follows:

All Regulated species were directly included in the Priority List, whereas invasive species were considered for impact assessment (see method below).

Naturalised species were identified as invasive elsewhere, based on the CABI Datasheets (2018) and the Global Invasive Species Database (Invasive Species Specialist Group 2015). Naturalised species that are invasive elsewhere were regarded as potentially invasive species and were considered for impact assessment. Naturalised species not invasive elsewhere were included in the Uncertainty List.

Casual and not in the wild species were screened for climatic suitability in Spain (see method below). For species climatically suitable somewhere in the country, with a medium to high level of confidence in the likelihood, we checked whether they were invasive elsewhere (Roy et al. 2014). Species that were not climatically suitable and not registered as invasive elsewhere, were included in the Green List (Dehnen-Schmutz 2011), commonly known as the “*white list*” by decision-makers. In contrast, species that were climatically suitable and were invasive elsewhere were regarded as potentially invasive species and thus considered for impact assessment. On the other hand, species that were climatically suitable but not invasive elsewhere and species that were invasive elsewhere but not climatically suitable were included in the Uncertainty List.

Finally, all the species naturalised or casual in Spain, for which we could not find sufficient data about being invasive elsewhere and those for which we have a low level of confidence in the likelihood of climatic suitability or no data at all, were included in the Uncertainty List. This list also includes species not in the wild that are invasive elsewhere rather than Spain, species that are not climatic suitable or species in which the level of confidence in the likelihood of climatic suitability is very low.

In contrast, the Data deficient list includes species not in the wild, with no data on status elsewhere and on climate suitability.

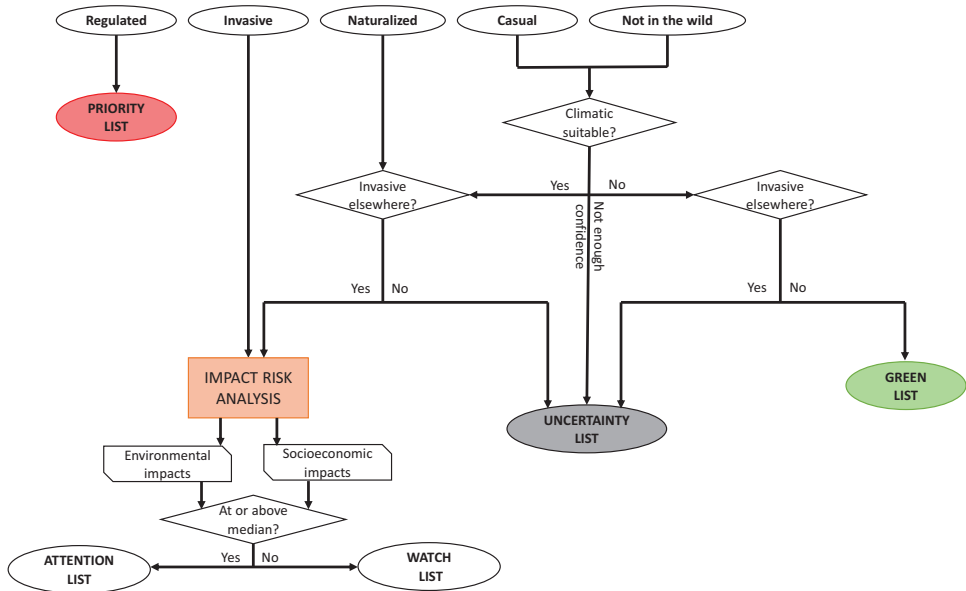


Figure 1. Flow diagram of horizon-scanning of commercial ornamental non-native plant species in Spain and their classification into respective lists. Colour codes correspond to those in Table 1.

Climatic suitability

The climate in Spain is a mosaic of three main climates: Oceanic in the NW, Mediterranean continental in the centre and Mediterranean maritime in the E and S of the country including semi-arid areas (Ninyerola et al. 2005). Furthermore, Spain is a mountainous country, in which elevations over 1500 m a.s.l. are common and the highest peak rises to 3480 m a.s.l. Mountainous areas impose sharp topographical-climatic gradients where these three climatic types gradually change to a Mountain climate, characterised by cold, strong winds and abundant rainfall or snowfall. We know from previous regional analyses that the establishment of non-native species is enhanced in mesic conditions (i.e. intermediate temperature and moisture levels), such as those close to coastal areas (Gassó et al. 2009, González-Moreno et al. 2014).

Precipitation was not considered as a criterion for climatic suitability because Spain has a wide rainfall range. Since our analysis is not spatially explicit, at the regional scale, there are suitable conditions for non-native species to establish and spread (González-Moreno et al. 2014). According to AEMET (2016), the town with the highest rainfall is Vigo (NW Spain), with an average of 1790 mm per year. The climatic station registering the lowest amount is Almería (SE Spain), with an average of 200 mm per year. Therefore, due to this wide range of rainfall in our study area, we did not consider tolerance to drought or waterlogging as climatic classification criteria for the risk of invasion at the country scale.

To follow the precautionary principle, our criteria on temperature suitability were based on the highest absolute minimum and the highest mean of the minimum in the coldest month. This implies that there are many territories in Spain that, having lower

minimum temperatures than the threshold chosen, will be less susceptible to invasion by the species of concern. In this way, we minimise the false negatives that may arise. Thus, we considered a plant to have climatic suitability to survive in Spain if it met two temperature criteria: (1) it can tolerate temperatures below the highest historical absolute minimum temperature in Spain, which was 0.2 °C in Almería (9 February 1935); and (2) it can tolerate temperatures below the highest mean minimum temperature in the coldest month in Spain, which in Tarifa is January at 10.8 °C (mean recorded from data between 1981 to 2010) (AEMET 2016). The air temperature tolerance for each species was consulted in the CABI Invasive Species Compendium (2018).

The level of confidence in the likelihood of climatic suitability was based on the quality of information available. A high level of confidence was assigned if both air temperature values were available; a medium level of confidence was assigned if only one of the temperature values was available but there was information on the species being naturalised or not elsewhere with similar climatic conditions to those in Spain (i.e. Mediterranean or temperate climate); and a low level of confidence was assigned if only one of the temperature values was available or if the species was naturalised or not elsewhere with similar climatic conditions to those in Spain.

Impact assessment

There are different ways to rate impacts in risk assessments. Some are based on their significance and intensity, some on the number of impacts (see table 3 in Vilà et al. 2019). To quantify the intensity of impacts requires a throughout screening of all the scientific literature, an aim that was above our man-power capacity. As we had many species to assess and our approach is by Horizon-scanning, we identified a broad range of potential impact types, including socioeconomic impacts. For each invasive or potentially invasive species, we assigned binary scores (yes/no) to the 11 potential impact mechanisms on the environment, following Blackburn et al. (2014): competition, hybridisation, disease transmission, parasitism, poisoning, toxicity and allelopathy, biofouling, interaction with other invasive non-native species, nutrient cycling, physical modification of the habitat, natural succession and disruption to food webs. We also included potential impacts on four socioeconomic aspects: human health (such as allergenic pollen), infrastructures, agriculture and forestry and other sectors (e.g. livestock, domestic animals). The vast majority of the data concerning impacts was retrieved from the CABI Invasive Species Compendium (2018). For cases in which the CABI compendium did not provide sufficient information, the Global Invasive Species Database (Invasive Species Specialist Group 2015) was consulted. Information on pollen allergenicity was found in the Allergome database (Mari et al. 2009).

We compared the numeric results of potential environmental (0–11) and socioeconomic (0–4) impacts between the different invasion status groups of non-native species (i.e. not in the wild, casual, naturalised and invasive). We used R software to perform a multiple comparison using Tukey's range test, fitted in the generalised linear model (glm) by quasi-Poisson regression.

We consider median values for both environmental and socioeconomic impacts as the threshold for the classification between species with a high and low number of impacts. Species with environmental or socioeconomic impacts at or above the thresholds were included in the Attention List, while species with both environmental and socioeconomic impacts below the threshold formed the Watch List.

Societal interest analysis of Attention List species

Google is currently the most popular information search engine (Purcell et al. 2012) and it is quite useful for forecasting consumption and commerce (Vosen and Schmidt 2011). Google Trends (<http://trends.google.es>) has turned out to be a valuable tool to measure the level of interest of internet users on topics, species, events, questions etc., based on keywords and thus it has already been applied for this purpose in other research (Vosen and Schmidt 2011, Burivalova et al. 2018). Google Trends provides monthly data in a defined temporal range of regional trends of five keywords at a time, always relative to the highest value which is set to 100. We used Google Trends to analyse the level of interest of Spanish users in the Attention List species. We are aware that a species ranking high in interest does not necessarily mean that users are more interested in purchasing them. The reasons behind the searches for these species are not known, but they indicate how popular the species are in society in general.

To standardise those relative values, we used the R pack “gtrendsR” v. 1.4.2. We first made a systematic examination of the scientific names of every species listed in the Attention List in the temporal range from January 2004 to December 2016 to identify the species with the highest trend value. We used the scientific names to standardise our search; some species consulted do not have vernacular names in Spanish and some others may have different names. As the Google Trends tool allows entering 5 keywords at a time, we carried out a first examination forming one initial group of five species to analyse and taking the highest value species in this first group. Then, we compared this highest ranked species with the next four species and again selected the species with the highest value in this new group. Systematically repeating this algorithm with the rest of the species allowed us to identify the species with the highest trend value, *Robinia pseudoacacia*. The highest value for this species is set equal to 100 and this was assigned as our control species. Then, in a second systematic consultation of Google Trends, we obtained the trend data for the rest of the species by comparing each one with the control, in order to standardise the values.

For each species, we obtained a standard trend value (STV) as the highest value of the monthly trend in the complete temporal range of each species, relative to the optimal value of 100 of the control species. After that, we also performed a systematic consultation of Google Trends for the species in the Green List and the Priority List.

We compared differences in STV of the Attention List species across the different invasion status groups of species within the list (i.e. not in the wild, casual, naturalised

and invasive). We used R software to perform a multiple comparison using Tukey's range test, fitted in the generalised linear model (glm) by quasi-Poisson regression. We also compared the STV of the species in the Priority list and the Green list, in order to check whether the STV index correlates with invasion itself.

Invasion risk assessment of Attention List species

We used an adaptation of the invasion risk assessment (WRA) protocol (Pheloung et al. 1999) for Spain (Gassó et al. 2010) in order to rank the species in the Attention list. The WRA scores range from -14 (benign species) to 29 (maximum risk). Three levels of invasion risk were considered: rejected, species likely to be high risk (score > 6); accepted, species with a low score (< 1); and species that need further evaluation, those with intermediate scores (1–6).

We compared the scores of the WRA of the Attention List species across the different invasion status groups of species within the list (i.e. not in the wild, casual, naturalised and invasive). We used R software to perform a multiple comparison using Tukey's range test, fitted in the generalised linear model (glm) by quasi-Poisson regression.

Prioritisation of Attention List species

We calculated a Priority Index for each species in the Attention list based on impact assessment, WRA score and STV according to the following equation:

$$PI_i = \left(\frac{100 \times E_i}{11} + \frac{100 \times S_i}{4} + \frac{100 \times WRA_i}{29} + STV_i \right) / 4$$

where: PI_i = Priority Index for species i ; E_i = number of environmental impacts for species i ; S_i = number of socioeconomic impacts for species i ; WRA_i = Weed Risk Assessment score for species i ; STV_i = Standard Trend Value for species i .

The impact factors were relative to the 11 environmental and 4 socioeconomic impacts which represent the maximum possible impacts in the assessment. The WRA-factor was relative to 29, which is the maximum possible value in the WRA protocol. The STV is already represented as a percentage and thus no conversion is needed.

Within each invasion status group, we listed species in decreasing order of their Priority Index and highlighted those with a Priority Index at or above the median.

Data resources

The data underpinning the analysis, reported in this paper, are deposited in the Zenodo repository at <https://doi.org/10.5281/zenodo.3367257> (Bayon and Vilà 2019).

Results

Of the 914 taxa identified to species, 199 were native to Spain and 15 were archaeophytes. Of the 700 remaining non-native species, we did not find sufficient information on invasion status, climatic suitability or invasiveness elsewhere for 430 species (Data deficient list; Appendix 4) in the consulted databases (Invasive Species Specialist Group 2015; CABI 2018). For the remaining 270 non-native species, 71 taxa were not in the wild, 99 were casual, 70 naturalised and 30 invasive in Spain. Of the invasive species in Spain, eight are regulated by the Spanish Catalogue of Non-native Invasive Species (BOE 2013) and one of them, *Pennisetum setaceum*, is also regulated by the List of Invasive Alien Species of Union Concern (2016, 2017).

Nineteen species not in the wild, 30 casual and 24 naturalised species are climatically suitable and invasive elsewhere and thus considered potential invaders. These species, in addition to the 22 already invasive non-regulated species, were assessed for impact (Table 1).

Impact Assessment

We assessed the potential impact of the above-mentioned 19 not in the wild, 30 casual, 24 naturalised and 22 invasive species that are climatically suitable and invasive elsewhere. The global median value for environmental impacts was three and the median for socioeconomic impacts was one. Therefore, species with impacts at or above these values were included in the Attention List. This included eleven not in the wild (58%), 22 casual (73%), 20 naturalised (83%) and 15 invasive species (68%). We did not find significant differences in the number of environmental or socioeconomic impacts across any pair of species status groups (Fig. 2).

Within each invasion status, the species with the highest number of environmental impacts included the invasive *Robinia pseudoacacia* (7), *Agave sisalana* (6) and *Elaeagnus angustifolia* (6); the naturalised *Ficus pumila* (7), *Ficus rubiginosa* (6), *Lupinus polyphyllus* (6) and *Sansevieria trifasciata* (6); the casual *Wisteria sinensis* (8) and *Grevillea robusta* (7); and the not in the wild *Nymphaea odorata* (7).

Species with the highest number of socioeconomic impacts were the invasive *Robinia pseudoacacia* (3), *Acacia longifolia* (3), *Eucalyptus globulus* (3) and *Lantana camara* (3); the naturalised *Lupinus polyphyllus* (3), *Rhus typhina* (3) and *Tagetes minuta* (3); the casual *Miscanthus sinensis* (3), *Portulaca oleracea* (3) and *Sesbania punicea* (3); and the not in the wild *Allamanda cathartica* (3).

Species listing

The 270 non-native species with available data were classified into the following five lists:

The Priority List contains eight regulated invasive species that were still commercially available in nurseries (Table 2).

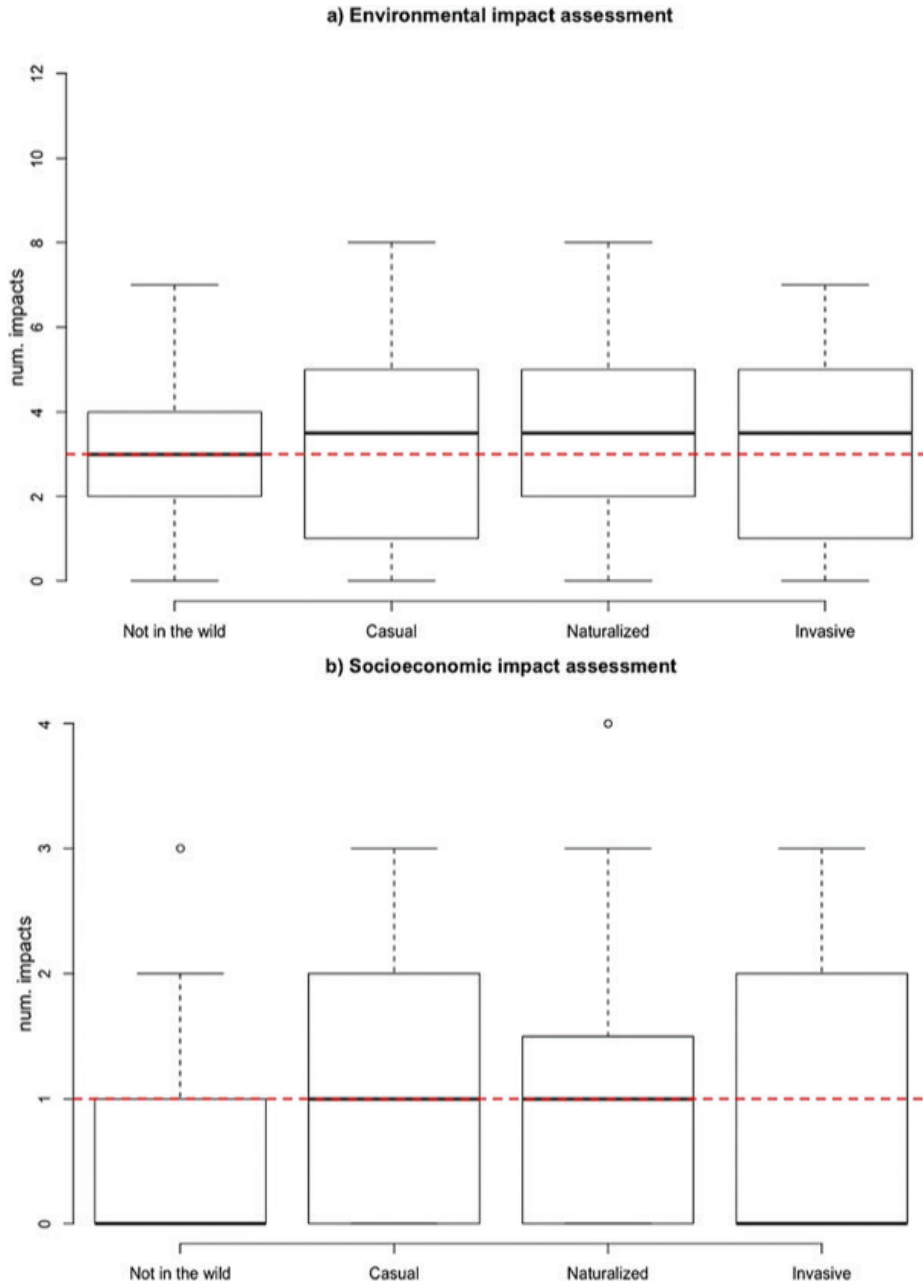


Figure 2. Environmental (a) and socioeconomic (b) impacts of invasive and potentially invasive ornamental plant species. P-values for Tukey’s range tests for environmental impacts: not in the wild – casual: $p = 0.833$; not in the wild – naturalised: $p = 0.498$; not in the wild – invasive: $p = 0.926$; casual – naturalised: $p = 0.904$; casual – invasive: $p = 0.997$; naturalised – invasive: $p = 0.845$. P-values for Tukey’s range tests for socioeconomic impacts: not in the wild – casual: $p = 0.790$; not in the wild – naturalised: $p = 0.526$; not in the wild – invasive: $p = 0.916$; casual – naturalised: $p = 0.947$; casual – invasive: $p = 0.994$; naturalised – invasive: $p = 0.875$. Dashed red line represents the global median of impacts and the threshold for species in the Attention List (at and above the line, Table 3) and Watch List (below the line, Appendix 2)

Table 1. Classification of commercial ornamental plant taxa in Spain according to their invasion status and climatic suitability. Colour codes correspond to those in Fig 1: Priority List (red, Table 2), Impact Risk Analysis (orange), Green List (green, Table 4) and Uncertainty List (grey, Appendix 3).

	N	Climatic suitable	Not Climatic suitable	Low confidence in likelihood on climatic suitability	Not enough information about climatic suitability	Invasive elsewhere	Not invasive elsewhere
Total taxa in nurseries	1036						
Taxa excluded	122						
Total species listed	914						
Native	199						
Archeophyte	15						
Non-native (non-archeophyte)	700						
Invasive – Regulated	8						
Invasive – Not Regulated	22						
Naturalised	70					24	46
Casual	100	36	2	4	58		
Casual – Climatic Suitable						30	6
Casual – Not Climatic Suitable						1	1
Not in the wild	71	34	10	27			
Not in the wild – Climatic Suitable						19	15
Not in the wild – Not Climatic Suitable						4	6
Data deficient	430						

Table 2. Priority List. Includes invasive species regulated by the Spanish Catalogue of Non-native Invasive Species (BOE 2013) or the List of Invasive Alien Species of Union Concern (European Commission 2016, 2017). Native distribution: Afr: Africa; As: Asia (Temperate); Aus: Australia; NAm: North America; SAm: South and Central America.

Species	Family	Native distribution	Regulated in Spain	Regulated in EU
<i>Acacia dealbata</i>	Fabaceae	Aus	Yes	No
<i>Agave americana</i>	Agavaceae	SAm	Yes	No
<i>Ailanthus altissima</i>	Simarubaceae	As	Yes	No
<i>Buddleja davidii</i>	Scrophulariaceae	As	Yes	No
<i>Cortaderia selloana</i>	Poaceae	SAm	Yes	No
<i>Opuntia ficus-indica</i>	Cactaceae	NAm	Yes	No
<i>Pennisetum setaceum</i>	Poaceae	Afr	Yes	Yes
<i>Tradescantia fluminensis</i>	Commelinaceae	SAm	Yes	No

The Attention List (Table 3) is composed of 68 species, including 11 not in the wild, 22 casual, 20 naturalised and 15 invasive.

The Watch List contains 27 species: eight not in the wild, eight casual, four naturalised and seven invasive, but below the threshold for environmental and socio-economic impacts (Appendix 2).

The Green List is represented by only seven species: one casual and six not in the wild taxa that are not climatically suitable nor invasive elsewhere (Table 4). Finally, the Uncertainty List was formed by 161 species, in which: 46 are not in the wild (27 with low confidence on climatic suitability, 15 not invasive elsewhere but climatically

Table 3. Attention List. Includes all invasive and potentially invasive species with ≥ 3 environmental or ≥ 1 socio-economic potential impacts, classified as: a) not in the wild, b) casual, c) naturalised and d) invasive species, presented in decreasing Priority Index order. Native distribution: Afr: Africa; As: Asia (Temperate); AT: Asia (Tropical); Aus: Australia; Eur: Europe; NAm: North America; Pac: Pacific; SAm: South and Central America. Weed Risk Assessment (WRA): scores 1–6 indicate that the species needs further evaluation; scores > 6 indicate that the species is rejected. STV: Standard Trend Value (0-100). Priority Index is calculated following the equation: Priority index = $((100 \times Ei) / 11 + (100 \times Si) / 4 + (100 \times WRA) / 29 + STV) / 4$ where: Ei = environmental impacts; Si = socioeconomic impacts. * Species with Priority Index ≥ 35 have been highlighted with an asterisk.

