

Invasion science, ecology and economics: seeking roads not taken

Mark Williamson¹, Laura A. Meyerson^{2,3}, Harald Auge⁴

1 Department of Biology, University of York, York YO10 5DD **2** Institute of Botany, Department of Invasion Ecology, Academy of Sciences of the Czech Republic, Průhonice, CZ 252 43, Czech Republic **3** University of Rhode Island, Department of Natural Resources Science, Kingston, RI 02881 **4** UFZ, Helmholtz Centre for Environmental Research-UFZ, Dept. Community Ecology, Theodor-Lieser-Str. 4, 06120 Halle, Germany

Corresponding author: Mark Williamson (mw1@york.ac.uk)

Academic editor: Ingolf Kühn | Received 3 October 2011 | Accepted 4 October 2011 | Published 5 October 2011

Citation: Williamson M, Meyerson LA, Auge H (2011) Invasion science, ecology and economics: seeking roads not taken. NeoBiota 10: 1–5. doi: 10.3897/neobiota.10.2194

Introduction

As members of the editorial board of NeoBiota who, for various reasons, didn't get our names on the original editorial (Kühn et al. 2011), we would like to add a coda to it. Even though there were 38 bullet points listing areas in invasion science where more work is needed, we would like to mention additional areas that we hope would be addressed in future issues of NeoBiota. Like the other editors, we would like this innovative and exciting new journal to lead the way in all areas of invasion science. As the graphs in Gurevitch et al. (2011) and Kühn et al. (2011) show, the literature on invasions has been increasing almost exponentially since the early 1980s and so we cannot expect any list of areas of interest to stay complete and up to date for very long.

Three areas that we would like to stress are the interaction between invasion science and economics and the role that invasion science should play in advancing pure ecology in two areas, population dynamics and ecosystem ecology. Neither ecology nor economics appears as a word in the original bullet list, but many of the topics are obviously ecological while none are obviously economic. For economics, we want to point out its relevance to invasion science and the feedback between the two disciplines, particularly in a rapidly changing world with powerful new emerging economies. For ecology, we want to emphasise not what ecology tells us about invasions but what invasions reveal about ecology and evolution at two scales.

Economics

There are two recent multi-author books that show the extent and variety of the interaction of economics with invasion science (Keller et al. 2009, Perrings et al. 2010) and also the variety of approaches to tackling these problems, though in this field models are almost always important. Both books also cover management and policy. As any manager knows, finance, either explicit in income or implicit from volunteers etc., determines what can be done and which problems can be tackled. But economics is about much more than costs. Economic analysis and theory are important in developing policy for dealing with invasive problems and serve as motivators for both the public and private sector to take action.

The ecological and economic dimensions of the problem of invasive species are connected at different levels. Many of the changes that lead ecosystems to be more vulnerable to the impact of invasives (e.g. fragmentation, disturbance, loss of diversity, pollution) are direct consequences of economic behaviour. The ecological mechanisms affecting invasives, such as functional diversity and dispersion, are correlated with trade, transport and travel. The consequences of the reduction in ecosystem functionality and the ability to provide ecological services have direct implications for the value of the output and ecological capital of the system.

At every level, the ecological impacts of economic activities are incidental to and usually ignored by the actors concerned. These impacts are externalities of the market transactions; they are not taken seriously by those making the transactions perhaps because they are not held legally responsible for the impacts nor are the markets directly affected by these impacts. Instead these impacts are often borne by those who receive little or no benefit from the market transactions. In addition, quantifying some ecosystem services (and disservices) is difficult and approaches to do so vary necessarily by scale, type of service, and region (Meyerson et al. 2005). Therefore, the major economic problems of invasions are first to understand the nature of invasive species externalities, second to evaluate the consequences they have for well-being, and third to develop policies and instruments for their internalisation.

Ecology

The intimate relation between ecology and invasion science is well known. Less recognised is that invasions throw light on some ecological processes that can be more difficult to study in uninvaded systems. Many ecosystems are close to equilibrium or are following a moving equilibrium from seasonal or longer changes which makes detecting significant changes a long-term prospect and out of sync with two to four year funding cycles. Invasions supply ample examples of unintended experiments with systems well away from equilibrium, often over relatively short time periods. The resultant changes are informative both for the population dynamics of individual species and for the coevolution of communities.

In population dynamics, the growth and spread of populations are natural aspects to study in invaded systems. We will just mention two aspects, lag and the pattern of spread.

There is much misunderstanding of lag. It occurs when a population is not growing in numbers at all. When there are, as so often, casuals, i.e. individuals not producing population growth, it can be difficult to be sure whether the population is growing or not. A common problem is to mistake the early stages of logarithmic or quadratic growth with lag. The quickest solution is usually to plot transformations, e.g. log or square root, of the species counts. Too many statisticians want arithmetic plots which frequently conceal the behaviour of a population. Lags are important for management as they result in invasive species that appear to be harmless, sleeper weeds and such, leading to a lack of action when it would still be relatively cheap and easy to control or even eradicate a population. The lengths of lags are surprisingly variable and some can be quite long. Williamson (2010) found lags from 7 to 154 years in some beautiful Czech plant data, though 22 of 50 species showed no lag. The median lag was 41 years, a period long enough to make a serious management problem. We would emphasize though that lag is an important and little understood aspect of population growth in every sort of species.

It is easy to suggest causes for lag, such as the wrong habitat at introduction, the wrong genotype first introduced or Allee effects, but we know of very few cases when the cause can even be guessed let alone demonstrated. One such is in *Epilobium ciliatum*, a willow herb native to North America, first established in England in the midlands before 1891 but which didn't spread though it did establish. Another introduction into south-east England in the 1920s spread rapidly throughout Britain, overrunning the midlands. It is the plant species with the fastest known spread in Britain so far (Williamson 2011). In that case, the failure of the 19th century introduction to spread can be ascribed with some confidence to genotype. Not that that helps much without knowing the genes and what characters they affect and why those characters prevent spread in England. Lags, though important, are difficult to study and much neglected by ecologists.