	Family	Native distribution	Impacts		WRA			Trends	Prior. Index
			Environment	Socio-economics	Score	Evaluation	STV	Evaluation	
a) Species not in the wild									
<i>Cinnamomum camphora</i> *	Lauraceae	As	4	2	17	Reject	35	Less Interesting	45
<i>Cotoneaster horizontalis</i> *	Rosaceae	As, AT	3	1	26	Reject	37	Less Interesting	45
<i>Physalis angulata</i> *	Solanaceae	NAm, SAm, Pac	4	2	22	Reject	0	Not Interesting	41
<i>Allamanda cathartica</i> *	Apocynaceae	SAm	4	3	11	Reject	0	Not Interesting	37
<i>Nymphaea odorata</i> *	Nymphaeaceae	NAm	7	2	9	Reject	0	Not Interesting	36
<i>Leptospermum scoparium</i> *	Myrtaceae	Aus	3	1	13	Reject	43	Less Interesting	35
<i>Cornus sericea</i>	Cornaceae	NAm	4	1	22	Reject	0	Not Interesting	34
<i>Berberis thunbergii</i>	Berberidaceae	As	4	1	12	Reject	27	Less Interesting	32
<i>Alocasia macrorrhizos</i>	Araceae	AT	4	0	13	Reject	0	Not Interesting	20
<i>Euonymus fortunei</i>	Celastraceae	As	4	0	7	Reject	0	Not Interesting	15
<i>Archontophoenix cunninghamiana</i>	Arecaceae	Aus	4	0	4	Evaluating	0	Not Interesting	13
b) Casual species									
<i>Portulaca oleracea</i> *	Portulacaceae	Afr, EUr	4	3	15	Reject	54	Interesting	54
<i>Cestrum nocturnum</i> *	Solanaceae	SAm	4	2	9	Reject	80	Very Interesting	49
<i>Wisteria sinensis</i> *	Fabaceae	As	8	2	9	Reject	43	Less Interesting	49
<i>Kalanchoe daigremontiana</i> *	Crassulaceae	Afr	5	1	22	Reject	37	Less Interesting	46
<i>Pinus radiata</i> *	Pinaceae	NAm	3	2	12	Reject	60	Interesting	45
<i>Nandina domestica</i> *	Berberidaceae	As, AT	5	2	9	Reject	43	Less Interesting	42
<i>Casuarina equisetifolia</i> *	Casuarinaceae	Aus	5	2	7	Reject	45	Less Interesting	41
<i>Miscanthus sinensis</i> *	Poaceae	AT	6	3	9	Reject	0	Not Interesting	40
<i>Paulownia tomentosa</i> *	Paulowniaceae	As, AT	4	1	19	Reject	27	Less Interesting	38
<i>Zantedeschia aethiopica</i> *	Araceae	Afr	0	1	15	Reject	70	Interesting	37
<i>Physalis peruviana</i> *	Solanaceae	SAm	5	2	8	Reject	22	Not Interesting	36
<i>Grevillea robusta</i> *	Proteaceae	Aus	7	1	2	Evaluating	45	Less Interesting	35
<i>Sesbania punicea</i> *	Fabaceae	SAm	2	3	13	Reject	0	Not Interesting	35
<i>Gypsophila paniculata</i>	Caryophyllaceae	As, Eur	6	1	6	Evaluating	17	Not Interesting	29
<i>Eugenia uniflora</i>	Myrtaceae	SAm	5	0	18	Reject	0	Not Interesting	27

	Family	Native distribution	Impacts		WRA		Trends Evaluation	Prior. Index	
			Environment	Socio-economics	Score	Evaluation			
<i>Spiraea japonica</i>	Rosaceae	As, AT	4	0	11	Reject	28	Less Interesting	26
<i>Tecoma stans</i>	Bignoniaceae	NAm, SAm	4	1	11	Reject	0	Not Interesting	25
<i>Prunus serotina</i>	Rosaceae	NAm	6	0	12	Reject	0	Not Interesting	24
<i>Morus nigra</i>	Moraceae	As	3	0	4	Evaluating	45	Less Interesting	22
<i>Eucalyptus sideroxylon</i>	Myrtaceae	Aus	3	0	14	Reject	0	Not Interesting	19
<i>Yucca aloifolia</i>	Agavaceae	NAm	3	1	4	Evaluating	0	Not Interesting	17
<i>Cereus uruguayanus</i>	Cactaceae	SAm	3	0	3	Evaluating	0	Not Interesting	9
c) Naturalised species									
<i>Lupinus polyphyllus*</i>	Fabaceae	NAm	6	3	27	Reject	0	Not Interesting	56
<i>Canna indica*</i>	Cannaceae	SAm	8	1	24	Reject	35	Less Interesting	54
<i>Rhus typhina*</i>	Anacardiaceae	NAm	5	4	15	Reject	0	Not Interesting	49
<i>Phragmites australis*</i>	Poaceae	NAm	2	2	27	Reject	35	Less Interesting	49
<i>Tagetes minuta*</i>	Asteraceae	NAm	4	3	22	Reject	0	Not Interesting	47
<i>Imperata cylindrica*</i>	Poaceae	AT	7	1	24	Reject	0	Not Interesting	43
<i>Ficus pumila*</i>	Moraceae	AT	3	3	5	Evaluating	35	Less Interesting	39
<i>Phoenix canariensis*</i>	Arecaceae	Afr	4	1	6	Evaluating	71	Interesting	38
<i>Melia azedarach*</i>	Meliaceae	AT, Aus	4	0	12	Reject	71	Interesting	37
<i>Psidium cattleianum*</i>	Myrtaceae	SAm	6	1	20	Reject	0	Not Interesting	37
<i>Albizia julibrissin</i>	Fabaceae	As	3	0	14	Reject	62	Interesting	34
<i>Ficus rubiginosa</i>	Moraceae	Aus	6	1	7	Reject	26	Less Interesting	32
<i>Broussonetia papyrifera</i>	Moraceae	As	5	2	2	Evaluating	27	Less Interesting	32
<i>Ziziphus jujuva</i>	Rhamnaceae	As, AT, Aus	5	1	17	Reject	0	Not Interesting	32
<i>Pennisetum villosum</i>	Poaceae	Afr	3	0	25	Reject	0	Not Interesting	28
<i>Sansevieria trifasciata</i>	Asparagaceae	Afr	4	0	12	Reject	35	Less Interesting	28
<i>Bacopa monnieri</i>	Plantaginaceae	NAm, SAm, As, Eur	2	1	16	Reject	10	Not Interesting	27
<i>Adiantum raddianum</i>	Pteridaceae	SAm	3	1	13	Reject	7	Not Interesting	26
<i>Atriplex semibaccata</i>	Amaranthaceae	Aus	3	0	15	Reject	0	Not Interesting	20
<i>Annona cherimola</i>	Annonaceae	SAm	1	1	0	Accepted	0	Not Interesting	9
d) Invasive species									
<i>Robinia pseudoacacia*</i>	Fabaceae	NAm	7	3	15	Reject	100	Very Interesting	73
<i>Lantana camara*</i>	Verbenaceae	SAm	5	3	25	Reject	67	Interesting	68
<i>Eucalyptus globulus*</i>	Myrtaceae	Aus	4	3	21	Reject	35	Less Interesting	55
<i>Acacia longifolia*</i>	Fabaceae	Aus	4	3	23	Reject	0	Not Interesting	48
<i>Acacia saligna*</i>	Fabaceae	Aus	5	1	22	Reject	23	Not Interesting	42
<i>Leucaena leucocephala*</i>	Fabaceae	NAm	5	0	21	Reject	35	Less Interesting	38
<i>Elaeagnus angustifolia*</i>	Elaeagnaceae	As	6	0	21	Reject	19	Not Interesting	36
<i>Lonicera japonica*</i>	Caprifoliaceae	As, AT	3	1	14	Reject	39	Less Interesting	35

	Family	Native distribution	Impacts		WRA		Trends Evaluation	Prior. Index	
			Environment	Socio-economics	Score	Evaluation			
<i>Agave sisalana*</i>	Agavaceae	SAm	6	2	10	Reject	0	Not Interesting	35
<i>Psidium guajava</i>	Myrtaceae	NAm	4	1	19	Reject	0	Not Interesting	32
<i>Gledisia triacanthos</i>	Fabaceae	NAm	4	0	10	Reject	41	Less Interesting	28
<i>Phormium tenax</i>	Xanthorrhoeaceae	Pac	3	0	10	Reject	35	Less Interesting	24
<i>Bidens aurea</i>	Asteraceae	NAm	1	2	5	Evaluating	18	Not Interesting	24
<i>Stenotaphrum secundatum</i>	Poaceae	Afr	5	0	13	Reject	0	Not Interesting	23
<i>Passiflora caerulea</i>	Passifloraceae	SAm	3	0	6	Evaluating	0	Not Interesting	12

Table 4. Green List. Includes non-native non-invasive species with very low invasion potential. Native distribution: As: Asia (Temperate); AT: Asia (Tropical); SAm: South and Central America. Status in Spain: N: Not in the wild, C: Casual.

Species	Family	Native distribution	Status in Spain
<i>Averrhoa carambola</i>	Oxalidaceae	AT	N
<i>Celosia argentea</i>	Amaranthaceae	AT	N
<i>Ficus benjamina</i>	Moraceae	AT	N
<i>Mangifera indica</i>	Anacardiaceae	As – AT	N
<i>Nelumbo nucifera</i>	Nelumbonaceae	AT	N
<i>Pogostemon helferi</i>	Lamiaceae	AT	N
<i>Senna corymbosa</i>	Fabaceae	SAm	C

suitable, four not climatically suitable but invasive elsewhere), 69 are casual (4 with low confidence on climatic suitability, 58 with no available information on climatic suitability, six not invasive elsewhere but climatically suitable and one not climatically suitable but invasive elsewhere) and 46 are naturalised not invasive elsewhere (Appendix 3).

Societal interest analysis of Attention List species

In the Google Trends systematic examination of the 68 Attention List species, maximum trend values were observed for *Robinia pseudoacacia* – March 2004 – and therefore we used this record as our control species.

Within the Attention list, the most noteworthy species (higher STV) included: the invasive *Robinia pseudoacacia* (100) and *Lantana camara* (67); the naturalised *Phoenix canariensis* (71) and *Melia azedarach* (71); the casual *Cestrum nocturnum* (80) and *Zantedeschia aethiopica* (70); and, far from the previous groups, the not in the wild *Leptospermum scoparium* (43). Complete results of the STV analysis are shown in Table 3. There were no significant differences in STV between any pair of invasion status groups of species (Fig. 3). Similarly, there were no differences between the species in the Priority list and the Green List ($p=0.967$).

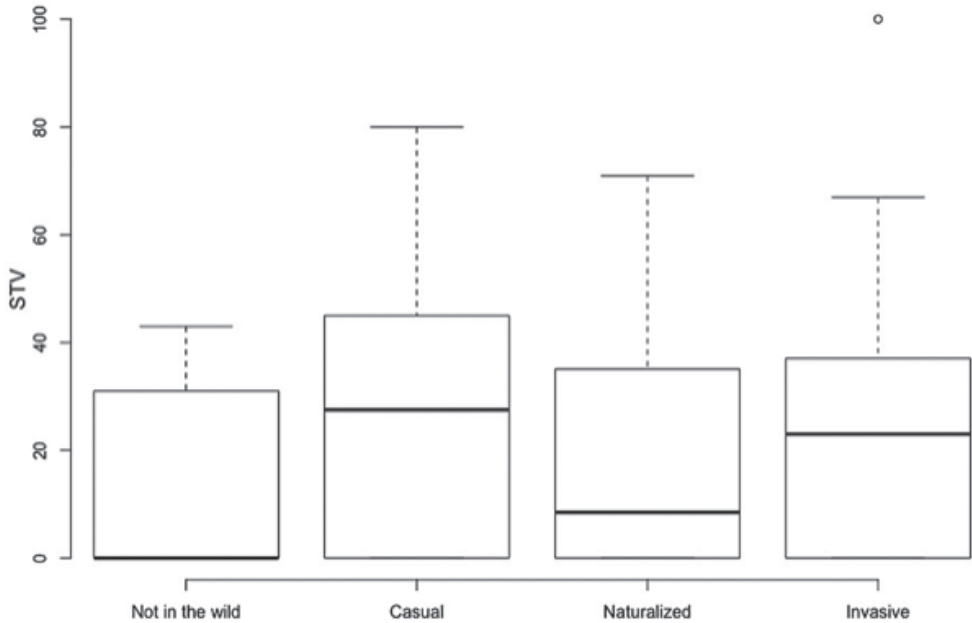


Figure 3. Society interest in ornamental non-native plant species classified by their invasion status. STV: Standard Trend Value. P-values for Tukey's range tests: not in the wild – casual: $p = 0.373$; not in the wild – naturalised: $p = 0.783$; not in the wild – invasive: $p = 0.436$; casual – naturalised: $p = 0.794$; casual – invasive: $p = 1$; naturalised – invasive: $p = 0.860$.

Invasion risk assessment of Attention List species

In the WRA, all species in the Attention List were rejected, except for 11 that required further evaluation and only one, *Annona cherimola*, that was accepted (Table 3).

Within each invasion status, the highest WRA scores were for the invasive *Lantana camara* (25), *Acacia longifolia* (23), *Acacia saligna* (22), *Elaeagnus angustifolia* (21), *Eucalyptus globulus* (21) and *Leucana leucocephala* (21); the naturalised *Phragmites australis* (27), *Lupinus polyphyllus* (27), *Pennisetum villosum* (25), *Canna indica* (24) and *Imperata cylindrica* (24); the casual *Kalanchoe daigremontiana* (22), *Pawlonia tomentosa* (19) and *Eugenia uniflora* (18); and the not in the wild *Cotoneaster horizontalis* (26), *Cornus sericea* (22) and *Physalis angulata* (22). For every invasion status, the species requiring further evaluation accounted for less than 25%. There were no significant differences in WRA scores between any pair of invasion status groups of species (Fig. 4).

Prioritisation of Attention List species

The median value of Priority Indices was 35. Species with a Priority Index ≥ 35 are highlighted in Table 3. Within each invasion status, the highest Priority Indices in invasive species were found for *Robinia pseudoacacia* (73), *Lantana camara* (68) and

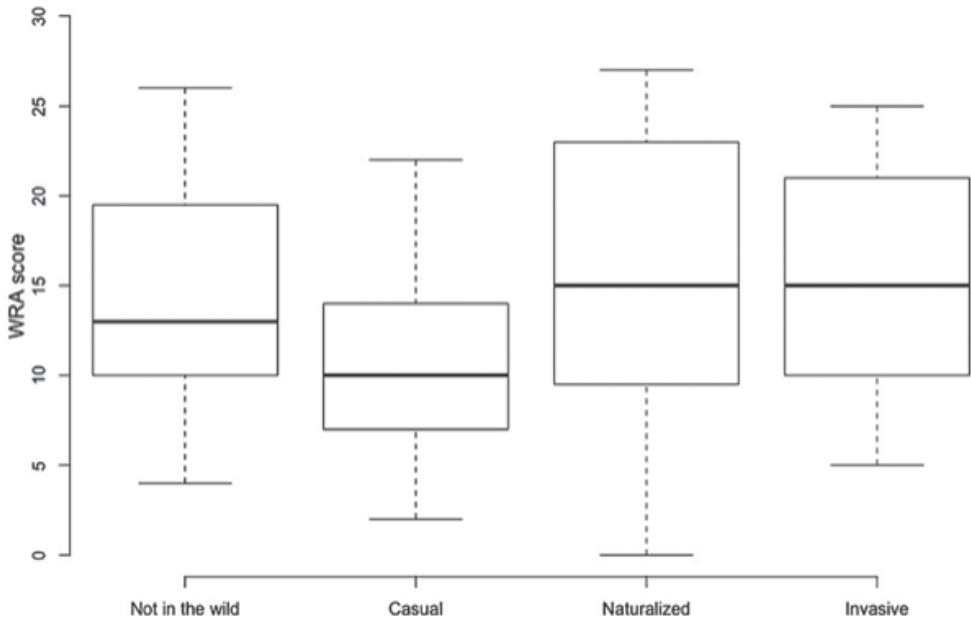


Figure 4. Weed risk assessment (WRA) score in ornamental non-native plant species classified by their invasion status in Spain. P-values for Tukey's range tests: not in the wild – casual: $p = 0.392$; not in the wild – naturalised: $p = 0.983$; not in the wild – invasive: $p = 0.951$; casual – naturalised: $p = 0.101$; casual – invasive: $p = 0.086$; naturalised – invasive: $p = 0.997$.

Eucalyptus globulus (55); in naturalised species *Lupinus polyphyllus* (56) and *Canna indica* (54); in casual species *Portulaca oleracea* (54), *Cestrum nocturnum* (49) and *Wisteria sinensis* (49); and in not in the wild species *Cinnamimum camphora* (45) and *Cotoneaster horizontalis* (45). There were no significant differences between any pair of invasion status groups of species (Fig. 5).

Discussion

Nurseries and the commercial introduction of non-native plant species are the main deliberate pathways for plant invasions (Van Kleunen et al. 2018). Some of the most harmful invasive plant species in the wild are non-native species introduced for commercial purposes (Hulme 2007). In Spain, non-native plants represent the vast majority of species sold by nurseries (77%) and 30 of these species have been reported as invasive in the peninsular territory of Spain. The regulation of non-native invasive plant species is necessary. However, nurseries often do not fully comply with commercial restrictions (Wirth et al. 2004; Cronin et al. 2017; Touza et al. 2014). Besides the Spanish (BOE 2013) and European (European Commission 2016, 2017) regulations on non-native invasive species and similar to what happens in other countries, there are eight regulated species that, although being regulated, were still commercially available

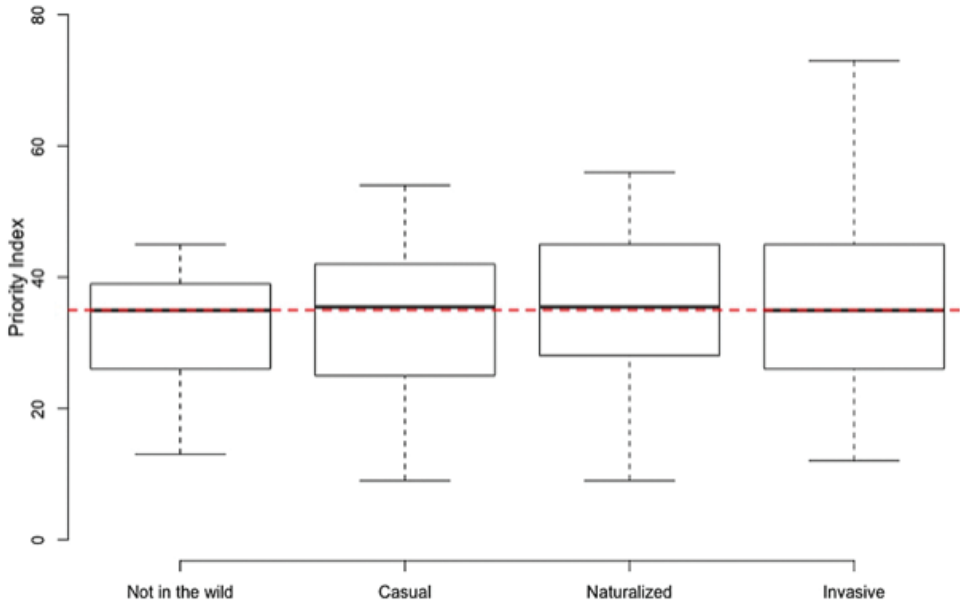


Figure 5. Priority Index in ornamental non-native plant species classified by their invasion status in Spain. P-values for Tukey's range tests: not in the wild – casual: $p = 0.981$; not in the wild – naturalised: $p = 0.860$; not in the wild – invasive: $p = 0.633$; casual – naturalised: $p = 0.958$; casual – invasive: $p = 0.748$; naturalised – invasive: $p = 0.953$. Dashed red line represents the global median of Priority Index (=38). Species at or above this line should be considered in prioritisation, as shown in table 3.

in the country at the time of this study (Appendix 1), as indicated in the Priority List. One of them, *Pennisetum setaceum*, was also been included under European regulation, although this inclusion is more recent than the study of the nurseries for this study. Therefore, there is a pressing need to enforce the current legislation, as well as to raise public awareness to prohibit the trade of these species.

Furthermore, because the deliberate transport, commerce and planting of non-native plant species can be controlled, all the invasive and potentially invasive species compiled into the Attention List could be considered for regulation, following the advice of the European Parliament and Council (2014). While some of these species have been introduced to provide an immediate economic benefit, such as *Eucalyptus globulus* and other species of the same genus (Touza et al. 2014), their impacts on the environment, as well as on some human activities besides the forestry sector, suggest that their regulation should be considered. In addition, the costs derived from the control of invasive species can be quite significant (Pimentel et al. 2005) and are not compensated for by their economic benefits.

The levels of potential impacts of species in the Attention List are independent of their invasion status in Spain. That is, current non-invasive species have the potential to cause as many impacts as invasive species. This result supports previous empirical studies indicating that invasiveness does not always translate to impacts (Ricciardi

and Cohen 2007). Despite the fact that some of these species were introduced a long time ago and are already invasive, such as *Ailanthus altissima* introduced into Spain in 1818 or *Acacia dealbata* in 1824 (Sanz Elorza et al. 2004), others have possibly been introduced recently as ornamental plants and thus have not had enough time for establishment and dispersal (Pemberton and Liu 2009). As a precautionary measure to avoid their impacts, there is a need to prevent the introduction of any non-native species listed in the Attention List and to conduct a complete risk assessment to study the possibility of their being regulated.

As the threshold number of environmental and socioeconomic impacts required for a species to be included or not in the Attention List is based on median values, it may exclude some species that have high risks of invasion despite a low number of impact types or species with still unknown impacts. In fact, the Watch List contains species that are well known to be invasive elsewhere, such as *Acer negundo* or *Eriobotrya japonica*, which cause few, but important, impacts. More detailed research on the potential type of impacts of the species in the Watch List, as well as conducting a WRA for these species, would allow for more adequate prioritisation of these species that are of major concern after those in the Priority and Attention Lists.

We are confident that the potential invasion of Attention List species is robust given the positive results of the WRA, in which only one of the 68 species listed was classified as accepted (i.e. low invasion risk). The proportion of species rejected by the WRA was very high and similar in all status groups of species, with a likely low incorporation of false positives (Andreu and Vilà 2010). Furthermore, our WRA analysis warns that species which are not in the wild, still have the potential to become invasive, reaching scores as high as those of already naturalised or invasive plants.

Likewise, with our analysis on the STV, we cannot infer causality between societal interest and increased commerce. In fact, the STV is not a good predictor of invasion status; the absence of differences between STV of the species in the Priority list and the Green list shows that the STV is not related with invasion. Nevertheless, greater interest, as reflected in Google statistics, can still be an indicator of increased consumption and trade (Vosen and Schmidt 2011) and greater interest might promote greater propagule pressure and greater potential to become established (Dehnen-Schmutz et al. 2007a; Johnston et al. 2009; Blackburn et al. 2013; García-Díaz et al. 2015). Thus, we think that the STV continues to have value, not as a predictor of invasion, but as a factor to be considered during prioritisation of the species within each invasion group.

Our approach is similar to previous Horizon-scanning analyses for non-native species (Roy et al. 2014, Roy et al. 2019) with the differences being that, in our study case, all the species are already in the region of analysis and the scoring is based on more parameters than just their potential to establish and cause impacts. We provide a Priority Index that includes the risk of invasion, the level of potential impacts and the popularity of the species. Therefore, it offers an integrative score that may be of interest to environmental administrations and management services as a valuable tool to support decision-making. The homogeneity in the Priority Index across the invasion status groups of species confirms that the potential for invasion and the impact

risks are independent of the actual invasion status of the species (Roberts et al. 2011; Gassó et al. 2010). Therefore, this index may even be useful for identifying current non-invasive species that, even if not in the wild, are potentially invasive. Indeed, our species Prioritisation List has already been used to identify species with the potential to be invasive in Gibraltar, an overseas territory of the United Kingdom which buys all its ornamental plants from neighbouring Spain according to the UKOTs Horizon Scanning and Biosecurity Workshop that took place on 21–24 January 2019 (K. Bensusan, pers. Com).

We also generated an Uncertainty List composed of species that probably do not represent an immediate invasion risk. For fifty-six percent of the species listed, we lack sufficient confidence in the likelihood of climatic suitability (or we have no information about it). Even if the species in the Uncertainty List do not become established in Spain due to their climatic requirements, or they are not invasive elsewhere, we need to be aware that these two criteria can change over time. For example, a particular climate change scenario could cause climatically unsuitable species to become suitable in the future (Mainka and Howard 2010).

Unfortunately, we could not find information on the status, invasive potential and climatic suitability of 61% of the non-native species sold in nurseries. There is a worrying possibility that the Data Deficient List includes some potentially invasive species that are not considered in the two major databases consulted (CABI Datasheets 2018; Invasive Species Specialist Group 2015). Additional research, as well as consultation of the primary literature, is needed to allow reclassifying species from the Data Deficient List, a task that would require the expertise of a larger team of scientists (Roy et al. 2019; González-Moreno et al. 2019). The immediate task would be to use the new available GLONAF database to identify invasive species elsewhere (van Kleunen et al. 2019).

Finally, we provide a Green List of non-native species with very low invasion potential. Promoting preferences for non-invasive species in horticulture can be a valuable endeavour in order to make regulations easier to comply with (Gagliardi and Brand 2007). Involving the horticultural industry in the dissemination of plant invasion risks and in the development of regulations has been shown to be effective (Humair et al. 2014). This Green List can be a starting point for the establishment of voluntary codes of conduct amongst nursery owners (Reichard 2004; Gagliardi and Brand 2007; Robinson et al. 2017). However, it is prudent not to forget that propagule pressure is an important factor determining invasion (Lockwood et al. 2005; 2009; Johnston et al. 2009).

If species in the Green List are planted frequently, in large quantities and in many locations, this scenario can be changed. For this reason, the Green List presented here is short and tentative; further and more in-depth research is needed on the Uncertainty List so as to possibly enlarge this Green List. Planting native species will always be the preferable alternative.

The present research is preliminary in nature and the authors are aware of the clear limitations of the conclusions. However, we consider it can be a very useful and complete tool to establish priorities in long lists of species for which not much information is available and it represents a good starting point for more thorough and detailed risk

analyses that allow the improvement and implementation of new and more efficient forms of regulation of invasive species.

Based on our prioritization list analysis, we provide the following recommendations: 1) there is a need to reinforce the current legislation and implement systems that guarantee its compliance regarding the species of the Priority List; 2) invasive species in the Attention List should be considered for regulation; 3) established, casual and not in the wild species in the Attention List, especially those with higher Priority Index values, should be included in a monitoring programme to prevent future invasions; 4) species in the Watch List should be included in an early warning programme if they are not yet in the wild and monitored if they are already established in a few localities; 5) species in the Uncertainty List require further evaluation in order to be reclassified into Attention, Watch or Green Lists; finally 6) species in Data Deficient List require further information on their status, invasive potential or climatic suitability in order to be reclassified into Attention, Watch or Green lists.

This research also reveals the limited responsibility and awareness by some commercial nurseries regarding the sale of invasive species. A better monitoring and tracking system for the species for sale and more rigorous inspections in nurseries are very necessary (Touza et al. 2014). Citizen awareness through the dissemination of knowledge about invasive non-native species, as well as citizen science projects working with gardeners, can be useful tools to reduce their demand and consumption as suggested in other studies (Reichard 2004; Gagliardi and Brand 2007; Robinson et al. 2017; Dehnen-Schmutz and Conroy 2018). Having a national registry of ornamental plant species available for sale and the requirement of a risk analysis for the introduction of new species in it, is also a recommendation to be considered.

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References

- AEMET (2016) AEMET (Agencia Estatal de Meteorología). <http://www.aemet.es/es/servicio-sclimaticos/datosclimatologicos> [Accessed 22 May 2016]
- Andreu J, Vilà M (2010) Risk analysis of potential invasive plants in Spain. *Journal for Nature Conservation* 18: 34–44. <https://doi.org/10.1016/j.jnc.2009.02.002>

- Bayón Á, Vilà M (2019) Dataset of Horizon scanning to identify invasion risk of ornamental plants marketed in Spain [Data set]. Neobiota. Zenodo. <http://doi.org/10.5281/zenodo.3367257>
- Blackburn TM, Essl F, Evans T, et al. (2014) A unified classification of alien species based on the magnitude of their environmental impacts. *PLOS Biology* 12(5): e1001850. <https://doi.org/10.1371/journal.pbio.1001850>
- Blackburn TM, Prowse TAA, Lockwood JL, Cassey P (2013) Propagule pressure as a driver of establishment success in deliberately introduced exotic species: Fact or artefact? *Biological Invasions* 15: 1459–1469. <https://doi.org/10.1007/s10530-013-0451-x>
- BOE (2013) Real Decreto 630/2013, de 2 de agosto, por el que se regula el Catálogo español de especies exóticas invasoras. *BOE* 185: 56764–56786
- Burivalova Z, Butler RA, Wilcove DS (2018) Analyzing Google search data to debunk myths about the public's interest in conservation. *Frontiers in Ecology and the Environment* 16(9):509–514. <https://doi.org/10.1002/fee.1962>
- CABI (2018) *Invasive Species Compendium*. CAB International, Wallingford. <https://www.cabi.org/isc> [Accessed 30 Jan 2016]
- Chrobock T, Kempel A, Fischer M, van Kleunen M (2011) Introduction bias: Cultivated alien plant species germinate faster and more abundantly than native species in Switzerland. *Basic and Applied Ecology* 12: 244–250. <https://doi.org/10.1016/j.baae.2011.03.001>
- Convention on Biological Diversity (2010) *Strategic Plan for Biodiversity 2011–2020*. <https://www.cbd.int/sp/default.shtml> [Accessed 12 May 2016]
- Cronin K, Kaplan H, Gaertner M, et al. (2017) Aliens in the nursery: assessing the attitudes of nursery managers to invasive species regulations. *Biological Invasions* 19: 925–937. <https://doi.org/10.1007/s10530-016-1363-3>
- Dehnen-Schmutz K (2011) Determining non-invasiveness in ornamental plants to build green lists. *Journal of Applied Ecology* 48: 1374–1380. <https://doi.org/10.1111/j.1365-2664.2011.02061.x>
- Dehnen-Schmutz K, Conroy J (2018) Working with gardeners to identify potential invasive ornamental garden plants: testing a citizen science approach. *Biological Invasions* 20: 3069–3077. <https://doi.org/10.1007/s10530-018-1759-3>
- Dehnen-Schmutz K, Touza J, Perrings C, Williamson M (2007) A century of the ornamental plant trade and its impact on invasion success. *Diversity and Distributions* 13: 527–534. <https://doi.org/10.1111/j.1472-4642.2007.00359.x>
- European Commission (2016) Commission Implementing Regulation (EU) 2016/1141 of 13 July 2016 adopting a list of invasive alien species of Union concern pursuant to Regulation (EU) No 1143/2014 of the European Parliament and of the Council.
- European Commission (2017) Commission Implementing Regulation (EU) 2017/1263 of 12 July 2017 updating the list of invasive alien species of Union concern established by Implementing Regulation (EU) 2016/1141 pursuant to Regulation (EU) No 1143/2014 of the European Parliament and of the Council.
- European Parliament and the Council of the European Union (2014) Regulation (EU) No 1143/2014 of 22 October on the prevention and management of the introduction and spread of invasive alien species. *Official Journal of the European Union*. L 317/35 – 317/55.

- Gagliardi JA, Brand MH (2007) Connecticut Nursery and Landscape Industry Preferences for Solutions to the Sale and Use of Invasive Plants. *HortTechnology* 17: 39–45. <https://doi.org/10.21273/HORTTECH.17.1.39>
- García-Díaz P, Ross JV, Ayres C, Cassey P (2015) Understanding the biological invasion risk posed by the global wildlife trade: propagule pressure drives the introduction and establishment of Nearctic turtles. *Global Change Biology* 21: 1078–91. <https://doi.org/10.1111/gcb.12790>
- Gassó N, Basnou C, Vilà M (2010) Predicting plant invaders in the Mediterranean through a weed risk assessment system. *Biological Invasions* 12: 463–476. <https://doi.org/10.1007/s10530-009-9451-2>
- Gassó N, Sol D, Pino J, Dana ED, Lloret F, Sanz-Elorza M, Sobrino E, Vilà M (2009) Exploring species attributes and site characteristics to assess plant invasions in Spain. *Diversity and Distribution* 15: 50–58. <https://doi.org/10.1111/j.1472-4642.2008.00501.x>
- Gederas L, Moen TL, Skjelseth S, Larsen L-K (Eds) (2012) Alien species in Norway – with the Norwegian Black List 2012. The Norwegian Biodiversity Information Centre, Norway.
- González-Moreno P, Diez JD, Ibáñez I, Font X, Vilà M (2014) Plant invasions are context-dependent: multiscale effects of climate, human activity and habitat. *Diversity and Distributions* 20: 720–731. <https://doi.org/10.1111/ddi.12206>
- Gordon DR, Onderdonk DA, Fox AM, Stocker RK (2008) Consistent accuracy of the Australian weed risk assessment system across varied geographies. *Diversity and Distributions* 14: 234–242. <https://doi.org/10.1111/j.1472-4642.2007.00460.x>
- Hulme PE (2007) Biological invasions in Europe: drivers, pressures, states, impacts and responses. *Issues in Environmental Science and Technology* 25: 56–80. <https://doi.org/10.1039/9781847557650-00056>
- Humair F, Humair L, Kuhn F, Kueffer C (2015) E-commerce trade in invasive plants. *Conservation Biology* 29: 1658–1665. <https://doi.org/10.1111/cobi.12579>
- Humair F, Siegrist M, Kueffer C (2014) Working with the horticultural industry to limit invasion risks: the Swiss experience. *EPPPO Bulletin* 44: 232–238. <https://doi.org/10.1111/epp.12113>
- Invasive Species Specialist Group ISSG (2015) The Global Invasive Species Database. Version 2015.1. <http://www.issg.org/database> [Accessed 23 May 2016]
- Johnston EL, Piola RF, Clark GF (2009) The Role of Propagule Pressure in Invasion Success. In: Rilov G, Crooks JA (Eds) *Biological Invasions in Marine Ecosystems. Ecological Studies (Analysis and Synthesis)* 204: 133–151. https://doi.org/10.1007/978-3-540-79236-9_7
- Lenda M, Skórka P, Knops JMH, et al. (2014) Effect of the internet commerce on dispersal modes of invasive alien species. *PLOS One* 9: e99786. <https://doi.org/10.1371/journal.pone.0099786>
- Leung B, Roura-Pascual N, Bacher S, et al. (2012) TEASIng apart alien species risk assessments: a framework for best practices. *Ecology Letters* 15: 1475–1493. <https://doi.org/10.1111/ele.12003>
- Lockwood JL, Cassey P, Blackburn TM (2009) The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions* 15: 904–910. <https://doi.org/10.1111/j.1472-4642.2009.00594.x>

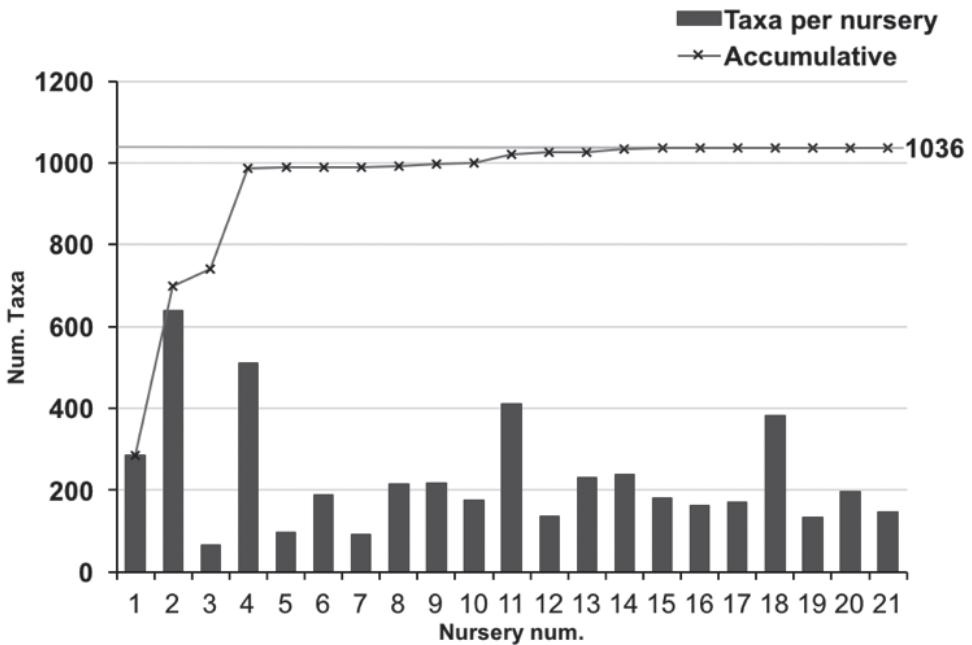
- Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution* 20: 223–228. <https://doi.org/10.1016/j.tree.2005.02.004>
- Mack RN, Simberloff D, Lonsdale WM, et al. (2000) Biotic Invasions: Causes, Epidemiology, Global Consequences, and Control. *Ecological Applications* 10: 689. <https://doi.org/10.2307/2641039>
- Mainka SA, Howard GW (2010) Climate change and invasive species: double jeopardy. *Integrative Zoology* 5(2):102–111. <https://doi.org/10.1111/j.1749-4877.2010.00193.x>
- Maurel N, Hanspach J, Kühn I, et al. (2016) Introduction bias affects relationships between the characteristics of ornamental alien plants and their naturalization success. *Global Ecology and Biogeography* 25: 1500–1509. <https://doi.org/10.1111/geb.12520>
- Niinemets Ü, Peñuelas J (2008) Gardening and urban landscaping: significant players in global change. *Trends in Plant Science* 13: 60–65. <https://doi.org/10.1016/j.tplants.2007.11.009>
- Ninyerola M, Pons X, Roure JM (2005) Atlas climático digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica. Universidad Autónoma de Barcelona, Bellaterra.
- Oftinowski R, Kenkel NC, Dixon P, Wilmschurst JF (2007) Integrating climate and trait models to predict the invasiveness of exotic plants in Canada's Riding Mountain National Park. *Canadian Journal of Plant Science* 87(5): 1001–1012. <https://doi.org/10.4141/CJPS07117>
- Parker JD, Torchin ME, Hufbauer RA, et al. (2013) Do invasive species perform better in their new ranges? *Ecology* 94: 985–994. <https://doi.org/10.1890/12-1810.1>
- Pemberton RW, Liu H (2009) Marketing time predicts naturalization of horticultural plants. *Ecology* 90: 69–80. <https://doi.org/10.1890/07-1516.1>
- Pheloung PC, Williams PA, Halloy SR (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *Journal of Environmental Management* 57: 239–251. <https://doi.org/10.1006/jema.1999.0297>
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273–288. <https://doi.org/10.1016/j.ecolecon.2004.10.002>
- Purcell K, Brenner J, Rainie L (2012) Search Engine Use 2012. In: Pew Research Center Internet and Technology. <http://www.pewinternet.org/2012/03/09/search-engine-use-2012> [Accessed 22 Jan 2018]
- Pyšek P, Richardson D M, Rejmánek M, Webster G, Williamson M, Kirschner J (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* 53: 131–143. <https://doi.org/10.2307/4135498>
- Reichard SH (2004) Conflicting Values and Common Goals: Codes of Conduct to Reduce the Threat of Invasive Species. *Weed Technology* 18: 1503–1507. [https://doi.org/10.1614/0890-037X\(2004\)018\[1503:CVACGC\]2.0.CO;2](https://doi.org/10.1614/0890-037X(2004)018[1503:CVACGC]2.0.CO;2)
- Ricciardi A, Cohen J (2007) The invasiveness of an introduced species does not predict its impact. *Biological Invasions* 9: 309–315. <https://doi.org/10.1007/s10530-006-9034-4>
- Richardson DM, Pyšek P, Rejmanek M, et al. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6: 93–107. <https://doi.org/10.1046/j.1472-4642.2000.00083.x>

- Roberts W, Harrod O, Mitterdorfer B, Pheloung P (2011) Regulating invasive plants and use of weed risk assessments. *Current Opinion in Environmental Sustainability* 3(1–2): 60–65. <https://doi.org/10.1016/j.cosust.2010.11.007>
- Robinson BS, Inger R, Crowley SL, Gaston KJ (2017) Weeds on the web: conflicting management advice about an invasive non-native plant. *Journal of Applied Ecology* 54: 178–187. <https://doi.org/10.1111/1365-2664.12712>
- Roy HE, Bacher S, Essl F, et al. (2019) Developing a list of invasive alien species likely to threaten biodiversity and ecosystems in the European Union. *Global Change Biology* 25: 1032–1048. <https://doi.org/10.1111/gcb.14527>
- Roy HE, European Commission, Directorate-General for the Environment, CEH (Centre of Ecology and Hydrology) (2015) Invasive alien species: prioritising prevention efforts through horizon scanning: final report. Publications Office, Luxembourg.
- Roy HE, Peyton J, Aldridge DC, et al. (2014) Horizon scanning for invasive alien species with the potential to threaten biodiversity in Great Britain. *Global Change Biology* 3859–3871. <https://doi.org/10.1111/gcb.12603>
- Sanz Elorza M, Dana ED, Sobrino E (Eds) (2004) Atlas de las Plantas Alóctonas Invasoras en España. Dirección General para la Biodiversidad, Madrid.
- Simberloff D, Martin J-L, Genovesi P, et al. (2013) Impacts of biological invasions: what's what and the way forward. *Trends in Ecology and Evolution* 28: 58–66. <https://doi.org/10.1016/j.tree.2012.07.013>
- Touza J, Pérez-Alonso A, Chas-Amil ML, Dehnen-Schmutz K (2014) Explaining the rank order of invasive plants by stakeholder groups. *Ecological Economics* 105: 330–341. <https://doi.org/10.1016/j.ecolecon.2014.06.019>
- Van Kleunen M, Dawson W, Essl F, et al. (2015) Global exchange and accumulation of non-native plants. *Nature* 525: 100–103. <https://doi.org/10.1038/nature14910>
- Van Kleunen M, Essl F, Pergl J, et al. (2018) The changing role of ornamental horticulture in alien plant invasions. *Biological Reviews* 93(3): 1421–1437 <https://doi.org/10.1111/brv.12402>
- Van Kleunen M, Pyšek P, Dawson W, et al. (2019) The Global Naturalized Alien Flora (GloNAF) database. *Ecology* 100: e02542. <https://doi.org/10.1002/ecy.2542>
- Vilà M, Gallardo B, Preda C, et al. (2019) A review of impact assessment protocols of non-native plants. *Biological Invasions* 21: 709–723. <https://doi.org/10.1007/s10530-018-1872-3>
- Vosen S, Schmidt T (2011) Forecasting private consumption: survey-based indicators vs. Google trends. *Journal of Forecasting* 30: 565–578. <https://doi.org/10.1002/for.1213>
- Walters LJ, Brown KR, Stam WT, Olsen JL (2006) E-commerce and *Caulerpa*: unregulated dispersal of invasive species. *Frontiers in Ecology and the Environment* 4: 75–79. [https://doi.org/10.1890/1540-9295\(2006\)004\[0075:EACUDO\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2006)004[0075:EACUDO]2.0.CO;2)
- Weber E, Gut D (2004) Assessing the risk of potentially invasive plant species in central Europe. *Journal for Nature Conservation* 12: 171–179. <https://doi.org/10.1016/j.jnc.2004.04.002>
- Wirrh FF, Davis KJ, Wilson SB (2004) Florida Nursery Sales and Economic Impacts of 14 Potentially Invasive Landscape Plant Species. *Journal of Environmental Horticulture* 22: 12–16. <https://doi.org/10.24266/0738-2898-22.1.12>

Appendix I

Table AI. Nurseries. The list of taxa was compiled through the systematic consultation of Spanish nursery catalogs which provide information on plants for sale. As shown in the graph below, the number of taxa did not increase after the 15th catalog was consulted. Our database included a total of 1036 taxa from 21 nurseries. Notice that these nurseries are distributed across all biogeographic regions of mainland Spain.

	Nursery	Source	Access date	Province	Num. taxa
1	Viveros Plantamus	https://plantamus.com	11/12/15	A Coruña	286
2	Viveros Sanchez	http://viverossanchez.com	01/04/16	Guadalajara	638
3	Viveros Maiplant	http://www.maiplant.com	02/23/16	Alicante	66
4	Alberola Viveros	http://www.alberolaviveros.com	02/23/16	Valencia	510
5	Viveros Bargas	http://www.viverosbargas.com	02/24/16	Valencia	97
6	Viveros Rucat	http://www.viverosrucat.es	01/26/16	Madrid	189
7	Viveros Veron	http://viverosveron.com	01/26/16	Zaragoza	92
8	Garden Center Campo Grande	http://www.campogrande.es	01/31/16	Valladolid	214
9	Plantas del Sueve	http://www.delsueve.com	02/01/16	Asturias	217
10	Viveros Urkiondo	http://www.urkiondo.com	02/09/16	Guipuzkoa	174
11	Viveros Barra	http://viverosbarra.es	05/01/16	Leon	410
12	Viveros Coplant	http://www.coplant.es	05/20/16	Pontevedra	137
13	Viveros Borrazas	http://www.viverosborrazas.com	06/11/16	A Coruña	231
14	Viveros Zuaime	http://www.viveroszuaime.es	06/14/16	Granada	238
15	Viveros Sevilla	http://www.viverossevilla.com	06/16/16	Sevilla	180
16	Viveros Ferca	http://viverosferca.com	07/28/16	Ciudad Real	162
17	Viveros Ibañez	http://www.viverosibanez.es	09/20/16	Zaragoza	171
18	Viveros Corma	http://www.corma.es	09/30/16	Barcelona	383
19	Viveros Canós	http://viveroscanos.com	09/30/16	Badajoz	132
20	Viveros Perica	http://viverosperica.com	10/03/16	La Rioja	195
21	Viveros Ametza	http://www.viverosametza.com	10/03/16	Navarra	147



Appendix 2

Table A2. Watch list. The Watch List includes invasive and potentially invasive species with potential impacts below median; classified as: a) not in the wild, b) casual, c) naturalized and d) invasive species. Native distribution: Afr: Africa; As: Asia (Temperate); AT: Asia (Tropical); Aus: Australia; NAm: North America; SAm: South and Center America.

	Family	Native distribution	Impacts	
			Environment	Socioeconomics
a) Species not in the wild				
<i>Berberis darwinii</i>	Berberidaceae	SAm	2	0
<i>Euonymus alata</i>	Celastraceae	As	2	0
<i>Ficus elastica</i>	Moraceae	As	2	0
<i>Fraxinus americana</i>	Oleaceae	NAm	0	0
<i>Gunnera manicata</i>	Gunneraceae	SAm	2	0
<i>Pyrus calleryana</i>	Rosaceae	As, AT	0	0
<i>Thevetia peruviana</i>	Apocynaceae	NAm, SAm	0	0
<i>Zelkova serrata</i>	Ulmaceae	As, AT	0	0
b) Casual species				
<i>Ageratum houstonianum</i>	Asteraceae	SAm	0	0
<i>Aloe vera</i>	Liliaceae	Afr	0	0
<i>Corymbia citriodora</i>	Myrtaceae	Aus	0	0
<i>Erigeron karvinskianus</i>	Asteraceae	SAm	0	0
<i>Lagerstroemia indica</i>	Lythraceae	As, AT	2	0
<i>Salix babylonica</i>	Salicaceae	As	0	0
<i>Salvia microphylla</i>	Lamiaceae	NAm	1	0
<i>Trachycarpus fortunei</i>	Arecaceae	As	1	0
c) Naturalized species				
<i>Alpinia zerumbet</i>	Zingiberaceae	AT	2	0
<i>Berberis aquifolium</i>	Berberidaceae	NAm	1	0
<i>Parthenocissus quinquefolia</i>	Vitaceae	NAm	0	0
<i>Passiflora edulis</i>	Passifloraceae	SAm	2	0
d) Invasive species				
<i>Acer negundo</i>	Aceraceae	NAm	1	0
<i>Cyperus alternifolius</i>	Cyperaceae	Afr	0	0
<i>Eriobotrya japonica</i>	Rosaceae	As	0	0
<i>Eucalyptus camaldulensis</i>	Myrtaceae	Aus	1	0
<i>Oenothera biennis</i>	Onagraceae	NAm	1	0
<i>Pelargonium capitatum</i>	Geraniaceae	Afr	2	0
<i>Tropaeolum majus</i>	Tropaeolaceae	SAm	0	0

Appendix 3

Table A3. Uncertainty list. The Uncertainty List includes non-invasive and potentially non-invasive species which lack sufficient information, or those that do not meet the requirements to be included in the Green List; classified as: a) not in the wild, b) casual, and c) naturalized species. Native distribution: Afr: Africa; As: Asia (Temperate); AT: Asia (Tropical); Aus: Australia; Eur: Europe; NAm: North America; Pac: Pacific; SAM: South and Center America. Invasive elsewhere and climate suitability: Y: yes; N: no; Confidence in the likelihood of climatic suitability: H: high; M: med.