Conversely, spread is often quite easy to study though here again some biologists have made an elementary mistake, namely regarding the increase in records as an increase in population size, while nearly always it is only a measure of population range. Possibly this comes from models of spread involving population parameters such as the intrinsic rate of natural increase. Long term records of the ranges of invading species show much variation in the rate and pattern of spread, phenomena complicated by the heterogeneity of natural systems (Williamson 2010). Again, practically nothing is known of the causes of such variation. Yet such knowledge would be most useful in predicting the behaviour of new invaders. It would also, importantly, advance our understanding of basic ecology, and perhaps also provide insights into range expansions and spread under global climate change. The quantitative study of both lag and spread depends on long term, good quality and consistent data. So invasions can be of benefit to ecological science by strengthening the case for long term studies.

The other ecological topic we would like to mention is that species invasions may help us to better understand the mechanisms which generally govern ecosystems. How does co-evolutionary history among species shape the diversity, functioning and stability of ecosystems? Although this topic is somewhat related to the bullet point “Eco-evolutionary feedback between invasive traits and ecosystem function” in the original list, it focuses on different processes.

Interactions among plants, herbivores and microbes influence ecosystem functions (Stein et al. 2009, 2010) and are commonly thought to be shaped by joint evolutionary history (Thompson 1994); exotic species are disconnected from such coevolved relationships and may encounter evolutionarily naïve communities. This in turn may affect competitive outcomes among species (Thorpe et al. 2011) and lead to the disruption of species interactions in the invaded ecosystem (Stinson et al. 2006). It is therefore reasonable to suggest that ecosystem properties are shaped by the coevolutionary history among species, but this hypothesis has been tested only in a very few studies. Recently, Wilsey et al. (2009) set up experimental communities either composed of native plants or composed of exotics which were phylogenetically related to the natives, and revealed that exotic communities declined faster in diversity, but showed higher productivity than the native communities. These findings demonstrate how fine-tuned species interactions within communities are, and suggest that not only the invasive traits of species, but also the novelty of exotic species *per se* may affect ecosystems. In another study, Maron and Marler (2008) showed that the diversity-productivity relationship was even reversed when native plant communities were experimentally invaded by exotics. Perhaps, the dislocation from co-evolved relationships may not only contribute to unifying theories explaining invasions (e.g. Hallett 2006), but also to a predictive framework for the ecosystem impact of invaders.

References

- Gurevitch J, Fox GA, Wardle GM, Inderjit, Taub D 2011 Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecology Letters* 14: 407–418. doi: 10.1111/j.1461-0248.2011.01594.x
- Hallett SG (2006) Dislocation from coevolved relationships: a unifying theory for plant invasion and naturalization? *Weed Science* 54: 282–290
- Keller RP, Lodge DM, Lewis MA, Shogren JF (Eds) (2009) *Bioeconomics of invasive species: integrating ecology, economics, policy, and management*. Oxford University Press, Oxford. 298 pp.
- Kühn I, Kowarik I, Kollman J, Starfinger U, Bacher S, Blackburn TM, Bustamente RO, Celesti-Gradow L, Chytrý M, Colautti RI, Essl F, Foxcroft LC, García-Berthou E, Gollasch S, Hierro J, Hufbauer RA, Hulme PE, Jarošík V, Jeschke JM, Karrer G, Mack RN, Molofsky J, Murray BR, Nentwig W, Osborne B, Pyšek P, Rabitsch W, Rejmánek M, Roques A, Shaw R, Sol D, Vilà M, van Kleunen M, von der Lippe M, Wolfe LM, Penev L (2011)

- Open minded and open access: introducing Neobiota, a new peer reviewed journal of biological invasions. *Neobiota* 9: 1–11. doi: 10.3987/neobiota.9.1835
- Maron JL, Marler M (2008) Effects of native species diversity and resource additions on invader impact. *American Naturalist* 172: S18–S33. doi: 10.1086/588303
- Meyerson LA, Baron J, Melillo JM, Naiman RJ, O'Malley RI, Orians G, Palmer MA, Pfaff ASP, Running SW, Sala OE (2005) Aggregate measures of ecosystem services: can we take the pulse of nature? *Frontiers in Ecology and the Environment* 3: 56–59. doi: 10.1890/1540-9295(2005)003[0056:AMOESC]2.0.CO;2
- Perrings C, Mooney H, Williamson M (Eds) (2010) *Bioinvasions & globalization: ecology, economics, management, and policy*. Oxford University Press, Oxford, 267 pp.
- Stein C, Rißmann C, Hempel S, Renker C, Buscot F, Prati D, Auge H (2009) Interactive effects of mycorrhizae and a hemiparasite on plant community productivity and diversity. *Oecologia* 159: 191–205. doi: 10.1007/s00442-008-1192-x
- Stein C, Unsicker S, Kahmen A, Wagner M, Audorff V, Auge H, Prati D, Weisser WW (2010) Impact of invertebrate herbivory in grasslands depends on plant species diversity. *Ecology* 91: 1639–1650. doi: 10.1890/09-0600.1
- Stinson KA, Campbell SA, Powell JR, Wolfe BE, Callaway RM, Thelen GC, Hallett SG, Prati D, Klironomos JN (2006) Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *PLoS Biology* 4: 727–731. doi: 10.1371/journal.pbio.0040140
- Thompson JN (1994) *The coevolutionary process*. University of Chicago Press, Chicago, 376 pp.
- Thorpe AS, Aschehoug ET, Atwater DZ, Callaway RM (2011) Interactions among plants and evolution. *Journal of Ecology* 99: 729–740. doi: 10.1111/j.1365-2745.2011.01802.x
- Williamson M (2010) Variation in the rate and pattern of spread in introduced species and its implications. In: Perrings C, Mooney H, Williamson M (Eds) *Bioinvasions & globalization: ecology, economics, management, and policy*. Oxford University Press, Oxford, 54–63.
- Williamson M (2011) Alien plants in Britain. In: Pimentel D ed, *Biological invasions: economic and environmental costs of alien plant, animal, and microbe species*, 2nd edition. CRC Press, Boca Raton, FL, 107–128. doi: 10.1201/b10938-9
- Wilsey BJ, Teaschner TB, Daneshgar PP, Isbell FI, Polley HW (2009) Biodiversity maintenance mechanisms differ between native and novel exotic-dominated communities. *Ecology Letters* 12: 432–442. doi: 10.1111/j.1461-0248.2009.01298.x

Beyond EICA: understanding post-establishment evolution requires a broader evaluation of potential selection pressures

Joshua P. Atwood, Laura A. Meyerson

Department of Natural Resources Science, University of Rhode Island, 1 Greenhouse Rd, Kingston, RI, 02881

Corresponding author: *Joshua P. Atwood* (josh.atwood@gmail.com)

Academic editor: *Ingolf Kühn* | Received 25 January 2011 | Accepted 12 April 2011 | Published 5 October 2011

Citation: Atwood JP, Meyerson LA (2011) Beyond EICA: understanding post-establishment evolution requires a broader evaluation of potential selection pressures. *NeoBiota* 10: 7–25. doi: 10.3897/neobiota.10.954

Abstract

Research on post-establishment evolution in nonnative plant populations has focused almost exclusively on testing the Evolution of Increased Competitive Ability (EICA) hypothesis, which posits that the lack of specialized herbivores in the invaded range drives evolution in nonnative plant populations. Fifteen years of conflicting EICA test results suggest that selection pressures other than specialized herbivory are important in driving post-establishment evolution in invasive species. Alternative hypotheses, such as the Evolution of Reduced Competitive Ability (ERCA) hypothesis, have been proposed but have received little attention or testing. We argue that the lack of consensus across studies that test EICA may be due in part to the lack of consistent definitions and varying experimental design parameters, and that future research in this field would benefit from new methodological considerations. We examined previous work evaluating post-establishment evolution and evaluated the range of study systems and design parameters used in testing the EICA hypothesis. Our goal was to identify where different uses of ecological terms and different study parameters have hindered consensus and to suggest a path forward to move beyond EICA in post-establishment evolution studies. We incorporated these methods into a design framework that will increase data harmony across future studies and will facilitate examinations of any potential selection pressure driving evolution in the invaded range.

Keywords

EICA, ERCA, invasion ecology, invasive plants, natural selection

Introduction

It has been commonly observed that life-history traits of nonnative plant species vary across habitats in native and introduced ranges, most conspicuously as either increased growth (Crawley 1987; Thebaud and Simberloff 2001) or decreased growth (Crawley 1987; Siemann and Rogers 2003a; Bossdorf et al. 2004). While trait variations across habitats may in some cases be plastic (i.e., non-genetic) responses to local environmental conditions (e.g., Fowler et al. 1996; Willis et al. 2000; Keane and Crawley 2002), a growing number of studies have examined this variation from an evolutionary perspective: the characteristics of the invaded habitat amount to a suite of novel selection pressures that drive post-establishment evolution in invading populations (e.g., Blossey and Nötzold 1995; Cody and Overton 1996; Table 1). To date research regarding post-establishment evolution has been heavily focused on testing the Evolution of Increased Competitive Ability (EICA) hypothesis. This hypothesis posits that nonnative plant populations may evolve a modified energetic tradeoff in which vegetative growth is increased while herbivore defense is decreased due to the lack of specialized herbivores in the invaded range. The potential for increased reproductive effort was also discussed, though not tested (Blossey and Nötzold 1995). Increases in vegetative growth were interpreted broadly by Blossey and Nötzold (1995) as “increased competitive ability.”

Because research regarding post-establishment evolution has been so tightly focused on testing the EICA hypothesis, much of the literature in this field evaluates a single reduced selection pressure: the lack of specialized herbivores in the invaded range. However, the inconclusive support found for the EICA hypothesis suggests that factors other than herbivore release may drive post-establishment evolution in some systems (Bossdorf et al. 2005; Fornoni 2010). To this end, researchers have called for an expanded consideration of habitat characteristics that may act as selection pressures in the invaded range (Callaway and Maron 2006; Whitney and Gabler 2008). As this field expands, however, the approaches to testing hypotheses focused on post-establishment evolution merit careful consideration so that results across studies can be more easily used to form generalized conclusions. In addition, transitioning the focus from “competitive ability” (which is not well defined in this context) would enhance future research by more broadly focusing on evolved trait modifications that impact survival and fecundity.

There have been a handful of studies evaluating selection pressures other than specialized herbivory, although they have not received the attention and scrutiny given to the EICA hypothesis. Maron et al. (2004), for example, demonstrated morphological adaptations associated with latitude in nonnative populations of *Hypericum perforatum*, and Van Grunsven et al. (2009) found that a lack of soil pathogens resulted in increased growth for nonnative populations of *Carpobrotus edulis*. More broadly, Bossdorf et al. (2004) proposed the Evolution of Reduced Competitive Ability (ERCA) hypothesis, which posits that post-establishment evolution can be driven by the amount of plant competition found in the invaded habitat. Specifically, plant populations invading areas with fewer competitors should evolve an energetic tradeoff in which vegetative growth is decreased while other traits such as reproductive effort or herbivore defense

Table 1. Published hypotheses related to post-establishment evolution.

Reference	Description
Blossey and Nötzold 1995	<i>Evolution of Increased Competitive Ability (EICA)</i> : Evolved increase in growth, decrease in defense associated with lack of herbivores in invaded range.
Sexton et al. 2002	Invading populations benefit first from plasticity, then from local adaptation
Maron et al. 2004	Latitudinal clines drive local adaptations in nonnative populations.
Bosssdorf et al. 2004	<i>Evolution of Reduced Competitive Ability (ERCA)</i> : Low amounts of plant competition result in an evolved decrease in growth, increase in reproduction, and defense.
Roman 2006	Multiple introductions and hybridization increase invasion success through increased genetic variability.
Blumenthal 2006	<i>Resource-Enemy Release Hypothesis (R-ERH)</i> : Resource availability effects how enemy release drives plastic and genetic trait variation.
Van Grunsven et al. 2009	The absence of soil pathogens results in an evolved increase in growth.

are increased (Bosssdorf et al. 2004). One potential implication of this hypothesis is that intraspecific competitive interactions may be reduced in monotypic or near-monotypic stands, increasing stand-level fitness while decreasing individual growth. A test of this hypothesis in any organism or geographic system has not yet been published.