	Family	Native distribution	Invasive elsewhere	Climate suitability	Confidence
a) Species not in the wild					
<i>Agave vivipara</i>	Agavaceae	SAM	Y	Y	L
<i>Anubias barteri</i>	Araceae	Afr	N	N	L
<i>Anubias hastifolia</i>	Araceae	Afr	Y	N	L
<i>Anubias heterophylla</i>	Araceae	Afr	Y	N	L
<i>Bacopa caroliniana</i>	Plantaginaceae	NAm	N	Y	L
<i>Bismarckia nobilis</i>	Arecaceae	Afr	N	N	L
<i>Blyxa japonica</i>	Hydrocharitaceae	NAm	N	Y	H
<i>Brabea armata</i>	Arecaceae	NAm	N	Y	L
<i>Brabea edulis</i>	Arecaceae	NAm	N	Y	L
<i>Butia capitata</i>	Arecaceae	SAM	N	Y	L
<i>Cabomba furcata</i>	Cabombaceae	SAM	N	Y	L
<i>Campanula portenschlagiana</i>	Campanulaceae	Eur	N	Y	H
<i>Carex buchananii</i>	Cyperaceae	Aus	N	Y	L
<i>Chamaedorea seifrizii</i>	Arecaceae	NAm	N	Y	L
<i>Clematis montana</i>	Ranunculaceae	As	N	Y	M
<i>Cordyline australis</i>	Asparagaceae	Aus	N	Y	L
<i>Corymbia ficifolia</i>	Myrtaceae	Aus	N	Y	L
<i>Cotinus coggygria</i>	Anacardiaceae	As	N	Y	H
<i>Cryptostegia madagascariensis</i>	Apocynaceae	Afr	Y	N	H
<i>Cycas revoluta</i>	Cycadaceae	As	N	Y	L
<i>Delonix regia</i>	Fabaceae	Afr	Y	N	H
<i>Euphorbia lactea</i>	Euphorbiaceae	SAM	Y	N	M
<i>Ficus lyrata</i>	Moraceae	Afr	N	Y	M
<i>Ficus microcarpa</i>	Moraceae	Aus	Y	Y	L
<i>Freesia alba</i>	Iridaceae	Afr	N	Y	M
<i>Fuchsia magellanica</i>	Onagraceae	SAM	Y	N	M
<i>Gardenia jasminoides</i>	Rubiaceae	As, AT	N	Y	M
<i>Gaultheria mucronata</i>	Ericaceae	SAM	N	Y	L
<i>Gaura lindheimeri</i>	Onagraceae	NAm	N	Y	M
<i>Geum coccineum</i>	Rosaceae	Eur	N	Y	M
<i>Glossostigma elatinoides</i>	Phrymaceae	Aus	N	Y	H
<i>Lilaeopsis brasiliensis</i>	Apiaceae	SAM	N	Y	L
<i>Liriope muscari</i>	Liliaceae	As, NAm	N	Y	L
<i>Livistona chinensis</i>	Arecaceae	As	Y	N	L
<i>Lonicera pileata</i>	Caprifoliaceae	As	N	Y	L
<i>Loropetalum chinense</i>	Hamamelidaceae	As	N	Y	M
<i>Mayaca fluviatilis</i>	Mayacaceae	SAM	N	Y	L

	Family	Native distribution	Invasive elsewhere	Climate suitability	Confidence
<i>Myoporum tetrandrum</i>	Scrophulariaceae	Aus	N	Y	L
<i>Ophiopogon japonicus</i>	Asparagaceae	As	N	Y	H
<i>Opuntia microdasys</i>	Cactaceae	NAm	N	Y	H
<i>Perovskia atriplicifolia</i>	Lamiaceae	As	N	Y	M
<i>Pittosporum tenuifolium</i>	Pittosporaceae	Pac	N	Y	L
<i>Pogostemon stellatus</i>	Lamiaceae	AT, Aus	N	N	L
<i>Rotala wallichii</i>	Lythraceae	As	N	Y	L
<i>Serenoa repens</i>	Arecaceae	NAm	N	Y	L
<i>Vaccinium corymbosum</i>	Ericaceae	NAm	N	Y	M
b) Casual species					
<i>Acacia baileyana</i>	Fabaceae	Aus	N	NA	NA
<i>Acer campestre</i>	Sapindaceae	Afr, Eur	N	NA	NA
<i>Aloe arborescens</i>	Liliaceae	Afr	N	NA	NA
<i>Aloe maculata</i>	Liliaceae	Afr	N	Y	H
<i>Aloysia citrodora</i>	Verbenaceae	SAm	N	Y	H
<i>Anthriscus cerefolium</i>	Apiaceae	Eur	N	NA	NA
<i>Artemisia dracunculus</i>	Asteraceae	As, Eur, NAm	N	NA	NA
<i>Brachychiton populneus</i>	Malvaceae	Aus	N	NA	NA
<i>Caesalpinia gilliesii</i>	Fabaceae	SAm	N	NA	NA
<i>Callistemon citrinus</i>	Myrtaceae	Aus	N	NA	NA
<i>Calocedrus decurrens</i>	Cupressaceae	NAm	N	NA	NA
<i>Campsis radicans</i>	Bignoniaceae	NAm	N	NA	NA
<i>Catalpa bignonioides</i>	Bignoniaceae	NAm	N	NA	NA
<i>Catharanthus roseus</i>	Apocynaceae	Afr	N	NA	NA
<i>Cedrus deodara</i>	Pinaceae	As	N	NA	NA
<i>Cedrus libani</i>	Pinaceae	Eur	N	NA	NA
<i>Cercis siliquastrum</i>	Fabaceae	Eur	N	NA	NA
<i>Coffea arabica</i>	Rubiaceae	Afr	N	NA	NA
<i>Crassula ovata</i>	Crassulaceae	Afr	N	Y	M
<i>Cupressus arizonica</i>	Cupressaceae	NAm	N	NA	NA
<i>Cupressus macrocarpa</i>	Cupressaceae	NAm	N	NA	NA
<i>Cydonia oblonga</i>	Rosaceae	Eur	N	NA	NA
<i>Diospyros kaki</i>	Ebenaceae	As	N	NA	NA
<i>Eucalyptus gunnii</i>	Myrtaceae	Aus	N	NA	NA
<i>Euonymus japonicus</i>	Celastraceae	As	N	NA	NA
<i>Euphorbia candelabrum</i>	Euphorbiaceae	Afr	N	NA	NA
<i>Helianthus annuus</i>	Asteraceae	NAm	N	NA	NA
<i>Hibiscus rosa-sinensis</i>	Malvaceae	As	N	NA	NA
<i>Hibiscus syriacus</i>	Malvaceae	As	N	NA	NA
<i>Hyacinthus orientalis</i>	Asparagaceae	Afr, AT	N	NA	NA
<i>Jacaranda mimosifolia</i>	Bignoniaceae	SAm	N	NA	NA
<i>Jasminum nudiflorum</i>	Oleaceae	As	N	NA	NA
<i>Jasminum officinale</i>	Oleaceae	As	N	Y	H
<i>Juglans nigra</i>	Juglandaceae	NAm	N	NA	NA
<i>Koeleruteria paniculata</i>	Sapindaceae	As	N	NA	NA
<i>Lagunaria patersonii</i>	Malvaceae	Aus	N	NA	NA
<i>Larix decidua</i>	Pinaceae	Eur	N	NA	NA

	Family	Native distribution	Invasive elsewhere	Climate suitability	Confidence
<i>Lepidium sativum</i>	Brassicaceae	Afr	N	NA	NA
<i>Ligustrum ovalifolium</i>	Oleaceae	As	N	NA	NA
<i>Lobelia erinus</i>	Campanulaceae	Afr	N	NA	NA
<i>Lycium barbarum</i>	Solanaceae	As	N	NA	NA
<i>Malus domestica</i>	Rosaceae	As	N	NA	NA
<i>Mimosa pudica</i>	Fabaceae	SAm	Y	Y	L
<i>Monstera deliciosa</i>	Araceae	SAm	N	NA	NA
<i>Origanum majorana</i>	Lamiaceae	As, Eur	N	NA	NA
<i>Phytolacca dioica</i>	Phytolaccaceae	SAm	N	NA	NA
<i>Pinus canariensis</i>	Pinaceae	Afr	N	NA	NA
<i>Pinus strobus</i>	Pinaceae	NAm	N	NA	NA
<i>Pistacia vera</i>	Anacardiaceae	As, Eur	N	NA	NA
<i>Pittosporum tobira</i>	Pittosporaceae	As	N	NA	NA
<i>Plumbago auriculata</i>	Plumbaginaceae	Afr	N	NA	NA
<i>Populus simonii</i>	Salicaceae	As	N	NA	NA
<i>Prunus armeniaca</i>	Rosaceae	NAm	N	NA	NA
<i>Prunus domestica</i>	Rosaceae	Eur	N	NA	NA
<i>Pseudotsuga menziesii</i>	Pinaceae	NAm	N	NA	NA
<i>Ruta graveolens</i>	Rutaceae	Eur	N	NA	NA
<i>Salvia splendens</i>	Lamiaceae	SAm	Y	N	M
<i>Sedum sexangulare</i>	Crassulaceae	Eur	N	Y	H
<i>Sedum spurium</i>	Crassulaceae	Eur	N	NA	NA
<i>Solanum pseudocapsicum</i>	Solanaceae	SAm	N	NA	NA
<i>Spathodea campanulata</i>	Bignoniaceae	SAm	Y	N	L
<i>Syringa vulgaris</i>	Oleaceae	Eur	N	NA	NA
<i>Tagetes erecta</i>	Asteraceae	NAm	N	Y	M
<i>Tagetes patula</i>	Asteraceae	SAm	N	NA	NA
<i>Thunbergia alata</i>	Acanthaceae	Afr	Y	N	L
<i>Tipuana tipu</i>	Fabaceae	SAm	N	NA	NA
<i>Ulmus pumila</i>	Ulmaceae	As, AT	Y	Y	L
<i>Washingtonia filifera</i>	Arecaceae	NAm	N	NA	NA
<i>Zinnia elegans</i>	Asteraceae	SAm	N	NA	NA
c) Naturalized species					
<i>Actinidia chinensis</i>	Actinidiaceae	As	N		
<i>Aeonium arboreum</i>	Crassulaceae	Afr	N		
<i>Aesculus hippocastanum</i>	Sapindaceae	Eur	N		
<i>Alnus cordata</i>	Betulaceae	Eur	N		
<i>Ammannia coccinea</i>	Lythraceae	NAm	N		
<i>Anethum graveolens</i>	Apiaceae	Afr	N		
<i>Anthurium scherzerianum</i>	Anthuriaceae	As-Eur	N		
<i>Aptenia cordifolia</i>	Aizoaceae	Afr	N		
<i>Aquilegia vulgaris</i>	Ranunculaceae	As, Eur	N		
<i>Austrocylindropuntia cylindrica</i>	Cactaceae	SAm	N		
<i>Bougainvillea glabra</i>	Nyctaginaceae	SAm	N		
<i>Cedrus atlantica</i>	Pinaceae	Afr	N		
<i>Cerastium tomentosum</i>	Caryophyllaceae	Eur	N		
<i>Chamaecyparis lawsoniana</i>	Cupressaceae	NAm	N		

	Family	Native distribution	Invasive elsewhere	Climate suitability	Confidence
<i>Chamaedorea elegans</i>	Arecaceae	NAm	N		
<i>Crataegus azarolus</i>	Rosaceae	Afr, As, Eur	N		
<i>Cuminum cyminum</i>	Apiaceae	Eur	N		
<i>Cupressus sempervirens</i>	Cupressaceae	Eur	N		
<i>Erysimum odoratum</i>	Brassicaceae	Eur	N		
<i>Euphorbia millii</i>	Euphorbiaceae	Afr	N		
<i>Hydrangea macrophylla</i>	Hydrangeaceae	As	N		
<i>Hydrocotyle verticillata</i>	Araliaceae	NAm	N		
<i>Hypericum calycinum</i>	Hypericaceae	Eur	N		
<i>Impatiens walleriana</i>	Balsaminaceae	Afr	N		
<i>Laburnum anagyroides</i>	Fabaceae	Eur	N		
<i>Lonicera nitida</i>	Caprifoliaceae	AS	N		
<i>Mespilus germanica</i>	Rosaceae	As, Eur	N		
<i>Parthenocissus tricuspidata</i>	Vitaceae	As, AT	N		
<i>Pelargonium graveolens</i>	Geraniaceae	Afr	N		
<i>Pelargonium peltatum</i>	Geraniaceae	Afr	N		
<i>Petroselinum crispum</i>	Apiaceae	Eur	N		
<i>Phoenix dactylifera</i>	Arecaceae	As	N		
<i>Physocarpus opulifolius</i>	Rosaceae	NAm	N		
<i>Picea abies</i>	Pinaceae	Eur	N		
<i>Picea omorika</i>	Pinaceae	Eur	N		
<i>Prunus cerasifera</i>	Rosaceae	Eur	N		
<i>Prunus laurocerasus</i>	Rosaceae	As	N		
<i>Pyrostegia venusta</i>	Bignoniaceae	SAm	N		
<i>Quercus rubra</i>	Fagaceae	NAm	N		
<i>Salix viminalis</i>	Salicaceae	Eur	N		
<i>Sequoiadendron giganteum</i>	Cupressaceae	NAm	N		
<i>Styphnolobium japonicum</i>	Fabaceae	As	N		
<i>Tamarix parviflora</i>	Tamaricaceae	Afr	N		
<i>Vitis vinifera</i>	Vitaceae	Eur	N		
<i>Washingtonia robusta</i>	Arecaceae	NAm	N		
<i>Yucca gloriosa</i>	Agavaceae	NAm	N		

Appendix 4

Table A4. Data deficient list. The Data Deficient List includes species for which we did not have sufficient data for analysis. Native distribution: Afr: Africa; As: Asia (Temperate); AT: Asia (Tropical); Aus: Australia; Eur: Europe; NAM: North America; Pac: Pacific; SAM: South and Center America.

Species with deficient data	Family	Native distribution
<i>Abelia chinensis</i>	Caprifoliaceae	As
<i>Abelia floribunda</i>	Caprifoliaceae	Nam
<i>Abies concolor</i>	Pinaceae	NAM
<i>Abies koreana</i>	Pinaceae	As
<i>Abies nordmanniana</i>	Pinaceae	As, Eur
<i>Abies procera</i>	Pinaceae	NAM
<i>Acacia floribunda</i>	Fabaceae	Aus
<i>Acacia pendula</i>	Fabaceae	Aus
<i>Acca sellowiana</i>	Myrtaceae	SAM
<i>Acer palmatum</i>	Sapindaceae	As
<i>Acer rubrum</i>	Sapindaceae	NAM
<i>Acer saccharinum</i>	Sapindaceae	NAM
<i>Acorus gramineus</i>	Acoraceae	AT, AS
<i>Actinidia arguta</i>	Actinidiaceae	As
<i>Actinidia deliciosa</i>	Actinidiaceae	As
<i>Adenium obesum</i>	Apocynaceae	Afr
<i>Aechmea fasciata</i>	Bromeliaceae	SAM
<i>Agapanthus africanus</i>	Amaryllidaceae	Afr
<i>Agave attenuata</i>	Agavaceae	SAM
<i>Agave bracteosa</i>	Agavaceae	NAM
<i>Agave filifera</i>	Agavaceae	SAM
<i>Agave guiengola</i>	Agavaceae	SAM
<i>Agave horrida</i>	Agavaceae	SAM
<i>Agave lechuguilla</i>	Agavaceae	SAM
<i>Agave macroacantha</i>	Agavaceae	SAM
<i>Agave salmiana</i>	Agavaceae	SAM
<i>Agave victoriae-reginae</i>	Agavaceae	SAM
<i>Agave xylonacantha</i>	Agavaceae	SAM
<i>Allagoptera arenaria</i>	Arecaceae	SAM
<i>Allium schoenoprasum</i>	Amaryllidaceae	NAM
<i>Alocasia wentii</i>	Araceae	Aus
<i>Aloe marlothii</i>	Liliaceae	Afr
<i>Aloe variegata</i>	Xanthorrhoeaceae	Afr
<i>Alpinia caerulea</i>	Zigimberaceae	Aus
<i>Alternanthera peruensis</i>	Amaranthaceae	SAM
<i>Alternanthera reinekii</i>	Amaranthaceae	SAM
<i>Alternanthera rosaeivolia</i>	Amaranthaceae	SAM
<i>Anacardium occidentale</i>	Anacardiaceae	SAM
<i>Andromeda polifolia</i>	Ericaceae	Eur, As, NAM
<i>Anemantele lessoniana</i>	Poaceae	Aus
<i>Anemone blanda</i>	Ranunculaceae	Eur
<i>Anisodonte capensis</i>	Malvaceae	Afr

Species with deficient data	Family	Native distribution
<i>Aphelandra squarrosa</i>	Acanthaceae	SAm
<i>Arabis alpina</i>	Brassicaceae	AT
<i>Araucaria araucana</i>	Araucariaceae	SAm
<i>Araucaria heterophylla</i>	Araucariaceae	Aus
<i>Archontophoenix alexandreae</i>	Arecaceae	Aus
<i>Archontophoenix purpurea</i>	Arecaceae	Aus
<i>Arctotis fastuosa</i>	Asteraceae	Afr
<i>Arenga engleri</i>	Arecaceae	AT
<i>Argyranthemum frutescens</i>	Asteraceae	Afr
<i>Arrojadoa rhodantha</i>	Cactaceae	SAm
<i>Asparagus setaceus</i>	Asparagaceae	Afr
<i>Aspidistra elatior</i>	Asparagaceae	AT
<i>Athyrium nipponicum</i>	Athyriaceae	As
<i>Aucuba japonica</i>	Garryaceae	As
<i>Balantium antarcticum</i>	Dicksoniaceae	Aus
<i>Banksia integrifolia</i>	Proteaceae	Aus
<i>Bauhinia purpurea</i>	Fabaceae	SAm
<i>Beaucarnea recurvata</i>	Asparagaceae	SAm
<i>Begonia cucullata</i>	Begoniaceae	AT
<i>Begonia rex</i>	Begoniaceae	AT
<i>Berberis julianae</i>	Berberidaceae	As
<i>Berberis microphylla</i>	Berberidaceae	SAm
<i>Bergenia cordifolia</i>	Saxifragaceae	As
<i>Beschorneria yuccoides</i>	Agavaceae	NAm
<i>Betula papyrifera</i>	Betulaceae	NAm
<i>Betula utilis</i>	Betulaceae	As
<i>Boronia crenulata</i>	Rutaceae	Aus
<i>Boswellia carterii</i>	Burseraceae	Afr
<i>Brachychiton acerifolius</i>	Malvaceae	Aus
<i>Brachychiton bidwillii</i>	Malvaceae	Aus
<i>Brachychiton discolor</i>	Malvaceae	Aus
<i>Brachychiton rupestris</i>	Malvaceae	Aus
<i>Brachyscome multifida</i>	Asteraceae	Aus
<i>Brasiliopuntia brasiliensis</i>	Cactaceae	SAm
<i>Bulbine frutescens</i>	Liliaceae	Afr
<i>Butia eriostatha</i>	Arecaceae	SAm
<i>Butia yatai</i>	Arecaceae	SAm
<i>Buxus microphylla</i>	Buxaceae	As
<i>Callistemon viminalis</i>	Myrtaceae	Aus
<i>Callistephus chinensis</i>	Asteraceae	As
<i>Callitropsis nootkatensis</i>	Cupressaceae	NAm
<i>Calothamnus quadrifidus</i>	Myrtaceae	Aus
<i>Camellia japonica</i>	Theaceae	As
<i>Camellia sasanqua</i>	Theaceae	As
<i>Campanula carpatica</i>	Campanulaceae	Eur
<i>Campanula isophylla</i>	Campanulaceae	Eur
<i>Carex comans</i>	Cyperaceae	Aus
<i>Carica papaya</i>	Caricaceae	SAm

Species with deficient data	Family	Native distribution
<i>Carissa macrocarpa</i>	Apocynaceae	Afr
<i>Carya illinoensis</i>	Juglandaceae	NAm
<i>Caryota maxima</i>	Arecaceae	Eur
<i>Caryota mitis</i>	Arecaceae	AT
<i>Caryota wrens</i>	Arecaceae	AT
<i>Casimiroa edulis</i>	Rutaceae	SAm
<i>Catalpa bungei</i>	Bignoniaceae	As
<i>Ceanothus integerrimus</i>	Rhamnaceae	NAm
<i>Ceiba speciosa</i>	Malvaceae	SAm
<i>Celtis occidentalis</i>	Cannabaceae	NAm
<i>Cephalocereus senilis</i>	Cactaceae	NAm
<i>Cercidiphyllum japonicum</i>	Cercidiphyllaceae	As
<i>Cereus jamacaru</i>	Cactaceae	SAm
<i>Ceropegia woodii</i>	Apocynaceae	Afr
<i>Chaenomeles japonica</i>	Rosaceae	As
<i>Chamaecyparis obtusa</i>	Cupressaceae	As
<i>Chamaecyparis pisifera</i>	Cupressaceae	As
<i>Chamaecyparis thuyoides</i>	Cupressaceae	NAm
<i>Chambeyronia macrocarpa</i>	Arecaceae	Aus
<i>Chamelaucium uncinatum</i>	Myrtaceae	Aus
<i>Chlorophytum comosum</i>	Agavaceae	Afr
<i>Choisya ternata</i>	Rutaceae	NAm
<i>Citronella mucronata</i>	Cardiopteridaceae	SAm
<i>Citrus limetta</i>	Rutaceae	As
<i>Citrus medica</i>	Rutaceae	AT
<i>Citrus reticulata</i>	Rutaceae	As
<i>Cleistocactus strausii</i>	Cactaceae	SAm
<i>Cleyera japonica</i>	Pentaphragmaceae	As
<i>Cocos nucifera</i>	Arecaceae	Afr, AT, SAm, Pac
<i>Codiaeum variegatum</i>	Euphorbiaceae	AT
<i>Convolvulus cneorum</i>	Convolvulaceae	Eur, Afr
<i>Copernicia alba</i>	Arecaceae	SAm
<i>Cordyline fruticosa</i>	Asparagaceae	AT
<i>Cordyline indivisa</i>	Asparagaceae	Aus
<i>Coreopsis grandiflora</i>	Asteraceae	NAm
<i>Cornus controversa</i>	Cornaceae	As
<i>Cornus forida</i>	Cornaceae	NAm
<i>Cornus kousa</i>	Cornaceae	As
<i>Corylus colurna</i>	Betulaceae	As, Eur
<i>Corylus maxima</i>	Betulaceae	Eur
<i>Cotoneaster coriaceus</i>	Rosaceae	AT
<i>Cotoneaster dammeri</i>	Rosaceae	As
<i>Cotoneaster salicifolius</i>	Rosaceae	As
<i>Crassula sarcocaulis</i>	Crassulaceae	Afr
<i>Crotalaria capensis</i>	Fabaceae	Afr
<i>Cryptocoryne albida</i>	Araceae	AT
<i>Cryptocoryne parva</i>	Araceae	AT
<i>Cryptocoryne pygmaea</i>	Araceae	AT