Expanding our knowledge of post-establishment evolution beyond evaluations of the EICA hypothesis would address the omission of evolutionary potential from invasive species weed risk assessments, which attempt to predict the impact of an invading species on a given habitat based on the combination of species traits and habitat characteristics (Whitney and Gabler 2008). A better understanding of how the traits of invading species may rapidly change over time via natural selection would facilitate predictions regarding the immediate and long-term impacts of a given invasion (Daehler et al. 2004; Whitney and Gabler 2008). Such an understanding requires evaluations of not only those selection pressures posited by EICA or ERCA, but any number of habitat characteristics that vary across the native and invaded ranges of a given species.

We examined previous work regarding post-establishment evolution in order to better understand why outcomes across studies have been inconsistent. Because this literature has focused primarily on testing the EICA hypothesis, we focused our analysis within the field of evolution and invasive species by specifically examining tests of the EICA. Unlike previous reviews, we specifically evaluated study systems and methodologies in order to identify design parameters that will allow better synthesis across research on post-establishment evolution. We also focused on the use of the term “competitive ability” and how its definition varied based on the context of experimental designs. We searched for relevant literature published since the introduction of EICA that explicitly tested the predictions of the EICA hypothesis in a common garden or reciprocal transplant design, resulting in 58 studies. We focused on common garden and reciprocal transplant designs because of their frequent use and their ability to minimize the effects of phenotypic plasticity in the examination of evolved trait differentiation. We reviewed each study and

recorded information regarding study systems and design parameters, including whether abiotic and biotic variables were reported for seed collection sites, the inclusion of introduction history, sample size, the traits measured and metrics used, and the incorporation (or lack thereof) of competition in experimental manipulations. We also noted whether each study ultimately found support for the predictions of the EICA hypothesis (Table 2).

Based on our results, we developed a framework that can be used to move beyond EICA to evaluate a broad range of habitat characteristics that can act as selection pressures driving post-establishment evolution. Our intent is to facilitate future research that expands the consideration of potential selection pressures and encourages integration of results across study species and organisms.

Methodological variability in evaluating selection pressures: lessons from tests of the EICA hypothesis

The variation in sample sizes of both native and nonnative populations used in common garden research is one of the most readily apparent differences among studies of post-establishment evolution (Table 2). The logistical difficulties of obtaining individuals from both the introduced and invaded ranges likely contribute to the small number of populations used to represent each range in most studies. Though a handful of studies used ten or more populations in each range (e.g., Blossey 1996; Blair and Wolfe 2004; Güsewell et al. 2006), most tests of the EICA hypothesis have used a small number of populations (e.g., <10) and 13 of the 58 studies we reviewed used just one population to represent a native or invaded range (e.g., Blossey and Nötzold 1995; Lankau et al. 2004; Rogers and Siemann 2005; Franks et al. 2008).

Most of the studies we examined measured only one trait despite the fact that hypotheses focused on post-establishment evolution generally discuss multiple traits related to one another through energetic tradeoffs. The EICA hypothesis makes two predictions that were explicitly tested by Blossey and Nötzold (1995): that nonnative populations will demonstrate increased growth and will also demonstrate decreased herbivore defense. Of the 58 studies we reviewed, only 15 examined differences in both growth and defense in the same species. Of these, only eight found support for both predictions of the EICA hypothesis (Table 2). Twelve of the 58 studies identified reproductive effort as a third energetic “sink” in evolved tradeoffs, though only three studies quantified all three of these traits in the same species (Fig. 1, Table 2).

Common garden designs also varied by study, either as outdoor gardens or greenhouse benches. Those studies that used outdoor gardens diverged further in whether plants were grown in pots (e.g., Willis and Blossey 1999) or were planted directly into the ground (e.g., Siemann and Rogers 2001). Each approach has its advantages and disadvantages: while greenhouse studies allow researchers to better control environmental variables such as temperature or photoperiod, some researchers have argued that growth under these conditions may be too artificial for evaluating growth in wild populations (Gibson et al. 1999).

Table 2. Design parameters of studies testing the EICA hypothesis. In the column labeled “Abiotic data,” “1” indicates that researchers tried to incorporate a variety of abiotic environments in seed collection sites while “2” indicates that researchers tried to utilize similar environments. In the column “Traits,” “G” = vegetative growth, “T” = herbivore tolerance, and “R” = reproductive effort. The column labeled “Comp.” indicates whether or not competition was incorporated into experimental manipulations. For “Metrics,” growth metrics are denoted by “B” = biomass, “H” = height, “NL” = number of leaves, “LA” = leaf area, “BA” = basal area; tolerance metrics are denoted by “HM” = herbivore mass, “HA” = herbivore abundance, “LD” = leaf damage, “DC” = defense chemicals, “TD” = trichome density; reproductive metrics are denoted by “RM” = reproductive mass, “ReMR” = reproductive mass ratio, and “NF” = number of fruits. In the column “Sample Size,” the values correspond to the number of native and nonnative populations used, respectively, unless the sample size was not differentiated by range. The column “EICA” indicates whether support was found, with “Partial” indicating that multiple traits were tested but not all results supported predictions, and “1” indicating that support was found, but only when plants were grown in the absence of competition.

Article	Abiotic data	Intro. Hist	Traits	Comp.	Metrics	Sample size	EICA
Abhilasha and Joshi 2009	No	Yes	G T R	No	B, HA, RM	8&22	Yes
Bastlová and Kvet 2002	Yes	No	G	No	B, ReMR	3&3	Yes
Blair and Wolfe 2004	No ¹	No	G T R	Yes	NL, TD, RM	20&20	Yes
Blossey 1996	No	Yes	G T	No	B, HA	13&23	Yes
Blossey and Nötzold 1995	No	Yes	G T	No	B, H, HM	1&1	Yes
Blumenthal and Hufbauer 2007	No ²	No	G	Yes	B	2&2	Yes ¹
Bossdorf et al. 2004	Yes ²	Yes	G R	Yes	H, B, RM	8&8	No
Bossdorf et al. 2008	Yes	Yes	G R	No	B, NF	11&12	No
Brown and Eckert 2005	No	Yes	R	No	RM	6&5	Yes
Buschmann et al. 2005	Yes ²	Yes	G T R	No	B, NL, NF	1&1	Partial
Cano et al. 2008	Yes ¹	Yes	G	No	LA	4&4	Yes
Cano et al. 2009	No	Yes	G T	No	B, LA	3&3	No
Cipollini et al. 2005	No	Yes	T	No	DC	4&7	No
Cripps et al. 2009	Yes ¹	Yes	G	No	B, HA	6&10	No
Daehler and Strong 1997	No	Yes	R	No	RM	4&1	Yes
DeWalt et al. 2004	Yes	Yes	G	No	B	4&4	No
Eigenbrode et al. 2008	No	Yes	T	No	DC	4&3	No
Erfmeier and Breulheide 2005	Yes ²	Yes	G	No	H	6&6	Yes
Franks et al. 2008	No	Yes	G T	No	B, HA	1&1	No
Genton et al. 2005	No	Yes	G T	No	B, LD	2&1	No
Güeswell et al. 2006	No	No	G	No	B, NL	20&22	Yes
Handley et al. 2008	No	Yes	T	No	LD	8&16	No
He et al. 2009	No	No	G	Yes	B	8&9	No
Henery et al. 2010	No	Yes	G	No	B	45	No
Herrera et al. 2011	No	Yes	T	No	HM	3&3	No
Huang et al. 2010	No	Yes	T	No	HM	6&6	Yes
Hull-Sanders et al. 2007	No	Yes	T	No	HM, DC	10&20	No
Johnson et al. 2007	No	Yes	T	No	DC	10&22	Yes
Joshi and Vrieling 2005	No	Yes	T	No	DC, HM	13&16	Partial
Lambert and Casagrande 2007	No	No	T	No	HA	6&4	No

Article	Abiotic data	Intro. Hist	Traits	Comp.	Metrics	Sample size	EICA
Lankau et al. 2004	No	Yes	G T	No	B, LD	1&1	No
Leger and Forister 2005	No ¹	Yes	T	No	HM	7&4	No
Leger and Rice 2003	Yes ²	Yes	G	Yes	B	10&10	Yes ¹
Lym and Carlson 2002	No	No	R	No	HA	1&6	No
Maron et al. 2004	No	Yes	G R	No	B, NF	18&32	No
McKenney et al. 2007	Yes	Yes	G	Yes	B	10&10	No
Meyer and Hull-Sanders 2008	No	Yes	G R	No	H, LA, ReMR	10&20	No
Meyer et al. 2005	No ¹	Yes	G T	No	H, HM	10&20	Partial
Müller and Martens 2005	Yes	Yes	G T	No	B, DC	11&10	No
Ridenour et al. 2008	No	No	G R	Yes	B, NF	22&23	Partial
Rogers and Siemann 2004	No	No	G	Yes	B	1&1	Yes
Rogers and Siemann 2005	No	Yes	T	No	HM	1&1	Yes
Rogers et al. 2003	No	No	T	No	NL	1&1	No
Siemann and Rogers 2001	No ¹	Yes	G T	No	BA, DC	1&1	Yes
Siemann and Rogers 2003a	No	Yes	G T	No	BA, LD, DC	1&1	Yes
Siemann and Rogers 2003b	No	Yes	G T	No	H, LD, HM	1&1	Yes
Stastny et al. 2005	Yes	No	G T	No	LA, DC	4&4	Partial
van Kleunen and Fischer 2008	Yes ²	Yes	G R	No	# Branches, Flowers	17&7	Yes
van Kleunen and Schmid 2003	No	Yes	T	No	H	9&10	No
Vilà and Gimeno 2005	Yes	Yes	R	No	NF	30&20	Yes
Vilà et al. 2003	No ¹	Yes	G	Yes	B	10&20	No
Widmer et al. 2007	No	Yes	G	No	H	7&8	Yes
Williams et al. 2008	Yes	Yes	G	No	Plant volume	10&10	No
Willis et al. 1999	No	No	G	No	B, H	10&10	Yes
Willis et al. 2000	No ¹	No	G	No	B	3&3	No
Zou et al. 2007	No	No	G	No	B, H	4&4	Yes
Zou, Rogers, and Siemann 2008	No	Yes	T	No	B, LD	9&9	Yes
Zou et al. 2008	No	Yes	G T	Yes	B, LD	2&2	Yes

The term “competitive ability” had multiple interpretations across the studies that we reviewed. In studies where individuals are grown alone (e.g., Blossey and Nötzold 1995; Maron et al. 2004), “competitive ability” appeared to be interpreted as the ability of an individual to secure resources for itself regardless of the presence of neighbors. Alternatively, studies in which individuals are grown alongside competitors (e.g., Leger and Rice 2003; Vilà et al. 2003; Bossdorf et al. 2004) appeared to interpret “competitive ability” as the ability of an individual to preempt resources for itself specifically in the presence of neighbors. The distinction is an important one: Blumenthal and Hufbauer (2007) found that biomass was higher in nonnative populations than native populations when grown in a common garden, but only when individuals were grown alone. When exposed to actual competition, there was no difference in biomass between nonnative and native populations. Of the 58 studies we examined, only

ten exposed individuals to actual competition by growing study individuals alongside competing neighbors. Of these, only one found support for both predictions of the EICA hypothesis (Fig. 1, Table 2).

These different definitions of competitive ability have also muddled our understanding of the energetic tradeoffs being examined in these studies. The focus on testing EICA has resulted in the general adoption of the term “competitive ability” as synonymous with “vegetative growth,” as it was interpreted by Blossey and Nötzold (1995). This is an oversimplification since EICA links multiple traits that are influenced by competition through energetic tradeoffs, including growth, defense, and, in more recent work, reproduction (Herms and Mattson 1992; Bazzaz and Grace 1997; Table 2). It is possible that, as predicted by the ERCA hypothesis, non-native plant populations could produce decreased total biomass but increased fruit mass, resulting in increased fecundity in future generations (Bossdorf et al. 2004). This would be considered reduced competitive ability despite the increased success of the nonnative plant population.