Species with deficient data	Family	Native distribution
<i>Cryptocoryne tonkinensis</i>	Araceae	AT
<i>Cryptocoryne walkeri</i>	Araceae	AT
<i>Cryptocoryne wendtii</i>	Araceae	AT
<i>Cryptomeria japonica</i>	Cupressaceae	As
<i>Cuphea hyssopifolia</i>	Lythraceae	NAM
<i>Cussonia spicata</i>	Araliaceae	Afr
<i>Cycas circinalis</i>	Cycadaceae	AT
<i>Cyclamen persicum</i>	Primulaceae	Eur
<i>Cyperus papyrus</i>	Cyperaceae	Afr
<i>Dasyllirion lucidum</i>	Asparagaceae	NAM
<i>Dasyllirion serratifolium</i>	Asparagaceae	NAM
<i>Delosperma congestum</i>	Aizoaceae	Afr
<i>Dianthus chinensis</i>	Caryophyllaceae	As
<i>Dieffenbachia seguine</i>	Araceae	SAM
<i>Dionaea muscipula</i>	Droseraceae	NAM
<i>Dioon edule</i>	Zamiaceae	NAM
<i>Dombeya tiliacea</i>	Malvaceae	Afr
<i>Dracaena braunii</i>	Asparagaceae	Afr
<i>Dracaena draco</i>	Asparagaceae	Afr
<i>Dracaena fragans</i>	Asparagaceae	Afr
<i>Dracaena reflexa</i>	Asparagaceae	Afr
<i>Drosanthemum speciosum</i>	Aizoaceae	Afr
<i>Dyopsis decaryi</i>	Arecaceae	Afr
<i>Dyopsis decipiens</i>	Arecaceae	Afr
<i>Dyopsis lutescens</i>	Arecaceae	Afr
<i>Echinodorus tenellus</i>	Alismataceae	NAM
<i>Echinocactus grusonii</i>	Cactaceae	NAM
<i>Echinocereus nivosus</i>	Cactaceae	NAM
<i>Echinodorus ozelot</i>	Alismataceae	NAM
<i>Echinodorus paniculatus</i>	Alismataceae	NAM
<i>Echinodorus parviflora</i>	Alismataceae	NAM
<i>Echinodorus tenellus</i>	Alismataceae	NAM
<i>Echinopsis eyriesii</i>	Cactaceae	SAM
<i>Echinopsis huascha</i>	Cactaceae	SAM
<i>Echinopsis macrogona</i>	Cactaceae	SAM
<i>Egeria najas</i>	Hydrocharitaceae	SAM
<i>Ensete ventricosum</i>	Musaceae	Afr
<i>Epipremnum aureum</i>	Araceae	AT
<i>Erythrina caffra</i>	Fabaceae	Afr
<i>Erythrina crista-galli</i>	Fabaceae	SAM
<i>Erythrina falcata</i>	Fabaceae	SAM
<i>Escallonia macrantha</i>	Escalloniaceae	SAM
<i>Espostoa guentheri</i>	Cactaceae	SAM
<i>Espostoa lanata</i>	Cactaceae	SAM
<i>Eucalyptus coccifera</i>	Myrtaceae	Aus
<i>Eucalyptus nitens</i>	Myrtaceae	Aus
<i>Eucalyptus parvifolia</i>	Myrtaceae	Aus
<i>Eugenia brasiliensis</i>	Myrtaceae	SAM

Species with deficient data	Family	Native distribution
<i>Euphorbia abyssinica</i>	Euphorbiaceae	Afr
<i>Euphorbia avasmontana</i>	Euphorbiaceae	SAM
<i>Euphorbia baioensis</i>	Euphorbiaceae	Afr
<i>Euphorbia ingens</i>	Euphorbiaceae	Afr
<i>Euphorbia martinae</i>	Euphorbiaceae	Afr
<i>Euphorbia pseudocactus</i>	Euphorbiaceae	Afr
<i>Euphorbia pulcherrima</i>	Euphorbiaceae	SAM
<i>Euphorbia trigona</i>	Euphorbiaceae	Afr
<i>Euryops chrysanthemoides</i>	Asteraceae	Afr
<i>Euryops pectinatus</i>	Asteraceae	Afr
<i>Exacum affine</i>	Gentianaceae	Afr
<i>Fatsia japonica</i>	Araliaceae	As
<i>Felicia amelloides</i>	Asteraceae	Afr
<i>Ferocactus emoryi</i>	Cactaceae	NAM
<i>Ferocactus glaucescens</i>	Cactaceae	NAM
<i>Ferocactus gracilis</i>	Cactaceae	NAM
<i>Ferocactus pilosus</i>	Cactaceae	NAM
<i>Ficus macrophylla</i>	Moraceae	Aus
<i>Firmiana simplex</i>	Malvaceae	As, AT
<i>Fissidens fontanus</i>	Flissidentaceae	NAM
<i>Fontinalis antipyretica</i>	Fontanilaceae	NAM
<i>Fortunella japonica</i>	Rutaceae	As
<i>Gazania splendens</i>	Asteraceae	Afr
<i>Gelsemium sempervirens</i>	Gelsemiaceae	NAM
<i>Genista lydia</i>	Fabaceae	Eur
<i>Ginkgo biloba</i>	Ginkgoaceae	As
<i>Grevillea juniperina</i>	Proteaceae	Aus
<i>Grevillea lanigera</i>	Proteaceae	Aus
<i>Griselinia littoralis</i>	Griselinaceae	Aus
<i>Hamamelis virginiana</i>	Hammamelidaceae	NAM
<i>Handroanthus chrysanthus</i>	Bignoniaceae	SAM
<i>Hardenbergia comptoniana</i>	Fabaceae	Aus
<i>Haworthia fasciata</i>	Xanthorrhoeaceae	Afr
<i>Hebe diosmifolia</i>	Plantaginaceae	Aus
<i>Hebe odora</i>	Plantaginaceae	Aus
<i>Hebe topiaria</i>	Plantaginaceae	Aus
<i>Hedera algeriensis</i>	Araliaceae	Afr
<i>Hedera canariensis</i>	Araliaceae	Afr
<i>Hottonia inflata</i>	Primulaceae	NAM
<i>Howea forsteriana</i>	Arecaceae	Pac
<i>Hoya carnosia</i>	Asclepiadaceae	AT, Aus
<i>Hydrangea paniculata</i>	Hydrangeaceae	As
<i>Hydrocotyle tripartita</i>	Araliaceae	Aus
<i>Impatiens hawkeri</i>	Balsaminaceae	Aus
<i>Jasminum grandiflorum</i>	Oleaceae	Afr, AT
<i>Jasminum mezyi</i>	Oleaceae	As
<i>Jubaea chilensis</i>	Arecaceae	SAM
<i>Juniperus chinensis</i>	Cupressaceae	As

Species with deficient data	Family	Native distribution
<i>Juniperus horizontalis</i>	Cupressaceae	NAm
<i>Juniperus scopulorum</i>	Cupressaceae	NAm
<i>Juniperus squamata</i>	Cupressaceae	As
<i>Justicia brandegeana</i>	Acanthaceae	SAm
<i>Kalanchoe beharensis</i>	Crassulaceae	Afr
<i>Kalanchoe blossfeldiana</i>	Crassulaceae	Afr
<i>Kerria japonica</i>	Rosaceae	As
<i>Koelreuteria bipinnata</i>	Sapindaceae	As
<i>Lampranthus spectabilis</i>	Aizoaceae	Afr
<i>Leucanthemum paludosum</i>	Asteraceae	Eur
<i>Leucothoe fontanesiana</i>	Ericaceae	NAm
<i>Licuala grandis</i>	Arecaceae	Aus
<i>Ligustrum japonicum</i>	Oleaceae	As
<i>Liquidambar styraciflua</i>	Hammamelidaceae	NAm
<i>Liriodendron tulipifera</i>	Magnoliaceae	NAm
<i>Litchi chinensis</i>	Sapindaceae	AT
<i>Livistona australis</i>	Arecaceae	Aus
<i>Lobelia cardinalis</i>	Campanulaceae	NAm
<i>Lomariopsis lineata</i>	Lomaropsidaceae	AT, Aus
<i>Lophophora williamsii</i>	Cactaceae	NAm
<i>Macrozamia communis</i>	Cicadaceae	Aus
<i>Magnolia denudata</i>	Magnoliaceae	As
<i>Magnolia grandiflora</i>	Magnoliaceae	NAm
<i>Magnolia stellata</i>	Magnoliaceae	As
<i>Malpighia emarginata</i>	Malpighiaceae	SAm
<i>Malus floribunda</i>	Rosaceae	As
<i>Mammillaria geminispina</i>	Cactaceae	NAm
<i>Mammillaria magnifica</i>	Cactaceae	NAm
<i>Mammillaria rhodantha</i>	Cactaceae	NAm
<i>Melaleuca ericifolia</i>	Myrtaceae	Aus
<i>Melaleuca linearis</i>	Myrtaceae	Aus
<i>Melocactus neryi</i>	Cactaceae	SAm
<i>Melocactus zehntneri</i>	Cactaceae	SAm
<i>Mentha crispata</i>	Lamiaceae	Cosm
<i>Metasequoia glyptostroboides</i>	Taxodiaceae	As
<i>Metrosideros excelsa</i>	Myrtaceae	Aus
<i>Micranthemum callitrichoides</i>	Scrophulariaceae	SAm
<i>Micranthemum micranthemoides</i>	Scrophulariaceae	NAm
<i>Micromeria fruticosa</i>	Lamiaceae	Eur
<i>Microsorium pteropus</i>	Polypodiaceae	AT
<i>Morus australis</i>	Moraceae	AT
<i>Musa acuminata</i>	Musaceae	AT, Aus
<i>Musa basjoo</i>	Musaceae	As
<i>Myriophyllum mattogrossense</i>	Haloragidaceae	SAm
<i>Myrtillocactus geometrizans</i>	Cactaceae	NAm
<i>Nannorrhops ritchieana</i>	Arecaceae	As
<i>Nasella tenuissima</i>	Poaceae	SAm
<i>Nemesia strumosa</i>	Scrophulariaceae	Afr

Species with deficient data	Family	Native distribution
<i>Nertera granadensis</i>	Rubiaceae	SAm, Pac
<i>Nolina longifolia</i>	Asparagaceae	NAm
<i>Nyssa sylvatica</i>	Cornaceae	NAm
<i>Opuntia macrocentra</i>	Cactaceae	NAm
<i>Opuntia pubescens</i>	Cactaceae	SAm
<i>Oreocereus celsianus</i>	Cactaceae	SAm
<i>Oreocereus doelzianus</i>	Cactaceae	SAm
<i>Oreocereus leucotrichus</i>	Cactaceae	SAm
<i>Osmanthus heterophyllus</i>	Oleaceae	As
<i>Ostrya carpinifolia</i>	Betulaceae	Eur
<i>Pachira aquatica</i>	Bombacaceae	SAm
<i>Pachycereus marginatus</i>	Cactaceae	NAm
<i>Pachycereus pecten-aboriginum</i>	Cactaceae	NAm
<i>Pachycereus pringlei</i>	Cactaceae	NAm
<i>Pachypodium lamerei</i>	Apocynaceae	Afr
<i>Pachysandra terminalis</i>	Buxaceae	As
<i>Pandanus utilis</i>	Pandanaceae	Afr
<i>Pandorea jasminoides</i>	Bignoniaceae	Aus
<i>Panicum virgatum</i>	Poaceae	NAm
<i>Parajubaea cocoides</i>	Arecaceae	SAm
<i>Parajubaea torrallyi</i>	Arecaceae	SAm
<i>Parrotia persica</i>	Hamamelidaceae	Eur
<i>Passiflora incarnata</i>	Passifloraceae	SAm
<i>Passiflora manicata</i>	Passifloraceae	SAm
<i>Pelargonium grandiflorum</i>	Geraniaceae	Afr
<i>Pellia epiphylla</i>	Pelliaceae	As, Eur, NAm, Afr
<i>Pennisetum alopecuroides</i>	Poaceae	As, AT, Aus
<i>Pennisetum mesaiacum</i>	Poaceae	Afr
<i>Pennisetum orientale</i>	Poaceae	Afr, AT
<i>Pentas lanceolata</i>	Rubiaceae	Afr
<i>Pereskiaopsis rotundifolia</i>	Cactaceae	NAm
<i>Persea americana</i>	Lauraceae	SAm
<i>Phanera variegata</i>	Fabaceae	AT
<i>Philodendron bipinnatifidum</i>	Araceae	SAm
<i>Philodendron tuxtla</i>	Araceae	SAm
<i>Phlox subulata</i>	Polemoniaceae	NAm
<i>Phoenix reclinata</i>	Arecaceae	Afr
<i>Phoenix roebelenii</i>	Arecaceae	As, AT
<i>Phoenix theophrasti</i>	Arecaceae	Eur
<i>Phyllostrachys aurea</i>	Poaceae	As
<i>Picea glauca</i>	Pinaceae	NAm
<i>Picea koraiensis</i>	Pinaceae	As
<i>Picea pungens</i>	Pinaceae	NAm
<i>Pieris japonica</i>	Ericaceae	As, AT
<i>Pilosocereus leucocephalus</i>	Cactaceae	NAm
<i>Pilosocereus pachycladus</i>	Cactaceae	SAm
<i>Pinus brutia</i>	Pinaceae	Eur
<i>Pinus mugo</i>	Pinaceae	SAm

Species with deficient data	Family	Native distribution
<i>Pinus palustris</i>	Pinaceae	NAM
<i>Pistacia atlantica</i>	Anacardiaceae	Afr
<i>Pistacia chinensis</i>	Anacardiaceae	As
<i>Platanus orientalis</i>	Platanaceae	Eur
<i>Plectranthus verticillatus</i>	Lamiaceae	Afr
<i>Plumeria alba</i>	Apocynaceae	SAM
<i>Plumeria rubra</i>	Apocynaceae	SAM
<i>Polaskia chichipe</i>	Cactaceae	NAM
<i>Polaskia chula</i>	Cactaceae	NAM
<i>Polianthes tuberosa</i>	Amaryllidaceae	SAM
<i>Polygala myrtifolia</i>	Polygalaceae	Afr
<i>Portulaca umbraticola</i>	Portulacaceae	NAM
<i>Primula obconica</i>	Primulaceae	As
<i>Pritchardia hillebrandii</i>	Arecaceae	Pac
<i>Prunus serrulata</i>	Rosaceae	As
<i>Prunus subhirtella</i>	Rosaceae	As
<i>Pseudophoenix sargentii</i>	Arecaceae	NAM
<i>Pterocarya fraxinifolia</i>	Juglandaceae	Eur
<i>Puya chilensis</i>	Bromeliaceae	SAM
<i>Pyrus pyrifolia</i>	Rosaceae	As
<i>Quercus palustris</i>	Fagaceae	NAM
<i>Radermachera sinica</i>	Bignoniaceae	AT
<i>Ranunculus asiaticus</i>	Ranunculaceae	Eur, Afr
<i>Ravenala madagascariensis</i>	Strelitziaceae	Afr
<i>Ravenea rivularis</i>	Arecaceae	Afr
<i>Rhapidophyllum hystrix</i>	Arecaceae	NAM
<i>Rhapis excelsa</i>	Arecaceae	As
<i>Rhododendron arboreum</i>	Ericaceae	AT
<i>Rhododendron molle</i>	Ericaceae	As
<i>Ribes nigrum</i>	Grossulariaceae	Eur
<i>Ribes sanguineum</i>	Grossulariaceae	NAM
<i>Rotala rotundifolia</i>	Lythraceae	AT
<i>Roystonea regia</i>	Arecaceae	NAM
<i>Rubus spectabilis</i>	Rosaceae	NAM
<i>Russelia equisetiformis</i>	Scrophulariaceae	NAM
<i>Sabal mexicana</i>	Arecaceae	NAM
<i>Sabal minor</i>	Arecaceae	NAM
<i>Sabal palmetto</i>	Arecaceae	NAM
<i>Salix integra</i>	Salicaceae	As
<i>Salix matsudana</i>	Salicaceae	As
<i>Sansevieria perrottii</i>	Asparagaceae	Afr
<i>Schefflera arboricola</i>	Araliaceae	AT
<i>Scindapsus pictus</i>	Araceae	AT
<i>Sedum spectabile</i>	Crassulaceae	As
<i>Selaginella lepidophylla</i>	Selaginellaceae	NAM
<i>Sequoia sempervirens</i>	Cupressaceae	NAM
<i>Skimmia japonica</i>	Rutaceae	As
<i>Sorbus intermedia</i>	Rosaceae	Eur

Species with deficient data	Family	Native distribution
<i>Sorbus torminalis</i>	Rosaceae	Eur, Afr
<i>Staurogyne repens</i>	Acanthaceae	SAM
<i>Stenocarpus sinuatus</i>	Proteaceae	Aus
<i>Stephanotis floribunda</i>	Apocynaceae	Afr
<i>Stetsonia coryne</i>	Cactaceae	SAM
<i>Stevia rebaudiana</i>	Asteraceae	SAM
<i>Strelitzia nicolai</i>	Stelitzziaceae	Afr
<i>Strelitzia reginae</i>	Stelitzziaceae	Afr
<i>Syagrus romanzoffiana</i>	Arecaceae	SAM
<i>Syagrus yungasensis</i>	Arecaceae	SAM
<i>Symphoricarpos orbiculatus</i>	Caprifoliaceae	NAM
<i>Taxiphyllum alternans</i>	Hypnaceae	AT
<i>Taxiphyllum barbieri</i>	Hypnaceae	AT
<i>Taxodium distichum</i>	Taxodiaceae	NAM
<i>Tetraclinis articulata</i>	Cupressaceae	Afr
<i>Thuja occidentalis</i>	Cupressaceae	NAM
<i>Thuja plicata</i>	Cupressaceae	NAM
<i>Thymus citriodorus</i>	Lamiaceae	Cosm
<i>Tilia americana</i>	Malvaceae	NAM
<i>Tilia tormentosa</i>	Malvaceae	Eur
<i>Tillandsia flabellata</i>	Bromeliaceae	SAM
<i>Trachelospermum jasminoides</i>	Apocynaceae	As, AT
<i>Trachycarpus martianus</i>	Arecaceae	As
<i>Trithrinax campestris</i>	Arecaceae	SAM
<i>Ugni molinae</i>	Myrtaceae	SAM
<i>Utricularia graminifolia</i>	Lentibulariaceae	AT
<i>Vaccinium macrocarpon</i>	Ericaceae	NAM
<i>Vallisneria americana</i>	Hydrocharitaceae	NAM
<i>Vallisneria caulescens</i>	Hydrocharitaceae	Aus
<i>Veitchia joannis</i>	Arecaceae	Aus
<i>Vesicularia dubyana</i>	Hypnaceae	AT
<i>Vesicularia montagnei</i>	Hypnaceae	AT
<i>Viburnum davidii</i>	Adoxaceae	As
<i>Viburnum plicatum</i>	Adoxaceae	As
<i>Viburnum sargentii</i>	Adoxaceae	As
<i>Vriesea splendens</i>	Bromeliaceae	SAM
<i>Weigela florida</i>	Diervillaceae	As
<i>Wodyetia bifurcata</i>	Arecaceae	Aus
<i>Xerochrysum bracteatum</i>	Asteraceae	Aus
<i>Yucca elephantipes</i>	Agavaceae	SAM
<i>Yucca filamentosa</i>	Agavaceae	NAM
<i>Yucca filifera</i>	Agavaceae	NAM
<i>Yucca glauca</i>	Agavaceae	NAM
<i>Yucca rostrata</i>	Agavaceae	NAM
<i>Zamia furfuracea</i>	Zamiaceae	NAM
<i>Zamioculcas zamiifolia</i>	Araceae	Afr
<i>Zelkova carpinifolia</i>	Ulmaceae	Eur

Composition patterns of ornamental flora in the Czech Republic

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Abstract

Ornamental plants are an important component of urban floras and a significant source of alien plant invasions to the surrounding landscapes. We studied ornamental flora across 174 settlements in the Czech Republic, Central Europe. The aims of the study were to (i) identify clusters of sites that are defined as distinctive groups of ornamental taxa reflecting environmental or socioeconomic factors and (ii) apply the classification approach which is traditionally used for spontaneous vegetation in order to evaluate the potential of different settlement types to act as source sites of invasive species. The inventories were classified in a similar manner that is generally applied to spontaneous vegetation using the COCKTAIL method. Diagnostic taxa were classified in a repeatable manner into 17 species groups, forming five distinctive clusters with ~70% of sites attributed to one cluster. The species pools of the clusters differed in their representation of species with native or alien status and different life forms. The following clusters were distinguished, based on the prevailing type of settlement: (1) old villas neighbourhoods of towns, (2) upland settlements, (3) modern neighbourhoods, (4) old rustic settlements and (5) modern rustic settlements. Similar to spontaneous vegetation, the classification of ornamental flora reflects both basic natural gradients (i.e. altitude) and man-made factors (i.e. the preferences for certain plants and associated management practices). Alien taxa associated with modern neighbourhoods are characterised by a relatively higher invasion potential than those from, for example, old rustic settlements. This is especially true for woody species which can spread in ruderal habitats as a result of urban sprawl. Our results showed that the classification method, commonly used to analyse vegetation data, can also be applied to ornamental flora.

Keywords

homegardens, invasion potential, urban, vegetation classification

Introduction

The recent increase in the knowledge of alien floras in countries worldwide (e.g. Pyšek et al. 2012, 2017; van Kleunen et al. 2015), as well as in the theory of biological invasions (e.g. Catford et al. 2009; Blackburn et al. 2011; Kueffer et al. 2013; Enders et al. 2019) has drawn the attention of researchers, amongst other topics, towards the ecological consequences of ornamental introductions (e.g. Thompson et al. 2003; Gaston et al. 2005, 2007; Smith et al. 2006; Loram et al. 2008a; van Heezik et al. 2013; Hulme et al. 2018; van Kleunen et al. 2018). Several studies integrate ecological data with socioeconomic aspects in ethnobotanical research, addressing the utilisation of plants by traditional societies (Vogl et al. 2004; Loram et al. 2008b; Davoren et al. 2016; Palliwoda et al. 2017), people's plants preferences (Kendal et al. 2012b) or with landscape design (Groening and Wolschke-Bulmahn 1989; Redman et al. 2004). However, the acquisition, cultivation, escape and formation of invading populations of ornamental aliens is a gradual process that is rarely studied in its entirety (but see Kowarik 2005; Daehler 2008; Cook et al. 2012; Kowarik and Pyšek 2012; Mayer et al. 2017; van Kleunen et al. 2018).

Ornamental plants represent an important component in the urban space (Chocholoušková and Pyšek 2003; Kowarik 2005; Botham et al. 2009; Pyšek and Chytrý 2014; Pergl et al. 2016b), as well as a significant source of invasive species as a result of escapes from private or public gardens (Reichard and White 2001; Dehnen-Schmutz et al. 2007; Hanspach et al. 2008; Hulme 2011; Pyšek et al. 2011; Gregor et al. 2012). Many taxa initially escape and spread in spatially restricted areas in the surroundings of gardens and then spread and colonise more distant vegetation. Such naturalisation foci may appear as a result of the combined effects of local popularity of a given taxon, regardless of its invasion status (Humair et al. 2014), suitable natural and cultural conditions (Marco et al. 2010), abundant propagation in cultivation and easy semi-spontaneous establishment in gardens. For example, many ornamental taxa become naturalised or even invasive in peri-urban belts or along motorways (Yang et al. 2015). This implies that (i) most naturalised ornamentals come from populations that are already pre-adapted to the local conditions (Mack 2000; Pyšek et al. 2011), (ii) the naturalised taxa are not distributed evenly across various natural and cultural gradients, but they are concentrated in specific conditions which are generally favourable for many escaping taxa and (iii) where there is a suitable set of introduction pathways and dispersal vectors (von der Lippe and Kowarik 2007; Wilson et al. 2009).

The horticulture industry is a major pathway for introductions of alien plants worldwide (Hulme et al. 2018; van Kleunen et al. 2018). It was shown that species introduced intentionally are more likely to have negative impact than those introduced unintentionally (Pergl et al. 2017) – many naturalised ornamentals have negative impacts on

native biodiversity (Vilà et al. 2010; Pyšek et al. 2012) or hybridise with native species (Klonner et al. 2017). However, it has also been shown that alien species introduced unintentionally can be successful invaders and also have high impact (Pyšek et al. 2011; Rumlerová et al. 2016). These factors may become significant in the era of changing climate (Klonner et al. 2017; Haeuser et al. 2018). Although the majority of alien species, grown as garden ornamentals, can only survive when planted under intensive management, a considerable number escape without human assistance and establish outside gardens (Pergl et al. 2016a; Dullinger et al. 2017; Mayer et al. 2017). In a previous study, we recorded 1,834 ornamental taxa in cultivated areas of 174 settlements in the Czech Republic, central Europe, of which 23% are known to escape from the cultivation (Pergl et al. 2016b). In the alien flora of the Czech Republic, 56% of the taxa have been recruited from escaping ornamental plants (Pyšek et al. 2012). Similarly, amongst 78 species cited in the Black List of alien species in the Czech Republic (i.e. national list of noxious weeds and pests), 51 species are planted as ornamentals and this includes some of the most invasive species such as *Heracleum mantegazzianum* or *Reynoutria* (syn. *Fallopia*) spp. (Pergl et al. 2016a). Detailed information on the origin, behaviour and secondary spread of the species at a site and in its neighbourhood can be obtained by questioning the local growers and horticulturalists and this knowledge can be useful in assessing the future risks of invasions (Kowarik 2005; Dehnen-Schmutz and Conroy 2018).

As shown by Lososová et al. (2012) and Štajerová et al. (2017), the composition of urban floras is determined by the availability of habitats and their spatial distribution, as well as by climate. Similarly, habitat heterogeneity influences the composition of ornamental flora in settlements. Moreover, the composition of ornamental flora reflects natural gradients in environmental conditions as well as the complex interplay of cultural and socioeconomic factors (e.g. Sukopp 2002; Loram et al. 2008a, b; Kendal et al. 2012a; Cubino et al. 2014, 2016; Lowenstein and Minor 2016). Reasons for planting are various and often remain hidden. Garden flora is dominated by rare and transient species that are surviving due to human care and are weakened by interspecific competition (Pergl et al. 2016b). The trade-off in research approaches between small-scale surveys of individual gardens covering restricted regions (e.g. Thompson et al. 2003) on one side and large scale studies on the other (e.g. Pergl et al. 2016a), shows that at the scale of individual gardens, some species appear to be rare (they occur at low abundances), but their local frequencies are rather high. Previous studies suggest that sampling whole settlements compared to inventories of individual gardens overestimates the proportion of rare species in the total flora, but this can be sufficiently compensated when accounting for the measures of abundance (Thompson et al. 2003; Smith et al. 2006; Acar et al. 2007; Pergl et al. 2016b).

Bearing this complexity in mind, we tested whether some repetitive ornamental species assemblages occur in human settlements. The main aim of the study is to identify clusters of sites that are defined as distinctive groups of ornamental taxa reflecting environmental or socioeconomic diversity by applying a modern vegetation classification approach and to assess the composition of ornamental flora at different settlement types in relation to aliens, therefore acting as source sites for the invasive species.

Methods

Study sites and recorded data

We used our previous research data on the ornamental flora in the Czech Republic (Pergl et al. 2016b). The ornamental flora was recorded at 174 urban localities (further referred to as ‘sites’) covering the main gradients of environmental (see Chytrý 2012) and socioeconomic conditions on the urban-rural gradient. Our study included records from ~ 3% of municipalities in the Czech Republic. The site sampling contained villages, towns, cities, garden allotments, cemeteries, areas of dispersed farmhouse settlement and new suburban residential areas. For relatively small villages of up to ~2000 inhabitants, the village was considered as a single site, whereas in towns and cities, several sites of similar urban character were included in this study. At each site, the ornamental flora was recorded in private gardens, as well as in public areas, with at least five gardens per site studied in detail. Sampling was based on the ability to enter private gardens and other gardens were surveyed from behind the fence (see Pergl et al. 2016b). Data were collected between June and August 2011–2013 by 11 botanists, most of them having met before fieldwork to adjust the methodology. At each site, we recorded both alien and native plants cultivated as ornamentals in private gardens and public spaces, except for spring geophytes and conifers that were excluded because this involved repeated visits to the sites to record both spring and summer aspects. To reduce the potential bias in sampling effort and different taxonomic expertise of involved botanists, an approach of aggregated taxa for complex taxon groups was used and the rarely recorded species were excluded from the analysis (see below). For each taxon at each site, the local population size (hereafter referred to as ‘abundance’) was estimated by using an ordinal scale, ranging from species present in a single garden (i.e. low abundance), species present in more than one garden but less than 30% of gardens (i.e. medium abundance), to commonly occurring taxa, recorded in more than 30% of gardens (i.e. high abundance). The final taxon × site matrix consisted of 35,725 records for 1,514 aggregated taxa (after taxonomic standardisation; see Pergl et al. 2016b, Supl. material 1 for a detailed description and data and Fig. 1 for data distribution).

Alien status was assigned to each taxon based on Pyšek et al. (2012). Definition of invasion status follows Richardson et al. (2000) and Blackburn et al. (2011). Persistence was classified as persistent (i.e. core) or transient part of the flora (MacArthur 1960; Magurran and Henderson 2003; Coyle et al. 2013). The categorisation is explained in detail in Pergl et al. (2016b) and was based on the taxon status, cultivation requirements and abundance. Data on species naturalisation status and abundance were taken from Pyšek et al. (2012). Native taxa (taxonomy taken from Danihelka et al. 2012) and all naturalised alien taxa with high abundance or scattered casual aliens were classified as core taxa. Frost-sensitive cultivated plants and casual aliens that vanished or were known from a single occurrence were classified as transient (see Supl. material 1 for further details on the sampling methods). If the aggregated taxon contained an alien taxon, then it was considered as alien in the analysis.

Classification of sites using the COCKTAIL method

We examined the compositional variation of ornamental flora in sites using the supervised classification of the COCKTAIL method (Bruehlheide 2000). The method is based on statistical measures of fidelity (i.e. the species concentration in a classification unit). Further, observed species frequencies within a classification unit (i.e. site) are compared with the frequencies expected under random distribution and this controlled procedure creates groups of species (Chytrý et al. 2002). The supervised classification is partially influenced by the observer by setting initial conditions of analysis (i.e. initial species with the highest fidelity values entering the process, see details below). The COCKTAIL method uses presence/absence data and is therefore appropriate for datasets with varying species abundances.

As a fidelity measure, we used the *phi* coefficient (Chytrý et al. 2002) that range from -1 to 1 . The *phi* value of 1 is for taxa occurring in all sites of a cluster and are absent elsewhere. The *phi* coefficient of association describes the correlation between two categorical factors in a 2×2 contingency table (Sokal and Rohlf 1995). A positive value of *phi* means that there is a positive correlation between a species and an existing species group. An advantage of the *phi* coefficient is its independence from the size of data; however, it depends on the relative cluster size. Therefore, we standardised the *phi* values to equate to the cluster size, according to Tichý and Chytrý (2006). Only taxa with both significant concentration in particular clusters (using Fisher's exact test and the significance level of $p < 0.01$) and a *phi* coefficient of ≥ 0.30 were considered as *diagnostic*. Fisher's test excludes some rare taxa that could become diagnostic by chance and is considered as a correction for the calculation of statistical significance for fidelity measures. The threshold value was selected subjectively in order to obtain a reasonable number of diagnostic species and is also comparable to other studies (see for example, Jarolímek and Šibík 2008 or Chytrý 2009). See Table 1 for the composition of assemblages and selected diagnostic taxa in all clusters.

First, we started the clustering algorithm with initial diagnostic species. In most cases, however, the same species group is obtained irrespective of which species of the group is chosen to start the algorithm (Bruehlheide 1995). Second, further species were added to the species group if their association to one or more species in the group exceeded a certain fidelity threshold (see above for details). The expected and observed cumulative distribution functions for sites were calculated using interspecific association between the selected species and other species in the dataset. Only groups that formed three or more sites were used for further analyses. We used the logical operator "AND" in our COCKTAIL definitions of classification units, when linking the plant assemblages in the JUICE 7.0 programme using a standardised process (Tichý 2002). Details on the COCKTAIL algorithm, defining the species groups, interspecific associations and group aggregation are described step by step at <http://www.sci.muni.cz/botany/juice/mang.htm>.

To describe gradients in environmental, social and economic traits, we used data from the Czech Statistical Office (www.cuzk.cz) and the Czech Hydrometeorological Institute (www.chmi.cz) shown in Table 2. The list of characteristics for individual sites with architectural structure, socioeconomic and environmental factors can be found in Suppl. material 2.

Table 1. Lists of diagnostic taxa composed of 17 COCKTAIL species groups (i.e. five clusters). The numbers of sites selected by a species group are presented in brackets. Planted species (in bold), casual aliens (*), naturalised incl. invasive aliens (†).

Cluster	Diagnostic taxa
1 – Old villas neighbourhoods of towns	
<i>Asarum europaeum</i> group (53): <i>Asarum europaeum</i> ; <i>Hepatica nobilis</i> ; <i>Impatiens balsamina</i> <i>Pseudofumaria lutea</i> group (85): <i>Asarum europaeum</i> ; <i>Dryas octopetala</i> ; <i>Lysimachia nummularia</i> ; <i>Pseudofumaria lutea</i> <i>Rhododendron</i> group (170): <i>Ligustrum vulgare</i> ; <i>Rhododendron</i> spp.; <i>Yucca filamentosa</i>	<i>Acaena</i> spp. , <i>Antennaria dioica</i> , <i>Aquilegia flabellata</i> *, <i>Asarum europaeum</i> , <i>Asplenium trichomanes</i> , <i>Athyrium nipponicum</i> , <i>Carex muricata</i> agg., <i>Cymbalaria muralis</i> *, <i>Daphne arbuscula</i> , <i>Datura stramonium</i> *, <i>Erica cinerea</i> , <i>Euphorbia milii</i> , <i>E. pulcherrima</i> , <i>Haecquetia epipactis</i> , <i>Heuchera sanguinea</i> , <i>Impatiens balsamina</i> *, <i>Lilium martagon</i> , <i>Lysimachia nummularia</i> , <i>Matteuccia struthiopteris</i> *, <i>Parnassia palustris</i> , <i>Phyllitis scolopendrium</i> , <i>Robinia pseudacacia</i> †, <i>Rosa xcentifolia</i> * et <i>R. damascena</i> *, <i>Sarracenia</i> sp.* et hybr., <i>Sedum hispanicum</i> †, <i>Verbascum thapsus</i>
2 – Upland settlements	
<i>Salix euxina</i> group (28): <i>Glebionis segetum</i> ; <i>Papaver croceum</i> ; <i>Salix euxina</i> <i>Aubrieta</i> group (134): <i>Aubrieta deltoidea</i> ; <i>Gentiana acaulis</i> et <i>G. clusii</i> ; <i>Saxifraga</i> sect. <i>Euaizoonia</i> <i>Athyrium filix-femina</i> group (113): <i>Athyrium filix-femina</i> ; <i>Helianthus xlaetiflorus</i> ; <i>Sedum anacampseros</i>	<i>Achillea ptarmica</i> , <i>Allium senescens</i> , <i>Arisaema</i> spp. , <i>Artemisia abrotanum</i> , <i>Begonia</i> aff. x<i>tuberhybrida</i> , <i>Callistephus chinensis</i> *, <i>Carex elata</i> , <i>Cymbalaria pallida</i> *, <i>Dianthus barbatus</i> †, <i>Digitalis purpurea</i> †, <i>Dryopteris carthusiana</i> , <i>Geranium ibericum</i> et <i>G. platypetalum</i> et <i>G. x<i>magnificum</i></i> , <i>Glebionis segetum</i> *, <i>Hebe</i> small-leaved spp. et hybr. , <i>Helianthus xlaetiflorus</i> †, <i>Heuchera cylindrica</i> , <i>Hordeum jubatum</i> †, <i>Iris pseudacorus</i> , <i>Jovibarba globifera</i> , <i>Kalanchoe blossfeldiana</i> , <i>Lilium bulbiferum</i> , <i>Magnolia kobus</i> , <i>Mauranthemum paludosum</i> , <i>Miscanthus floridulus</i> * et <i>M. xgiganteus</i> *, <i>Oxalis corniculata</i> †, <i>Papaver croceum</i> *, <i>Plectranthus forsteri</i> , <i>Primula denticulata</i> , <i>Pseudolysimachion spicatum</i> , <i>Salix euxina</i> , <i>Sedum anacampseros</i> , <i>S. forsterianum</i> *, <i>Sempervivum</i> sp.* et hybr., <i>Staphylea pinnata</i> , <i>Symphotrichum dumosum</i> *, <i>S. novae-angliae</i> †, <i>Tradescantia xandersoniana</i> *†
3 – Modern neighbourhoods	
<i>Acer palmata</i> group (131): <i>Acer</i> sect. <i>Palmata</i> ; <i>Campsis grandiflora</i> ; <i>C. radicans</i> et <i>C. x<i>tagliabuana</i></i> ; <i>Magnolia</i> aff. x <i>soulangiana</i> ; <i>Salix matsudana</i> cv. <i>Tortuosa</i> et <i>S. x<i>sempervirens</i></i> cv. <i>Erythroflexuosa</i> <i>Pennisetum alopecuroides</i> group (118): <i>Hydrangea arborescens</i> ; <i>Pennisetum alopecuroides</i> ; <i>Pyracantha coccinea</i> <i>Perovskia</i> spp. group (71): <i>Perovskia abrotanoides</i> et <i>P. atriplicifolia</i> ; <i>Caryopteris xclandonensis</i> ; <i>Jasminum nudiflorum</i> , <i>Santolina chamaecyparissus</i>	<i>Acer platanoides</i> , <i>A. sect. Palmata</i> , <i>Ailanthus altissima</i> †, <i>Aristolochia macrophylla</i> , <i>Asparagus densiflorus</i> , Bambusoideae tall small-leaved taxa , <i>Campsis grandiflora</i> et <i>C. radicans</i> et <i>C. x<i>tagliabuana</i></i> , <i>Caryopteris xclandonensis</i> , <i>Catalpa bignonioides</i> *, <i>Cortaderia selloana</i> , <i>Hamamelis</i> spp. , <i>Heuchera</i> aff. <i>americana</i> , <i>Hydrangea serrata</i> , <i>Jasminum nudiflorum</i> , <i>Koebertia paniculata</i> †, <i>Laburnum anagyroides</i> * et <i>L. x<i>watereri</i></i> †, <i>Lathyrus vernus</i> , <i>Lonicera</i> aff. <i>sempervirens</i> , <i>Magnolia</i> aff. <i>soulangiana</i> , <i>Nepeta racemosa</i> * et <i>M. xfaassenii</i> †, <i>Pennisetum alopecuroides</i> *, <i>Perovskia abrotanoides</i> et <i>P. atriplicifolia</i> , <i>Populus nigra</i> , <i>Prunus cerasifera</i> * et <i>P. x<i>cistena</i></i> †, <i>Pyracantha coccinea</i> †, <i>Santolina chamaecyparissus</i> *, <i>Silene uniflora</i> , <i>Spiraea</i> aff. <i>xcinerea</i> , <i>Syringa xprestoniae</i> , <i>Tradescantia pallida</i> , <i>Ulmus</i> aff. minor, <i>Viburnum rhytidophyllum</i> * et <i>V. xpragense</i> *, <i>V. tinus</i>
4 – Old rustic settlements	
<i>Calendula officinalis</i> group (162): <i>Calendula officinalis</i> ; <i>Callistephus chinensis</i> ; <i>Echinacea purpurea</i> ; <i>Tagetes erecta</i> <i>Mahonia aquifolium</i> group (166): <i>Alcea rosea</i> ; <i>Antirrhinum majus</i> ; <i>Asparagus officinalis</i> ; <i>Campanula persicifolia</i> ; <i>Mahonia aquifolium</i> <i>Agrimonia</i> aff. <i>eupatoria</i> group (84): <i>Agrimonia</i> aff. <i>eupatoria</i> ; <i>Allium schoenoprasum</i> ; <i>Anethum graveolens</i> ; <i>Levisticum officinale</i> ; <i>Rheum rhabarbarum</i> ; <i>Vaccinium corymbosum</i> <i>Nigella damascena</i> group (67): <i>Nigella damascena</i> ; <i>Lavatera trimestris</i> ; <i>Limonium sinuatum</i>	<i>Aconitum</i> aff. <i>napellus</i> , <i>Agrimonia</i> aff. <i>eupatoria</i> , <i>Anethum graveolens</i> †, <i>Asclepias tuberosa</i> , <i>Bassia scoparia</i> †, <i>Cleome hassleriana</i> , <i>Coreopsis basalis</i> , <i>C. rosea</i> , <i>Cosmos bipinnatus</i> *, <i>C. sulphureus</i> , <i>Cyclamen persicum</i> , <i>Dracaena</i> sp. , <i>Eupatorium purpureum</i> , <i>Iris ensata</i> , <i>Leucanthemopsis alpina</i> , <i>Levisticum officinale</i> *, <i>Ligularia stenocephala</i> , <i>Limonium sinuatum</i> , <i>Lonicera fragrantissima</i> et <i>L. xpurpurea</i> , <i>Malope trifida</i> *†, <i>Malus</i> spp.*†, <i>Mentha longifolia</i> , <i>Mentha xverticillata</i> , <i>Mimulus aurantiacus</i> , <i>Myrtus communis</i> , <i>Nigella damascena</i> †, <i>Pentas lanceolata</i> , <i>Polemonium caeruleum</i> , <i>Primula japonica</i> , <i>Rhodanthe chlorocephala</i> , <i>Sidalcea malviflora</i> , <i>Silene banksia</i> , <i>Skimmia japonica</i> , <i>Syringa xchinensis</i> , <i>Tiblidantha dubia</i> *†, <i>Vaccinium corymbosum</i> *, <i>Veronica virginica</i> , <i>Viburnum farfieri</i> et <i>V. x<i>bodnatsense</i></i>
5 – Modern rustic settlements	
<i>Rudbeckia laciniata</i> group (144): <i>Cosmos bipinnatus</i> ; <i>Delphinium xclutorum</i> ; <i>Heliopsis helianthoides</i> ; <i>Rudbeckia laciniata</i> ; <i>Salvia officinalis</i> <i>Commelina communis</i> group (81): <i>Portulaca grandiflora</i> et hybr.; <i>Euphorbia marginata</i> ; <i>Commelina communis</i> <i>Anemone sylvestris</i> group (87): <i>Anemone sylvestris</i> ; <i>Festuca gautieri</i> ; <i>Pseudolysimachion incanum</i> ; <i>Veronica austriaca</i> et <i>V. caespitosa</i> <i>Centaurea dealbata</i> group (115): <i>Centaurea dealbata</i> ; <i>Erigeron speciosus</i> ; <i>Prunus tenella</i>	<i>Androsace sarmentosa</i> * et <i>A. sempervirens</i> *, <i>Anemone sylvestris</i> , <i>Anthemis tinctoria</i> , <i>Antirrhinum majus</i> *, <i>Atriplex hortensis</i> *, <i>Campanula glomerata</i> , <i>Canna indica</i> , <i>Commelina communis</i> †, <i>Consolida ajacis</i> †, <i>Coreopsis grandiflora</i> et <i>C. lanceolata</i> , <i>Delphinium xclutorum</i> , <i>Eupatorium cannabinum</i> , <i>Euphorbia marginata</i> †, <i>Euryops</i> spp. , <i>Festuca gautieri</i> , <i>Festuca glauca</i> , <i>Gaura lindheimeri</i> et hybr. , <i>Geranium dalmaticum</i> et <i>G. x<i>cantabrigiense</i></i> , <i>Glebionis coronaria</i> , <i>Humulus lupulus</i> , <i>Chasmanthium latifolium</i> , <i>Inula ensifolia</i> , <i>Ipomoea purpurea</i> †, <i>Iris pumila</i> , <i>Linum austriacum</i> , <i>Lunaria annua</i> †, <i>Malva sylvestris</i> , <i>Nicandra physalodes</i> †, <i>Oenothera missouriensis</i> †, <i>Opuntia</i> spp. , <i>Portulaca grandiflora</i> * et hybr., <i>Prunus tenella</i> , <i>Pseudolysimachion incanum</i> , <i>Rudbeckia laciniata</i> †, <i>Ruta graveolens</i> †, <i>Santolina chamaecyparissus</i> , <i>Satureja hortensis</i> , <i>Sedum sarmentosum</i> †, <i>Sempervivum arachnoideum</i> , <i>Silene schafta</i> , <i>Stipa tenuissima</i> , <i>Streptocarpus saxorum</i> , <i>Tanacetum densum</i> et <i>T. baradjanii</i> , <i>Teucrium chamaedrys</i> , <i>Typha minima</i> , <i>Veronica austriaca</i> et <i>V. caespitosa</i> et <i>V. prostrata</i> , <i>Veronica</i> cf. <i>armena</i> et <i>V. pectinata</i>

Table 2. Basic environmental variables (mean \pm SD) characterising each cluster type. The data were obtained from the Czech Hydrometeorological Institute.

Cluster no., name and no. of cases	Altitude (m a.s.l.)	Annual mean temperature (°C)	Annual precipitation (mm/year)
1. old villas neighbourhoods of towns (N = 14)	358 \pm 103	8.4 \pm 1.1	724 \pm 171
2. upland settlements (N = 11)	612 \pm 224	6.8 \pm 1.2	901 \pm 149
3. modern neighbourhoods (N = 28)	312 \pm 114	8.9 \pm 0.9	610 \pm 115
4. old rustic settlements (N = 26)	395 \pm 86	8.3 \pm 0.7	683 \pm 102
5. modern rustic settlements (N = 40)	318 \pm 112	8.7 \pm 0.9	633 \pm 139
6. unclassified sites (N = 55)	398 \pm 181	8.1 \pm 4.2	710 \pm 508

Three statistical tests were performed to assess the differences between the clusters: proportion of alien taxa and proportion of transient and core taxa. Statistical differences between the clusters were tested using arc-transformed values, ANOVA and multiple comparisons by Tukey's test in R 3.2.1 for Windows (<https://cran.r-project.org/bin/windows/base/old/3.2.1>). Basic statistics on urban types were performed in STATISTICA 12 (www.statsoft.com) presented in Suppl. material 3.

Results

Assemblages of the ornamental flora

Using the COCKTAIL method, we defined 17 plant assemblages (i.e. species groups) across all sites. Based on the 17 plant species groups, five clusters were defined from the 119 sites using a logical operator, similar to classifying vegetation units. No reasonable pattern was found in the remaining cluster, which includes 55 sites (i.e. 32% of all sampled sites). This cluster was characterised as an unspecific ornamental flora, since no potential subgroup was sufficiently pronounced in its composition, habitat demands and cultural indication.

Clusters derived from lists of diagnostic taxa

The clusters were named according to the prevailing type of settlement: (1) old villas neighbourhoods of towns, (2) upland settlements, (3) modern neighbourhoods, (4) old rustic settlements and (5) modern rustic settlements. The taxa, reported below, represent examples of typical taxa (see Fig. 1 for the distribution of sites attributed to each cluster in the study area).

Cluster 1 – old villas neighbourhoods of towns (N = 14)

This cluster is characterised by (i) woodland understorey taxa, often growing semi-spontaneously in the shadow of trees and includes both native (e.g. *Asarum europaeum*,

Convallaria majalis) and alien species (e.g. *Helleborus* spp., *Matteuccia struthiopteris*); (ii) nutrient-demanding taxa domesticated on stone walls or in rockeries (*Asplenium trichomanes*, *Cymbalaria muralis*, *Pseudofumaria lutea* and *Sedum spurium*); (iii) indoor plants kept in the garden over the summer (*Erica cinerea* and *Euphorbia milii*) and (iv) ornamental shrubs (*Rhododendron* spp. and *Rosa ×centifolia*). These gardens were created around large villas built in wealthy residential areas between ~ 1870–1940. Their common style of an English garden is linked with the dominance of shrubs and trees along with lawns. Later, the need for easy and cheap upkeep of spacious gardens resulted in a selection of long-lived, undemanding and low-maintenance taxa (such as trees), persisting through clonal reproduction (such as shrubs) or even forming stable generative populations. Yet, these gardens harbour the lowest number of aliens amongst all the clusters.