The use of different metrics for quantifying plant traits presents further challenges for data comparison across studies. While Blossey and Nötzold (1995) utilized biomass and height as growth metrics, subsequent tests of EICA have used a wide variety of alternative metrics including plant volume (e.g., Maron et al. 2004), basal area (e.g., Siemann and Rogers 2003a), leaf area (e.g., Blair and Wolfe 2004), number of branches (e.g., van Kleunen and Fischer 2008), and leaf length (e.g., Stastny et al. 2005) (Table 2, 3). Similarly, the measurement of plant responses to herbivory has varied among studies and includes herbivore larval mass (e.g., Blossey and Nötzold 1995; Willis et al. 1999; Joshi and Vrieling 2005; Hull-Sanders et al. 2007), leaf damage (e.g., Buschmann et al. 2005; Genton et al. 2005), the number of herbivores present (e.g., Meyer et al. 2005; Franks et al. 2008), or concentrations of chemical defense compounds such as alkaloids, terpenes, and phenolics (e.g., Willis et al. 1999; Siemann and Rogers 2003a; Cipollini et al. 2005; Joshi and Vrieling 2005; Johnson et al. 2007) (Table 2, 3).

In evaluating specialized herbivory as a selection pressure, studies of post-establishment evolution have generally neglected other habitat characteristics that can act as confounding variables across seed collection sites. Because comparisons of native and nonnative populations often use seeds collected on different continents, abiotic characteristics such as photoperiod or climate may vary significantly across the study area. For example, of the 58 studies we reviewed, only 15 identified differences in abiotic conditions (e.g., climate and/or photoperiod) between the native and invaded ranges. None of the studies we reviewed recorded information regarding the biotic characteristics of the collection site (e.g., plant community composition) other than differences in herbivore assemblages (Fig. 1, Table 2). This is particularly significant in light of a study by Williams et al. (2008), which found that the results of common garden experiments change depending on the geographic location and habitat characteristics of the common garden.

Furthermore, the 15 studies that did report abiotic characteristics often disagreed as to whether consistency in abiotic factors across the sampling range was a desired

Table 3. The metrics used to quantify growth, herbivore tolerance and reproduction in studies examining post-establishment evolution. Data are aggregated from our review of design parameters detailed in Table 2.

Trait	Metric
Growth	Total biomass
	Aboveground biomass
	Belowground biomass
	Height
	Plant volume
	Basal area
	Leaf area
Reproduction	Number of flowers
	Fruit mass
Herbivore Tolerance	Herbivore mass
	Number of herbivores
	Defense chemical concentration
	Leaf damage

component of the experimental design, despite having similar aims in evaluating evolution in nonnative populations. Several studies noted that seeds utilized in a common garden were intentionally collected from a wide variety of habitat types in order to incorporate environmental heterogeneity across the distribution of the species (e.g., Siemann and Rogers 2001; Vilà et al. 2003; Cano et al. 2008; Cripps et al. 2009). Cripps et al. (2009), for example, chose populations “covering a wide geographic range to obtain representative samples” across the distribution of *Lepidium draba*. Conversely, other studies noted that seeds for common gardens were collected from very similar habitats in order to minimize the potential for confounding habitat variables (e.g., Leger and Rice 2003; Buschmann et al. 2005; Blumenthal and Hufbauer 2007). Erfmeier and Bruelheide (2005), collected seeds only from populations of *Rhododendron ponticum* growing on north-facing, forested slopes with an aspect of 10–20°. This variation in experimental design demonstrates a fundamental difference in how researchers assess the potential for confounding variables and leads to varying degrees of robustness across studies.

Introduction history and subsequent spread of an invader are potentially influential factors often missing in reports of post-establishment evolution. This history is fundamental to understanding the selection pressures to which a species has been exposed. For example, Maron et al. (2004) used genetic analyses to determine that multiple introductions of *Hypericum perforatum* had occurred in the US, thereby influencing the amount of genetic variability in nonnative populations. However, detailed introduction histories are often unavailable and genetic analyses can be time- and cost-intensive, likely contributing to the omission of such information from many studies. Of the 58 studies we examined, 44 studies reported some data regarding introduction history, though often this information was limited to the date of first introduction to a country or continent and as such does not provide a detailed description. The remain-

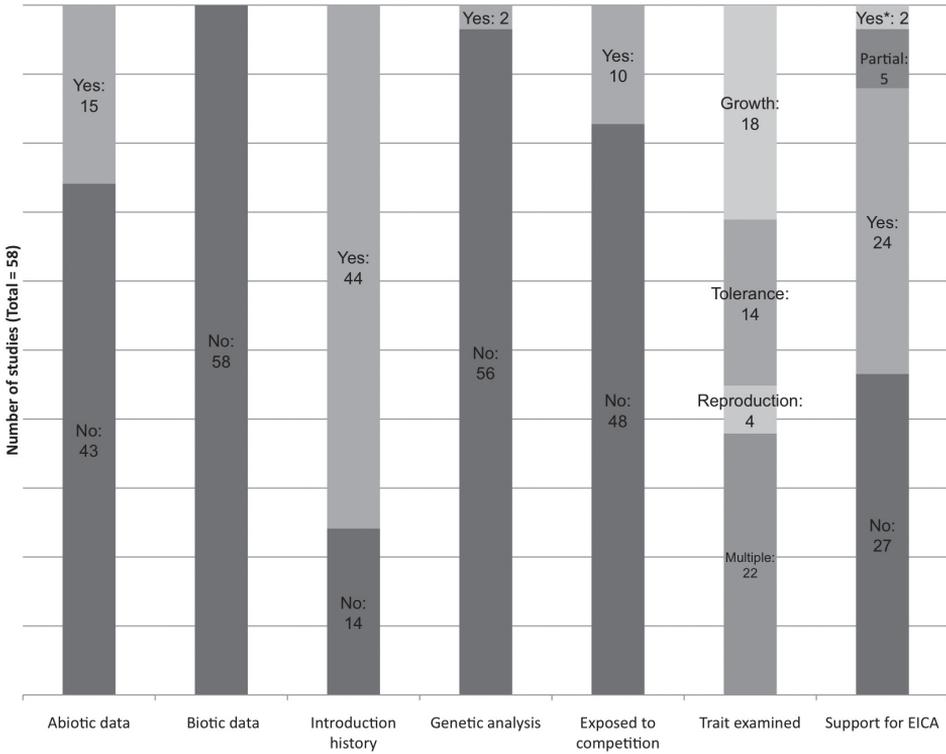


Figure 1. Frequencies of methodologies used in EICA studies. Data are aggregated from our review of design parameters detailed in Table 2. “*” Indicates that support for the EICA hypothesis was found only when plants were grown in the absence of competition.

ing 14 studies made no mention of introduction history. Only two studies conducted genetic analyses to assess variability among populations (Fig. 1, Table 2).