Cluster 2 – upland settlements (N = 11)

This cluster is rich in taxa tolerating cold climates and less fertile soils and demanding higher air moisture (e.g. *Primula denticulata*, *Papaver croceum*, *Begonia* aff. *×tuberhybrida*, *Athyrium filix-femina*). Extensive rockeries, rich in taxa from genera such as *Saxifraga*, *Sedum* and *Sempervivum*, are specific to these sites. Many of these uncompetitive and stress-tolerant taxa are of alpine or boreal origin and their local cultivation is enabled by nutrient poor soils, which are only rarely colonised by fast-growing competitive weeds, such as *Elymus repens* or tall annuals. Many alien taxa found in gardens maintain stable self-sowing or clonal populations (e.g. *Achillea ptarmica*, *Dianthus barbatus*). On the other hand, some taxa, which had been traditionally associated with this cluster (e.g. *Calystegia pulchra*, *Myrrhis odorata*, *Aconogonon polystachyum*), are infrequently planted in recent times. In dispersed mountain settlements, ruderal and semi-natural habitats bordering on gardens, these especially often comprise resistant and hardy herbs such as *Helianthus ×laetiflorus*, *Hemerocallis* spp. or taxa invading surrounding natural vegetation, such as *Digitalis purpurea*, *Lupinus polyphyllus* and *Telekia speciosa*.

Cluster 3 – modern neighbourhoods (N = 28)

This cluster includes many woody taxa which constitute ~70% of the local diagnostic taxa. Shrubs and trees are popular owing to their representative appearance and low maintenance. They include taxa with evergreen leaves (e.g. *Pyracantha coccinea* and many conifers), cultivars with columnar (*Populus nigra*) or tortuose habitus (*Corylus avellana*, *Salix matsudana*), coloured branches (*Cornus alba*) and variegated (*Salix integra* cv. Haruko-Nishiki) or dark leaves (*Prunus cerasifera* cv. *Pisardii*). Lianas (*Aristolochia macrophylla*, *Campsis radicans*, *Wistaria sinensis*), tall grasses (*Bambusoideae* family, *Cortaderia* spp., *Pennisetum* spp.) and virgate low shrubs and semi-shrubs (*Caryopteris ×clandonensis*, *Cotoneaster* spp., *Jasminum nudiflorum*, *Perovskia* spp.) are also very popular. On the contra-

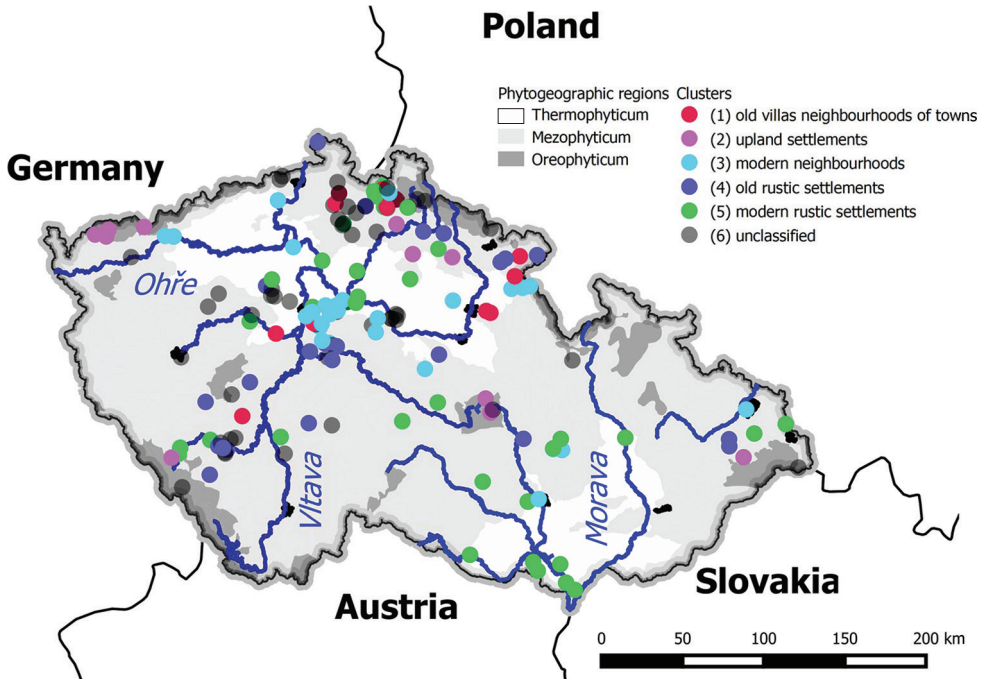


Figure 1. Map of sample sites in the Czech Republic. Phytogeographic regions, reflecting the climatic conditions, are indicated by three shades of grey. Thermophyticum includes warm areas with a thermophilous flora and vegetation. Mesophyticum harbours flora and vegetation typical of the central European temperate zone. Oreophyticum is a cold region with mountain flora and vegetation corresponding to forests of the boreal zone, with smaller areas above the timberline similar to habitats in the arctic zone (see Kaplan 2012).

ry, ornamental annuals, dependent on sowing and weeding, are entirely absent amongst the diagnostic taxa of this cluster. Gardens are typical of modern detached houses.

Cluster 4 – old rustic settlements (N = 26)

Joint cultivation of ornamental and utility plants in hoed beds characterise this cluster. Crops such as *Levisticum officinale* and *Rheum rhabarbarum* partly hold an ornamental function. *Anethum graveolens* is often combined with roses to grow under their protection. Some native taxa (e.g. *Agrimonia eupatoria*, *Rosa canina* and *Sambucus nigra*) often establish spontaneously and are tolerated both for ornamental and practical purposes. Hoeing, sowing and weeding are suitable management practices for cultivation of annuals (i.e. *Cosmos bipinnatus*, *Nigella damascena* or *Tagetes* spp.) or geophytes which are easily replanted (e.g. *Aconitum napellus*). Carnations (*Dianthus* spp.) along the edges of garden beds are another widely shared tradition. Amongst trees, taxa planted for fruits entirely prevail over ornamental trees. Low numbers of ornamental taxa and their arrays follow local tradition since the 19th century (e.g. *Polemonium caeruleum*, *Alcea*

rosea and *Phlox paniculata*). However, cultivation of, for example, *Syringa ×chinensis* and *Vaccinium corymbosum* is of modern origin.

Cluster 5 – modern rustic settlements (N = 40)

This cluster shares many taxa with cluster 3, but it has its own group of diagnostic taxa, such as (i) lianas (*Humulus lupulus*, *Ipomoea purpurea*), covering garden fences; (ii) taxa of rockeries, often robust and drought-resistant chamaephytes (genera *Iberis*, *Opuntia*, *Oenothera missouriensis*, *Ruta graveolens*, many taxa from the Lamiaceae family); (iii) self-spreading native taxa of dry grasslands (*Iris pumila*, *Anemone sylvestris*, *Linum austriacum*, *Prunus tenella*); (iv) annual self-sowing alien taxa (*Euphorbia marginata*, *Portulaca grandiflora*, *Commelina communis*, *Consolida ajacis*); and (v) tall nutrient-demanding perennials (*Canna indica*, *Rudbeckia laciniata*). These gardens usually border recently-built family houses.

Alien, core and transient taxa

The clusters significantly differed in the proportion of alien taxa, ranging from 73% (upland settlements) to 93% (unclassified cluster; Fig. 2). The highest number of aliens occurred in modern neighbourhoods and in old rustic settlements (Fig. 2). The multiple comparisons analysis revealed that the old villas neighbourhoods of towns comprise fewer aliens compared to other sites. There were no significant differences amongst the other groups.

The proportion of the transient taxa was not statistically different amongst the individual clusters. The lowest mean proportion of transient taxa was 29.7%. In addition, the clusters differed in the proportion of alien core (persistent) taxa (Fig. 3), with the highest proportion in the unclassified cluster (22.5%) and the lowest (7.1%) in modern neighbourhoods. The analysis showed a generally low number of taxa amongst the core aliens, indicating a higher probability of new introductions in the future.

Discussion

Classification of the ornamental flora

We based the categorisation of the ornamental flora on our field experience and used a formalised statistical approach to demonstrate that our assumptions about the assemblages of garden plant species can be expressed in a way that is usually applied to vegetation studies (see statistical forming of sociological species groups by Chytrý 2009 or Chytrý 2012 for a review). The COCKTAIL method allows for the transferability of species groups across scales, by combining grid-based distribution and vegetation data (Petřík and Bruelheide 2006). Although the method was not originally designed

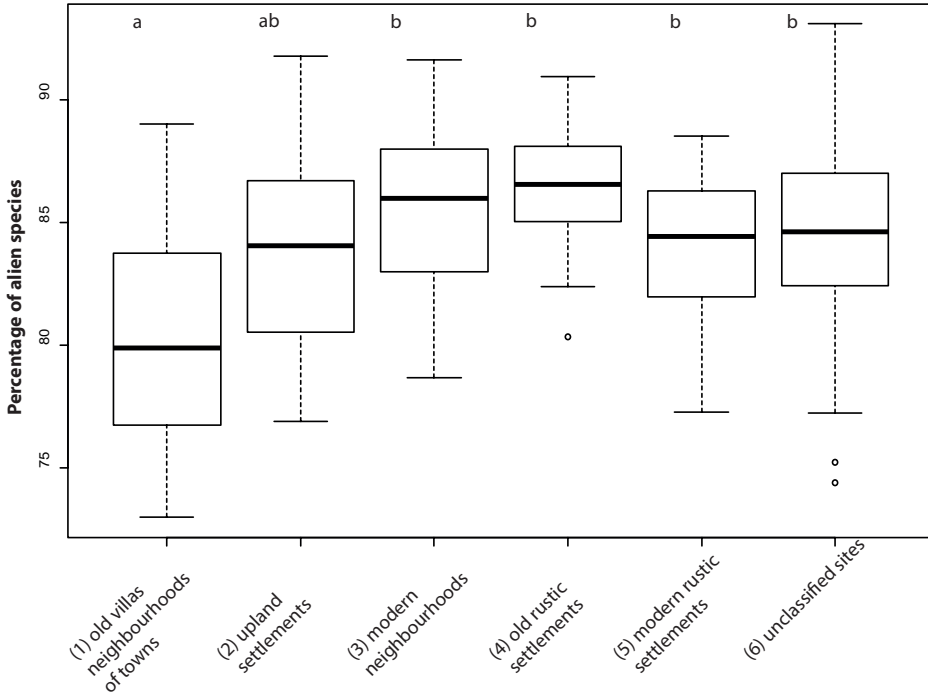


Figure 2. Differences in the percentages (i.e. median, 25th and 75th percentile and min/max values) of aliens amongst all ornamental taxa within clusters of the classified settlement types and within the unclassified cluster. Same letters above the boxes indicate insignificant differences between clusters (ANOVA $F = 5.35$, $df (5, 168)$, $p < 0.001$).

to study natural vegetation, our study is the first to apply COCKTAIL to artificial, non-spontaneous species groups. In most vegetation compendia, human-influenced vegetation is classified based on simple dominance; however, we used the COCKTAIL method to classify the traditionally recognised phytosociological units of various hierarchy (but see Fratarcangeli et al. 2019, who applied the concept of fidelity in the same way as in our study, but on spontaneous vegetation).

Cubino et al. (2014) and Kendal et al. (2012a) compared cultivated floras across urban and rural settlements and found that social factors (i.e. human behaviour) are more important than climate and environmental conditions in determining the distributions of floras. While both studies explored the diversity of ornamental floras in relation to socioeconomic aspects, only Cubino et al. (2016) interpreted plant communities with regard to urban characteristics. These authors found that the differences between the composition of natural vegetation and artificial plant assemblages could be related to permanent residencies of local inhabitants vs. temporal residencies occupied by tourists. In another study by the same authors, Cubino et al. (2017) separated ornamental gardens from irrigated lawns and vegetable gardens. This distinction could not be tested using our dataset, as the structure of our data is totally different from

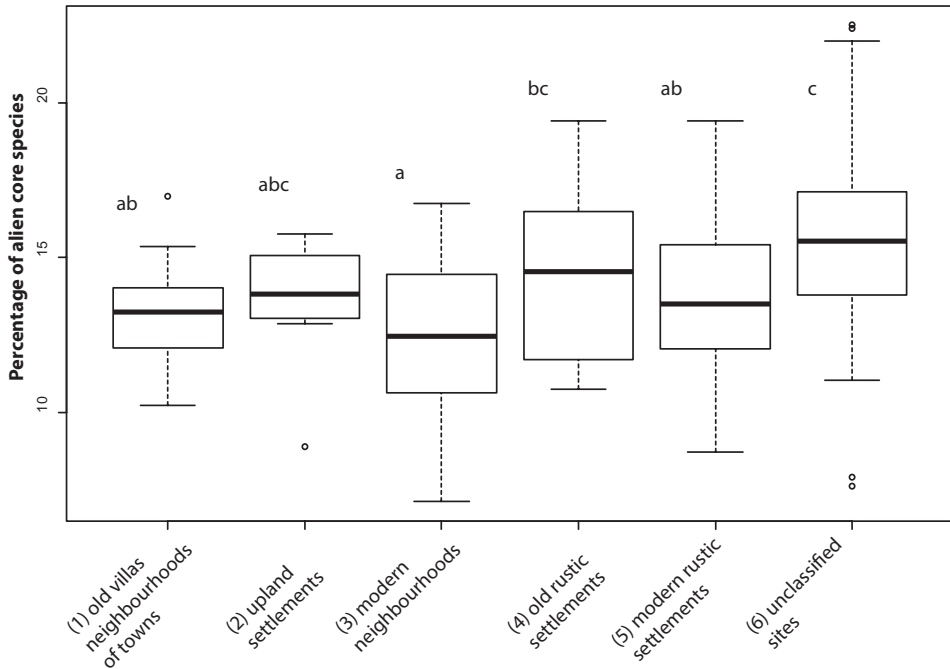


Figure 3. Differences in the percentages (i.e. median, 25th and 75th percentile and min/max values) of core alien ornamental taxa (i.e. frost-resistant cultivated plants that persisted for a long time after abandonment or taxa that occur at many sites) within clusters of classified settlement types and within the unclassified cluster. Same letters above the boxes indicate insignificant differences between clusters (ANOVA $F = 5.69$, $df (5, 168)$, $p < 0.001$).

the coastal ones. In addition, the sampling method and scale (questionnaire and home gardens), used by the cited authors, was sufficient to assess the socioeconomic characteristics which remained unknown to us, as we used data for the urban space only.

The concept of transient and core species, used in the analyses, shows the differences between established species, both naturalised aliens and native, and casual alien species. Both groups represent different levels of risk in the future. The core species have been present for a long time and many of them have the potential to spread after a lag phase; however, the transient taxa represent a larger pool of species waiting for opportunities to invade (Pergl et al. 2016b, Haeuser et al. 2018, van Kleunen et al. 2018). Additionally, potential time lags by core species may play a significant role after their long time of residence.

Ornamental flora and urban types

The information on the structure of settlements was not collected systematically. Therefore, we cannot provide percentage cover accounted for by individual clusters; however,

such information is clearly visible in the remote sensing images. Preliminary delimitation of individual clusters was therefore based on the structure of recorded sites that were chosen to cover relatively homogenous areas in the villages or in towns and cities. The clusters thus represent the structure of buildings and were mainly defined by expert knowledge.

We interpreted each cluster in terms of urban typology and environmental gradients (see Table 2). Our interpretation was based on the correspondence between the species composition of sites and their environmental, social and economic characteristics (Zerbe et al. 2003). Moreover, we carried out some preliminary analysis on the socioeconomic status of the sites, using the data from the Czech Statistical Office and this confirmed that our groups best describe the urban types that were delimited according to our field experience (see Suppl. material 2).

During our field assessment, we also evaluated some distinctive urban structures (see Suppl. material 2 and Suppl. material 3). Old villas neighbourhoods of towns are dominated by spacious gardens, surrounding wealthy houses (e.g. villas), built by the upper social classes between 1890 and 1930 (see Blažek 1998). These neighbourhoods are situated at different altitudes. Most upland settlements are situated in towns, villages or dispersed farmhouse settlements with a harsher climate (see Table 2). Upland settlements were mostly established by the former German population, which constituted an important, locally dominant ethnic minority prior to World War II. In the second half of the 20th century, many houses and gardens were renovated and new homes were built. The expansion of modern neighbourhoods dates back to the 1990s and occurred mainly in peri-urban lowlands with a mild climate. These neighbourhoods form a distinct urban type with a very specific composition of ornamental flora with the highest representations of specialists in gardening (see Suppl. material 2).

A modern style of garden design brought new practices, such as the use of bark chips or gravel (i.e. mulch). The activities of landscape architects and commercial gardening companies brought further radical changes to the local species composition. Old rustic settlements are characterised by cottage gardens in villages or peripheral parts of towns comprising a large number of farmhouses. Traditional rustic architecture is often replaced by modern single-family houses. However, the structure, composition and management of their gardens adheres to traditional habits (e.g. hoed patches, common cultivation of annuals, mixed plantations of ornamentals together with vegetables and a conservative selection of species). Some cemeteries were included because of the presence of folkish ornamental plants. Most sites are situated in lower altitudes. Modern and old rustic settlements share the same tradition of garden designs and gardening methods, except for the use of modern tools. Local fertile soils (often in lowland chernozem areas) and a warm climate allow for the development of species-rich and floriferous front gardens. Their structure is evidenced, for example, by luxuriant combinations of species, ranging from ornamental vines covering walls, unfenced gardens serving a semi-public function to narrow accessorial patches and lining pavements outside garden fences. Local emphasis on the representative role of these gardens is obvious. Most sites are villages or small towns with a significant proportion of new or renovated detached houses with front gardens and public green belts.

During our fieldwork, we identified other potentially important structures, besides the urban and rural structures listed above. Amongst others, these structures include cemeteries, public allotments, cottage colonies and crofts or gardens. We included public spaces such as cemeteries if these grounds were encountered during our urban district surveys. Therefore, these structures were included in all clusters but did not form an individual cluster. It was impossible to distinguish between private gardens and green public spaces in many cases, for example, green spaces in front of private houses. Surprisingly, none of these structures was differentiated as a unique cluster or species group. This may be due to their small size, floristic variability (i.e. cemeteries) or rather unspecific composition (i.e. allotments). However, it could also be that private gardens are over-represented in comparison to other “urban types” such as cemeteries, garden allotments or public parks.

Ornamental flora in various urban types as a source of plant invasions

The observed patterns suggest possible shifts in regional species pools which may correspond to the recent global shifts (van Kleunen et al. 2018). The detailed knowledge of these species pools is crucial for predicting future plant invasions. The invasion potential of species from private gardens differs according to the type of settlement. For example, a typical feature of old park-like gardens in towns (i.e. old villas neighbourhoods of towns) and gardens in upland settlements is the cultivation and successive domestication of ornamentals in semi-natural conditions. Plants in less-maintained parts of gardens or in semi-public spaces have been confronted with natural conditions for a long time, but also supported by episodic weeding or watering. Human assistance seems to be the best approach to promote naturalisation of new aliens (Mack 2000; Pyšek et al. 2011). Many shrubs (e.g. *Symphoricarpus albus* or *Cotoneaster* spp.) and tall herbs (*Rudbeckia laciniata*, *Reynoutria* spp., *Telekia speciosa*) can spread in these habitats for decades and establish invasive populations (e.g. Mandák et al. 2004). Other taxa are rarely cultivated, but form vigorous populations locally (e.g. *Heleborus foetidus*, *Celastrus orbiculatus*, *Cicerbita macrophylla* and *Veronica gentianoides*; see e.g. Červinka and Sádlo 2000). Many taxa spread within rockeries, but only few of these escape to natural rocky habitats (e.g. *Sedum* spp., *Alyssum murale*) or meadows (e.g. *Papaver nudicaule*, *Dianthus barbatus*). Some taxa may pose a threat to the native flora due to genetic erosion of the native taxa (e.g. *Hieracium aurantiacum* in its non-native areas, *Viola cornuta*, *Cerastium tomentosum* and cultivars of *Sedum album*, see Krahulcová et al. 1996) or appear as garden waste (e.g. *Cosmos* spp.).

Gardens in modern neighbourhoods and modern rustic settlements are very rich in taxa which were not present before the 1990s. Many of these escape, especially into novel habitats via interlocking concrete pavements or beds mulched with pebbles. For example, locally escaping populations of *Linaria purpurea*, *Pennisetum alopecuroides*,

Perovskia hybr. and *Thymophylla tenuiloba* have been observed during the surveys. In addition, these habitats also support the escape of some species that were traditionally cultivated but never escaped in the past, such as *Lavandula angustifolia*.

Many escaping aliens are already classified as invasive (Dehnen-Schmutz 2011), some of which are being eradicated or restricted to ornamental plantations, while others are still intentionally planted in the wild, such as *Rhus hirta* or *Symphoricarpos albus* (Pergl et al. 2016b). Our data allow us to comment on the invasion potential of rare taxa with small populations. Their local but copious spontaneous spread indicates that they may become invasive in the future (Dullinger et al. 2017). The high number of ornamental trees and shrubs planted in modern neighbourhoods potentially lead to invasions into the surrounding landscapes (Křivánek et al. 2006; Gregor et al. 2012; Aronson et al. 2015), especially near forests or shrubby vegetation (see e.g. Dobravolskaitė and Gudžinskas 2011). Abandoned private gardens in villas and residences in city centres represent a less serious threat, due to the lack of suitable habitats in the surroundings. Many alien taxa will overcome the climatic barrier in the future, as demonstrated with the ornamental flora of a small German city, where 45 garden-plant taxa are not yet naturalised but likely to become naturalised in the future (Mayer et al. 2017). The ability to naturalise is not directly linked with negative impacts; however, such studies can be used for horizon scanning (Roy et al. 2014) and for the early identification of potentially problematic taxa (Tanner et al. 2017; Roy et al. 2018). Consequently, the frequency of planting in different urban types, combined with the trait analysis of individual species and their ability to escape, can provide direct prioritisation schemes in the future (Kutlvašr et al. 2018).

Conclusions

In this study, we classified human-made assemblages of ornamental taxa. The results show that human-made assemblages of ornamental taxa can be classified using this method, which has been conceived for natural vegetation, formed by basic ecological gradients.

The detected variation of ornamentals mainly follows (i) altitude, associated with climatic or soil gradients and (ii) differences in local traditions, given by the socioeconomic drivers and cultural history. Similar compositional patterns can be expected in other countries, although particular clusters may differ substantially in their delimitation.

In view of the results, new neighbourhoods represent the greatest potential threat for future invasions. These gardens are species-rich, particularly in woody aliens and many of their taxa have been rarely cultivated or even absent until recently. Furthermore, these neighbourhoods are often constructed in peri-urban belts in which the abundance of newly disturbed habitats is suitable for new local escapees and invasions.

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References

- Acar C, Acar H, Eroglu E (2007) Evaluation of ornamental plant resources to urban biodiversity and cultural changing: A case study of residential landscapes in Trabzon city (Turkey). *Building and Environment* 42: 218–229. <https://doi.org/10.1016/j.buildenv.2005.08.030>
- Aronson MFJ, Handel SN, La Puma IP, Clemants SE (2015) Urbanization promotes non-native woody species and diverse plant assemblages in the New York metropolitan region. *Urban Ecosystems* 18: 31–45. <https://doi.org/10.1007/s11252-014-0382-z>
- Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. *Trends in Ecology and Evolution* 26: 333–339. <https://doi.org/10.1016/j.tree.2011.03.023>
- Blážek B (1998) Venkov, města, média (Villages, cities and media, in Czech). *SLON* (Praha): 1–362.
- Botham MS, Rothery P, Hulme PE, Hill MO, Preston CD, Roy DB (2009) Do urban areas act as foci for the spread of alien plant species? An assessment of temporal trends in the UK. *Diversity and Distributions* 15: 338–345. <https://doi.org/10.1111/j.1472-4642.2008.00539.x>
- Bruelheide H (1995) Die Grünlandgesellschaften des Harzes und ihre Standortsbedingungen. Mit einem Beitrag zum Gliederungssystem auf der Basis von statistisch ermittelten Artengruppen. *Dissertationes Botanicae* 244: 1–338.
- Bruelheide H (2000) A new measure of fidelity and its application to defining species groups. *Journal of Vegetation Science* 11: 167–178. <https://doi.org/10.2307/3236796>
- Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions* 15: 22–40. <https://doi.org/10.1111/j.1472-4642.2008.00521.x>
- Červinka Z, Sádlo J (2000) Neofyty *Ambrosia psilostachya* a *Celastrus orbiculatus* v městě Čelákovcích (Neophytes *Ambrosia psilostachya* and *Celastrus orbiculatus* in Čelákovice). *Muzeum a Současnost* 14: 65–68.