The broad range of approaches used in testing EICA may be one factor that limits consensus among the collective results. Twenty-four of the 58 studies we examined found support for the predictions of the EICA hypothesis, while 27 did not. Five studies found partial support, and two found support only when individuals were not exposed to competition (Fig. 1, Table 2). While EICA is likely an accurate predictor of evolutionary changes in some (but not all) of the species on which it has been tested, the fundamental differences in experimental designs and the use of loosely defined terms such as “competitive ability” in these studies may have hindered a more complete understanding of the applicability of the EICA hypothesis and of post-establishment evolution in general. While it is possible that meta-analyses could be used to make generalizations across methodologies (e.g., Colautti et al. 2009), the ecological relevance of results might be easier to interpret if some fundamental design parameters, such as the incorporation of competition into experimental manipulations, were similar across studies.

Post-establishment evolution is an area of research that has attracted substantial attention since the introduction of the EICA hypothesis, but the tests to date have not

yet provided a meaningful consensus. One approach to facilitate progress in this field is to move towards standard definitions and comparable approaches that will more specifically evaluate potential selection pressures beyond the predictions of the EICA hypothesis.

Moving forward: A framework for designing evaluations of selection pressures in post-establishment evolution

Based on our analysis, we developed a framework for future research on selection pressures potentially driving evolution. We focused our recommendations on experimental designs that reduce the potential for confounding factors and increase the ability to integrate results among studies (Table 4).

1. Consider abiotic and biotic conditions across ranges

Studies that examine a potential selection pressure should account for other habitat characteristics that may confound results. Ideally, the study system used for testing a post-establishment evolution hypothesis would use two ranges that are as similar as possible for all factors *except* for the characteristic being evaluated as a potential selection pressure. In particular, researchers can use seed collection sites at similar latitudes to partially control for photoperiod and climate (e.g., Blumenthal and Hufbauer 2007). Whether a study incorporates seed collections from separate continents or uses a smaller study area within a continent, a description of the environmental characteristics across the study system, including plant community composition, would inform comparisons across studies (e.g., Ebeling et al. 2008).

2. Choose study species with appropriate life-history strategies

Study species selected to test post-establishment evolution hypotheses are ideally those that have a high potential for rapid evolution. Species that reproduce primarily by seed rather than clonal growth will have a higher frequency of genetic recombination, as will species with relatively short generation times such as herbaceous perennials. As such, *r*-selected species may be good candidates for studying post-establishment evolution, though we do not suggest that the role of *K*-selected species should be ignored. In testing hypotheses related to herbivore damage, it is appropriate to consider the relative effects of specialist and generalist herbivores on a given study species (e.g., Huang et al. 2010). The ability of a species to self-fertilize may also affect the likelihood of adaptive evolution. Species that cannot self-fertilize will have higher outcrossing rates and accumulate beneficial adaptations more rapidly than self-fertilized species. However,

Table 4. A framework for testing post-establishment evolution hypotheses.

1.	Evaluate the variability in abiotic and biotic conditions across ranges
2.	Choose study species with appropriate life-history traits
3.	Include introduction history
4.	Incorporate competition in manipulations
5.	Measure multiple traits and avoid the term “competitive ability”
6.	Use standard metrics where possible

species that self-fertilize may exhibit stronger founder effects that could accelerate divergence from ancestral populations. Byers and Waller (1999) conducted an in-depth review of the evolutionary advantages and disadvantages of inbreeding, showing that while inbreeding populations tend to rapidly accumulate mutations, inbreeding may increase the likelihood of purging disadvantageous alleles from a population. Species that are known to hybridize with congeners may not be well suited for evolutionary studies, since the introduction of genetic material from other species may introduce novel traits that could mask the influence of selection (Roman 2006).

3. Consider introduction history

Documenting the introduction and historic spread of a given species can reveal the types and durations of selection pressures that the species has undergone. The possibility of multiple introductions should also be considered since repeated introductions can increase genetic variation and/or result in novel genetic admixtures not found in the native range (Maron et al. 2004). Where detailed records of species introduction are unavailable, genetic analyses can potentially determine relatedness of introduced populations. Hufbauer and Sforza (2008), for example, used chloroplast DNA to infer the history of introduction from Eurasia to North America for two species of *Centaurea*.

4. Incorporate competition in manipulations

Because individuals in nature rarely grow in isolation, tests in which individuals are exposed to actual competition are likely to be more ecologically relevant. Incorporation of multiple competitive scenarios in common garden experiments will enhance our understanding of traits that are affected by competition. For example, growing individuals along a gradient of competitive stress (measured as the number of individuals per pot) would provide more information on the ability of a given species to obtain and utilize resources. The ratio of the number of individuals in a pot to soil volume can also be kept constant to avoid confounding competition with density (Gurevitch et al. 1990).

5. Measure multiple traits and avoid the term “competitive ability”

Previous studies related to post-establishment evolution have used the term “competitive ability” as synonymous with vegetative growth, despite discussing growth in the context of energetic tradeoffs with other traits that may be affected by resource competition, including reproductive effort and herbivore tolerance (Blossey and Nötzold 1995; Bossdorf et al. 2004). A strict definition of “competitive ability” is lacking. Grime defined “competition” as the tendency of neighboring plants to use the same resources (Grime 1973), and thus “competitive ability” should be the ability to secure those resources. These resources may then be utilized for a variety of traits related to survival and fecundity, including (but not limited to) growth, reproduction, and herbivore tolerance, but the use of any one of these traits as being synonymous with “competitive ability” would be misleading. Future research could quantify variation in a broader suite of traits and refer more generally to survival and fecundity rather than using the loosely defined term “competitive ability.”