- Chocholoušková Z, Pyšek P (2003) Changes in composition and structure of urban flora over 120 years: A case study of the city of Plzeň. *Flora* 198: 366–376. <https://doi.org/10.1078/0367-2530-00109>
- Chytrý M (Ed.) (2009) *Vegetation of the Czech Republic. 2. Ruderal, weed, rock and scree vegetation*. Academia (Praha): 1–524.
- Chytrý M (2012) *Vegetation of the Czech Republic: Diversity, ecology, history and dynamics*. *Preslia* 84: 427–504.
- Chytrý M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science* 13: 79–90. <https://doi.org/10.1111/j.1654-1103.2002.tb02025.x>
- Cook EM, Hall SJ, Larson KL (2012) Residential landscapes as social-ecological systems: a synthesis of multi-scalar interactions between people and their home environment. *Urban Ecosystems* 15: 19–52. <https://doi.org/10.1007/s11252-011-0197-0>
- Cubino JP, Subirós JV, Lozano CB (2014) Examining floristic boundaries between garden types at the global scale. *Investigaciones Geográficas* 61: 71–86. <https://doi.org/10.14198/IN-GEO2014.61.05>
- Cubino JP, Subirós JV, Lozano CB (2016) Floristic and structural differentiation between gardens of primary and secondary residences in the Costa Brava (Catalonia, Spain). *Urban Ecosystems* 19: 505–521. <https://doi.org/10.1007/s11252-015-0496-y>
- Cubino JP, Kirkpatrick JB, Subirós JV (2017) Do water requirements of Mediterranean gardens relate to socio-economic and demographic factors? *Urban Water Journal* 14: 401–408. <https://doi.org/10.1080/1573062X.2016.1173219>
- Daehler CC (2008) Invasive plant problems in the Hawaiian Islands and beyond: Insights from history and psychology. In: Tokarska-Guzik B, Brock JH, Brundu G, Child L, Daehler CC, Pyšek P (Eds) *Plant Invasions: Human Perception, Ecological Impacts and Management*. Backhuys Publishers (Leiden), 3–20.
- Danihelka J, Chrtěk Jr J, Kaplan Z (2012) Checklist of vascular plants of the Czech Republic. *Preslia* 84: 647–811.
- Davoren E, Siebert S, Cilliers SS, du Toit M (2016) Influence of socioeconomic status on design of Botswana home gardens and associated plant diversity patterns in northern South Africa. *Landscape and Ecological Engineering* 12: 129–139. <https://doi.org/10.1007/s11355-015-0279-x>
- Dehnen-Schmutz K (2011) Determining non-invasiveness in ornamental plants to build green lists. *Journal of Applied Ecology* 48: 1374–1380. <https://doi.org/10.1111/j.1365-2664.2011.02061.x>
- Dehnen-Schmutz K, Conroy J (2018) Working with gardeners to identify potential invasive ornamental garden plants: testing a citizen science approach. *Biological Invasions* 20: 3069–3077. <https://doi.org/10.1007/s10530-018-1759-3>
- Dehnen-Schmutz K, Touza J, Perrings C, Williamson M (2007) The horticultural trade and ornamental plant invasions in Britain. *Conservation Biology* 21: 224–231. <https://doi.org/10.1111/j.1523-1739.2006.00538.x>
- Dobravolskaitė R, Gudžinskas Z (2011) Alien plant invasion to forests in the vicinity of communal gardens. *Botanica Lithuanica* 17: 73–84.

- Dullinger I, Wessely J, Bossdorf O, Dawson W, Essl F, Gatringer A, Klöner G, Kreft H, Kuttner M, Moser D, Pergl J, Pyšek P, Thuiller W, van Kleunen M, Weigelt P, Winter M, Dullinger S (2017) Climate change will increase the naturalization risk from garden plants in Europe. *Global Ecology and Biogeography* 26: 43–53. <https://doi.org/10.1111/geb.12512>
- Enders M, Havemann F, Jeschke JM (2019) A citation-based map of concepts in invasion biology. *NeoBiota* 47: 23–42. <https://doi.org/10.3897/neobiota.47.32608>
- Fratarcangeli C, Fanelli G, Franceschini S, De Sanctis M, Travaglini A (2019) Beyond the urban-rural gradient: Self-organizing map detects the nine landscape types of the city of Rome. *Urban Forestry and Urban Greening* 38: 354–370. <https://doi.org/10.1016/j.ufug.2019.01.012>
- Gaston KJ, Fuller RA, Loram A, MacDonald C, Power S, Dempsey N (2007) Urban domestic gardens (XI): Variation in urban wildlife gardening in the UK. *Biodiversity Conservation* 16: 3227–3238. <https://doi.org/10.1007/s10531-007-9174-6>
- Gaston KJ, Warren PH, Thompson K, Smith RM (2005) Urban domestic gardens (IV): The extent of the resource and its associated features. *Biodiversity and Conservation* 14: 3327–3349. <https://doi.org/10.1007/s10531-004-9513-9>
- Gregor T, Bonsel D, Starke-Ottich I, Zizka G (2012) Drivers of floristic change in large cities – A case study of Frankfurt/Main (Germany). *Landscape and Urban Planning* 104: 230–237. <https://doi.org/10.1016/j.landurbplan.2011.10.015>
- Groening G, Wolschke-Bulmahn J (1989) Changes in the philosophy of garden architecture in the 20th century and their impact upon the social and spatial environment. *Journal of Garden History* 9: 53–70. <https://doi.org/10.1080/01445170.1989.10408267>
- Haeuser E, Dawson W, Thuiller W, Dullinger S, Block S, Bossdorf O, Carboni M, Conti L, Dullinger I, Essl F, Klöner G, Moser D, Münkemüller T, Parepa M, Talluto MV, Kreft H, Pergl J, Pyšek P, Weigelt P, Winter M, Kühn I, Hermy M, Van der Veken S, Roquet C, van Kleunen M (2018) The European ornamental garden flora as an invasion debt under climate change. *Journal of Applied Ecology* 55: 2386–2395. <https://doi.org/10.1111/1365-2664.13197>
- Hanspach J, Kühn I, Pyšek P, Boos E, Klotz S (2008) Correlates of naturalization and occupancy of introduced ornamentals in Germany. *Perspectives in Plant Ecology, Evolution and Systematics* 10: 241–250. <https://doi.org/10.1016/j.ppees.2008.05.001>
- Hulme PE (2011) Addressing the threat to biodiversity from botanic gardens. *Trends in Ecology and Evolution* 26: 168–174. <https://doi.org/10.1016/j.tree.2011.01.005>
- Hulme PE, Brundu G, Carboni M, Dehnen-Schmutz K, Dullinger S, Early R, Essl F, Gonzalez-Moreno P, Groom Q, Kueffer C, Kühn I, Maurel N, Novoa A, Pergl J, Pyšek P, Seebens H, Tanner R, Touza J, van Kleunen M, Verbrugge L (2018) Integrating invasive species policies across ornamental horticulture supply chains to prevent biological invasions. *Journal of Applied Ecology* 55: 92–98. <https://doi.org/10.1111/1365-2664.12953>
- Humair F, Küffer C, Siegrist M (2014) Are non-native plants perceived to be more risky? Factors influencing horticulturists' risk perceptions of ornamental plant species. *PLoS ONE* 9: e102121. <https://doi.org/10.1371/journal.pone.0102121>
- Jarolímek I, Šibík J [Eds] (2008) Diagnostic, constant and dominant species of the higher vegetation units of Slovakia. *Veda (Bratislava)*: 1–332.
- Kaplan Z (2012) Flora and phytogeography of the Czech Republic. *Preslia* 84: 505–573.

- Kendal D, Williams NSG, Williams KJH (2012a) A cultivated environment: Exploring the global distribution of plants in gardens, parks and streetscapes. *Urban Ecosystems* 15: 637–652. <https://doi.org/10.1007/s11252-011-0215-2>
- Kendal D, Williams KJH, Williams NSG (2012b) Plant traits link people's plant preferences to the composition of their gardens. *Landscape and Urban Planning* 105: 34–42. <https://doi.org/10.1016/j.landurbplan.2011.11.023>
- Klonner G, Dullinger I, Wessely J, Bossdorf O, Carboni M, Dawson W, Essl F, Gattringer A, Haeuser E, van Kleunen M, Kreft H, Moser D, Pergl J, Pyšek P, Thuiller W, Weigelt P, Winter M, Dullinger S (2017) Will climate change increase hybridization risk between potential plant invaders and their congeners in Europe? *Diversity and Distributions* 23: 934–943. <https://doi.org/10.1111/ddi.12578>
- Kowarik I (2005) Urban ornamentals escaped from cultivation. In: Gressel J (Ed.) *Crop Fertility and Volunteerism: A Threat to Food Security in the Transgenic Era?* CRC Press (Boca Raton), 97–121. <https://doi.org/10.1201/9781420037999.ch7>
- Kowarik I, Pyšek P (2012) The first steps towards unifying concepts in invasion ecology were made one hundred years ago: revisiting the work of the Swiss botanist Albert Thellung. *Diversity and Distributions* 18: 1243–1252. <https://doi.org/10.1111/ddi.12009>
- Krahulcová A, Krahulec F, Kirschner J (1996) Introgressive hybridization between a native and an introduced species: *Viola lutea* subsp. *sudetica* versus *V. tricolor*. *Folia Geobotanica Phytotaxonomica* 31: 219–244. <https://doi.org/10.1007/BF02812066>
- Křivánek M, Pyšek P, Jarošík V (2006) Planting history and propagule pressure as predictors of invasions by woody species in a temperate region. *Conservation Biology* 20: 1487–1498. <https://doi.org/10.1111/j.1523-1739.2006.00477.x>
- Kueffer C, Pyšek P, Richardson DM (2013) Integrative invasion science: Model systems, multi-site studies, focused meta-analysis, and invasion syndromes. *New Phytologist* 200: 615–633. <https://doi.org/10.1111/nph.12415>
- Kutlvašr J, Pergl J, Baroš A, Pyšek P (2018) Survival, dynamics of spread and invasive potential of species in perennial plantations. *Biological Invasions* 21: 561–573. <https://doi.org/10.1007/s10530-018-1847-4>
- Loram A, Thompson K, Warren PH, Gaston KJ (2008a) Urban domestic gardens (XII): The richness and composition of the flora in five cities. *Journal of Vegetation Science* 19: 321–330. <https://doi.org/10.3170/2008-8-18373>
- Loram A, Warren PH, Gaston KJ (2008b) Urban domestic gardens (XIV): The characteristics of gardens in five cities. *Environmental Management* 42: 361–376. <https://doi.org/10.1007/s00267-008-9097-3>
- Lososová Z, Chytrý M, Tichý L, Danihelka J, Fajmon K, Hájek O, Kintrová K, Kühn I, Láníková D, Otýpková Z, Řehořek V (2012) Native and alien floras in urban habitats: A comparison across 32 cities of central Europe. *Global Ecology and Biogeography* 21: 545–555. <https://doi.org/10.1111/j.1466-8238.2011.00704.x>
- Lowenstein DM, Minor ES (2016) Diversity in flowering plants and their characteristics: Integrating humans as a driver of urban floral resources. *Urban Ecosystems* 19: 1735–1748. <https://doi.org/10.1007/s11252-016-0563-z>

- Mack RN (2000) Cultivation fosters plant naturalization by reducing environmental stochasticity. *Biological Invasions* 2: 111–122. <https://doi.org/10.1023/A:1010088422771>
- Mandák B, Pyšek P, Bímová K (2004) History of the invasion and distribution of *Reynoutria* taxa in the Czech Republic: A hybrid spreading faster than its parents. *Preslia* 76: 15–64.
- Marco A, Lavergne S, Dutoit T, Bertaudiere-Montes V (2010) From the backyard to the backcountry: How ecological and biological traits explain the escape of garden plants into Mediterranean old fields. *Biological Invasions* 12: 761–779. <https://doi.org/10.1007/s10530-009-9479-3>
- Mayer K, Haeuser E, Dawson W, Essl F, Kreft H, Pergl J, Weigelt P, Winter M, Lenzer B, van Kleunen M (2017) Naturalization of ornamental plant species in public green spaces and private gardens. *Biological Invasions* 19: 3613–3627. <https://doi.org/10.1007/s10530-017-1594-y>
- Palliwoda J, Kowarik I, von der Lippe M (2017) Human-biodiversity interactions in urban parks: The species level matters. *Landscape and Urban Planning* 157: 394–406. <https://doi.org/10.1016/j.landurbplan.2016.09.003>
- Pergl J, Pyšek P, Bacher S, Essl F, Genovesi P, Harrower CA, Hulme PE, Jeschke JM, Kenis M, Kühn I, Perglová I, Rabitsch W, Roques A, Roy DB, Roy HE, Vilà M, Winter M, Nentwig W (2017) Troubling travellers: Are ecologically harmful alien species associated with particular introduction pathways? *NeoBiota* 32: 1–20. <https://doi.org/10.3897/neobiota.32.10199>
- Pergl J, Sádlo J, Petrusek A, Laštůvka Z, Musil J, Perglová I, Šanda R, Šefrová H, Šíma J, Vohralík V, Pyšek P (2016a) Black, Grey and Watch Lists of alien species in the Czech Republic based on environmental impacts and management strategy. *NeoBiota* 28: 1–37. <https://doi.org/10.3897/neobiota.28.4824>
- Pergl J, Sádlo J, Petřík P, Danihelka J, Chrtek Jr J, Hejda M, Moravcová L, Perglová I, Štajerová K, Pyšek P (2016b) Dark side of the fence: Ornamental plants as a source for spontaneous flora of the Czech Republic. *Preslia* 88: 163–188.
- Petřík P, Bruelheide H (2006) Species groups can be transferred across scales. *Journal of Biogeography* 33: 1628–1632. <https://doi.org/10.1111/j.1365-2699.2006.01514.x>
- Pyšek P, Chytrý M (2014) Habitat invasion research: Where vegetation science and invasion ecology meet. *Journal of Vegetation Science* 25: 1181–1187. <https://doi.org/10.1111/jvs.12146>
- Pyšek P, Danihelka J, Sádlo J, Chrtek Jr J, Chytrý M, Jarošík V, Kaplan Z, Krahulec F, Moravcová L, Pergl J, Štajerová K, Tichý L (2012) Catalogue of alien plants of the Czech Republic (2nd edn). Checklist update, taxonomic diversity and invasion patterns. *Preslia* 84: 155–255.
- Pyšek P, Jarošík V, Pergl J (2011) Alien plants introduced by different pathways differ in invasion success: Unintentional introductions as greater threat to natural areas? *PLoS ONE* 6: e24890. <https://doi.org/10.1371/journal.pone.0024890>
- Pyšek P, Pergl J, Essl F, Lenzer B, Dawson W, Kreft H, Weigelt P, Winter M, Kartesz J, Nishino M, Antonova LA, Barcelona JF, Cabezas FJ, Cárdenas D, Cárdenas-Toro J, Castaño N, Chacón E, Chatelain C, Dullinger S, Ebel AL, Figueiredo E, Fuentes N, Genovesi P, Groom QJ, Henderson L, Inderjit, Kupriyanov A, Masciadri S, Maurel N, Meerman J, Morozova O, Moser D, Nickrent D, Nowak PM, Pagad S, Patzelt A, Pelser PB, Seebens H, Shu W, Thomas J, Velayos M, Weber E, Wieringa JJ, Baptiste MP, van Kleunen M (2017) Naturalized alien flora of the world: Species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. *Preslia* 89: 203–274. <https://doi.org/10.23855/preslia.2017.203>

- Redman CL, Grove JM, Kuby LH (2004) Integrating social science into the long-term ecological research (LTER) network: Social dimensions of ecological change and ecological dimensions of social change. *Ecosystems* 7: 161–171. <https://doi.org/10.1007/s10021-003-0215-z>
- Reichard SH, White P (2001) Horticulture as a pathway of invasive plant introductions in the United States. *BioScience* 51: 103–113. [https://doi.org/10.1641/0006-3568\(2001\)051\[0103:HAAPOI\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0103:HAAPOI]2.0.CO;2)
- Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6: 93–107. <https://doi.org/10.1046/j.1472-4642.2000.00083.x>
- Roy HE, Peyton J, Aldridge DC, Bantock T, Blackburn TM, Britton R, Clark P, Cook E, Dehnen-Schmutz K, Dines T, Dobson M, Edwards F, Harrower C, Harvey MC, Minchin D, Noble DG, Parrott D, Pocock MJO, Preston CD, Roy S, Salisbury A, Schönrogge K, Sewell J, Shaw RH, Stebbing P, Stewart AJA, Walker KJ (2014) Horizon scanning for invasive alien species with the potential to threaten biodiversity in Great Britain. *Global Change Biology* 20: 3859–3871. <https://doi.org/10.1111/gcb.12603>
- Roy HE, Rabitsch W, Scalera R, Stewart A, Gallardo B, Genovesi P, Essl F, Adriaens T, Bacher S, Booy O, Branquart E, Brunel S, Copp GH, Dean H, D'hondt B, Josefsson M, Kenis M, Kettunen M, Linnamagi M, Lucy F, Martinou A, Moore N, Nentwig W, Nieto A, Pergl J, Peyton J, Roques A, Schindler S, Schönrogge K, Solarz W, Stebbing PD, Trichkova T, Vanderhoeven S, van Valkenburg J, Zenetos A (2018) Developing a framework of minimum standards for the risk assessment of alien species. *Journal of Applied Ecology* 55: 526–538. <https://doi.org/10.1111/1365-2664.13025>
- Rumlerová Z, Vilà M, Pergl J, Nentwig W, Pyšek P (2016) Scoring environmental and socio-economic impacts of alien plants invasive in Europe. *Biological Invasions* 18: 3697–3711. <https://doi.org/10.1007/s10530-016-1259-2>
- Smith RM, Thompson K, Hodgson JG, Warren PH, Gaston KJ (2006) Urban domestic gardens (IX): Composition and richness of the vascular plant flora, and implications for native biodiversity. *Biological Conservation* 129: 312–322. <https://doi.org/10.1016/j.biocon.2005.10.045>
- Sokal RR, Rohlf FJ (1995) *Biometry* (3rd edn). Freeman, New York.
- Štajerová K, Šmilauer P, Brůna J, Pyšek P (2017) Distribution of invasive plants in urban environment is strongly spatially structured. *Landscape Ecology* 32: 681–692. <https://doi.org/10.1007/s10980-016-0480-9>
- Sukopp H (2002) On the early history of urban ecology in Europe. *Preslia* 74: 373–393.
- Tanner R, Branquart E, Brundu G, Buholzer S, Chapman D, Ehret P, Fried G, Starfinger U, van Valkenburg J (2017) The prioritisation of a short list of alien plants for risk analysis within the framework of the Regulation (EU) No. 1143/2014. *NeoBiota* 35: 87–118. <https://doi.org/10.3897/neobiota.35.12366>
- Thompson K, Austin K, Smith R, Warren P, Angold P, Gaston K (2003) Urban domestic gardens (I): Putting small-scale plant diversity in context. *Journal of Vegetation Science* 14: 71–78. <https://doi.org/10.1111/j.1654-1103.2003.tb02129.x>
- Tichý L (2002) JUICE, software for vegetation classification. *Journal of Vegetation Science* 13: 451–453. <https://doi.org/10.1111/j.1654-1103.2002.tb02069.x>

- Tichý L, Chytrý M (2006) Statistical determination of diagnostic species for site groups of unequal size. *Journal of Vegetation Science* 17: 809–818. <https://doi.org/10.1111/j.1654-1103.2006.tb02504.x>
- Tichý L, Holt J, Nejezchlebová M (2010) JUICE program for management, analysis and classification of ecological data, 2nd edition of the Program. http://www.sci.muni.cz/botany/juice/JCman2011_2nd.pdf
- van Heezik JM, Freeman CE, Porter S, Dickinson KJM (2013) Garden Size, Householder Knowledge, and Socio-Economic Status Influence Plant and Bird Diversity at the Scale of Individual Gardens. *Ecosystems* 16: 1442–1454. <https://doi.org/10.1007/s10021-013-9694-8>
- van Kleunen M, Dawson W, Essl F, Pergl J, Winter M, Weber E, Kreft H, Weigelt P, Kartesz J, Nishino M, Antonova LA, Barcelona JF, Cabezas FJ, Cárdenas D, Cárdenas-Toro J, Castaño N, Chacón E, Chatelain C, Ebel AL, Figueiredo E, Fuentes N, Groom QJ, Henderson L, Inderjit, Kupriyanov A, Masciadri S, Meerman J, Morozova O, Moser D, Nickrent DL, Patzelt A, Pelsers PB, Baptiste MP, Poopath M, Schulze M, Seebens H, Shu W, Thomas J, Velayos M, Wieringa JJ, Pyšek P (2015) Global exchange and accumulation of non-native plants. *Nature* 525: 100–103. <https://doi.org/10.1038/nature14910>
- van Kleunen M, Essl F, Pergl J, Brundu G, Carboni M, Dullinger S, Early R, González-Moreno P, Groom Q, Hulme PE, Kueffer C, Kühn I, Máguas C, Maurel N, Novoa A, Parepa M, Pyšek P, Seebens H, Tanner R, Touza J, Verbrugge L, Weber E, Dawson W, Kreft H, Weigelt P, Winter M, Klöner G, Talluto MV, Dehnen-Schmutz K (2018) The changing role of ornamental horticulture in plant invasions. *Biological Reviews* 93: 1421–1437. <https://doi.org/10.1111/brv.12402>
- Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE, DAISIE partners (2010) How well do we understand the impacts of alien species on ecological services? A pan-European cross-taxa assessment. *Frontiers in Ecology and the Environment* 8: 135–144. <https://doi.org/10.1890/080083>
- Vogl CR, Vogl-Lukasser B, Puri RK (2004) Tools and methods for data collection in ethnobotanical studies of homegardens. *Field Methods* 16: 285–306. <https://doi.org/10.1177/1525822X04266844>
- von der Lippe M, Kowarik I (2007) Do cities export biodiversity? Traffic as dispersal vector across urban-rural gradients. *Diversity and Distributions* 14: 18–25. <https://doi.org/10.1111/j.1472-4642.2007.00401.x>
- Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM (2009) Something in the way you move: dispersal pathways affect invasion success. *Trends in Ecology and Evolution* 24: 136–144. <https://doi.org/10.1016/j.tree.2008.10.007>
- Yang J, La Sorte FA, Pyšek P, Yan P, Nowak D, McBride J (2015) The compositional similarity of urban forests among the world's. *Global Ecology and Biogeography* 24: 1413–1423. <https://doi.org/10.1111/geb.12376>
- Zerbe S, Maurer U, Schmitz S, Sukopp H (2003) Biodiversity in Berlin and its potential for nature conservation. *Landscape and Urban Planning* 62: 139–148. [https://doi.org/10.1016/S0169-2046\(02\)00145-7](https://doi.org/10.1016/S0169-2046(02)00145-7)

Supplementary material 1

Sampling methods described in Pergl et al. (2016b)

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Data type: species data

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Link: <https://doi.org/10.3897/neobiota.52.39260.suppl1>

Supplementary material 2

List of characteristics for individual sites: architecture structure and socio-economic and environmental factors

Authors: Petr Petřík, Jiří Sádlo, Martin Hejda, Kateřina Štajerová, Petr Pyšek, Jan Pergl
Data type: measurement

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Supplementary material 3

Box plots for selected six clusters with subjectively recognized urban types

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Data type: statistical data

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