6. Use standard metrics where possible.

The variety of metrics used to measure growth, reproduction, and herbivore defense has made it difficult to integrate data across studies. Utilizing standard metrics or converting units to those of standard metrics could facilitate such comparisons. Vilà and Gimeno (2006), for example, used the number of stems of *Oxalis pes-caprae* as a growth metric, but converted their data to units of biomass using an allometric equation. Total biomass is non-dimensional and removes bias for vertical rather than lateral growth.

In studies measuring reproductive effort, a metric that demonstrates the energetic investment in reproductive biomass relative to total biomass is useful in accounting for the role of plant size in determining the amount of fruit produced. The reproductive mass ratio ($\text{ReMR} = [\text{fruit mass}] / [\text{total biomass}]^{-1}$) has been used to describe the production of reproductive structures relative to total biomass production (Abrahamson and Gadgil 1973; Bastlová and Kvet 2002; DeWalt et al. 2004).

Compensatory growth response is a good candidate as a standard measure for quantifying the effect of herbivory. While many studies have used quantified defense chemical concentrations, not all plant species utilize the same chemical pathways. As a metric of response to herbivory, compensatory growth is relevant across all species that utilize different chemical pathways and therefore facilitates comparisons across studies. Agrawal et al. (2005) used plant biomass to measure the response to herbivory for native and introduced species of Brassicaceae and found that exposure to herbivory resulted in a significant decrease in biomass production for native plants and no difference in biomass production in introduced plants.

Conclusion

Research on post-establishment evolution offers the potential for a better understanding of how nonnative plant populations interact with and adapt to their host environments. These data are relevant not only to invasion ecology, but also to studies of successional ecology and range expansions, as these fields also deal with new species interactions and novel habitat conditions (Davis et al. 2001; Simmons and Thomas 2004; Mitchell et al. 2006). The focus of previous work in this field on testing the EICA hypothesis has demonstrated that while EICA may describe evolution in some study systems, it does not fully explain the evolutionary response of nonnative plant populations to their invaded habitats. A broader examination of potential selection pressures is required to more fully understand post-establishment evolution. Careful consideration of experimental design parameters should be given to future research in this field. The lessons learned from tests of the EICA hypothesis can be used to guide future research that tests the EICA or ERCA hypotheses, or any other selection pressure that may drive post-establishment evolution.

Understanding how nonnative populations change over time is fundamental to their effective management, particularly with respect to weed risk assessments that attempt to predict the ways in which a given species might interact with a given habitat. Data on the evolutionary response of invading plant species can be used to incorporate evolutionary potential into such predictions, filling a knowledge gap that will allow researchers to predict not only the immediate impact of species invasions, but also how rapid evolutionary changes might over time alter the type or magnitude of those impacts (Whitney and Gabler 2008). Future studies that evaluate additional selection pressures will increase our understanding of how habitat characteristics drive adaptations. This information could be used to create regionally specific weed risk assessments that would prioritize management efforts and more effectively respond to current and potential threats (Daehler et al. 2004; Whitney and Gabler 2008). This enhanced understanding of how certain habitat characteristics drive rapid evolution will become increasingly relevant as trade, development, and global change alter habitat characteristics around the world.

Acknowledgements

We thank Elizabeth Farnsworth, Kimberly Lellis-Dibble, and two anonymous reviewers for comments and suggestions on early drafts of this manuscript.

References

Abhilasha D, Joshi J (2009) Enhanced fitness due to higher fecundity, increased defence against a specialist and tolerance towards a generalist herbivore in an invasive annual plant. *Journal of Plant Ecology* 2: 77–86. doi: 10.1093/jpe/rtp008

- Abrahamson WG, Gadgil M (1973) Growth form and reproductive effort in goldenrods (*Solidago*, Compositae). *The American Naturalist* 107: 651–661. doi: 10.1086/282864
- Agrawal AA, Kotanen PM, Mitchell CE, Power AG, Godsoe W, Klironomos JN (2005) Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. *Ecology* 86: 2979–2989. doi: 10.1890/05-0219
- Bastlová D, Kvet J (2002) Differences in dry weight partitioning and flowering phenology between native and non-native plants of purple loosestrife (*Lythrum salicaria* L.). *Flora* 197: 332–340. doi: 10.1078/0367-2530-00049
- Bazzaz FA, Grace J (1997) *Plant Resource Allocation*. Academic Press, London.
- Blair AC, Wolfe LM (2004) The Evolution Of an Invasive Plant: An Experimental Study with *Silene latifolia*. *Ecology* 85: 3035–3042. doi: 10.1890/04-0341
- Blossey B (1996) The search for patterns or what determines the increased competitive ability of invasive non-indigenous plants? Symposium proceedings, California Exotic Pest Plant Council, 1–7.
- Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology* 83: 887–889. doi: 10.2307/2261425
- Blumenthal DM, Huffbauer RA (2007) Increased plant size in exotic populations: a common garden test with 14 invasive species. *Ecology* 88: 2758–2765. doi: 10.1890/06-2115.1
- Bossdorf O, Auge H, Lafuma L, Rogers WE, Siemann E, Prati D (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* 144: 1–11. doi: 10.1007/s00442-005-0070-z
- Bossdorf O, Lipowsky A, Prati D (2008) Selection of preadapted populations allowed *Senecio inaequidens* to invade Central Europe. *Diversity and Distributions* 14:676–685. doi: 10.1111/j.1472-4642.2008.00471.x
- Bossdorf O, Prati D, Auge H, Schmid B (2004) Reduced competitive ability in an invasive plant. *Ecology Letters* 7: 346–353. doi: 10.1111/j.1461-0248.2004.00583.x
- Brown JS, Eckert CG (2005) Evolutionary increase in sexual and clonal reproductive capacity during biological invasion in an aquatic plant *Butomus umbellatus* (Butomaceae). *American Journal of Botany* 92: 495–502. doi: 10.3732/ajb.92.3.495
- Buschmann H, Edwards PJ, Dietz H (2005) Variation in growth pattern and response to slug damage among native and invasive provenances of four perennial Brassicaceae species. *Journal of Ecology* 93: 322–334. doi: 10.1111/j.1365-2745.2005.00991.x
- Byers DL, Waller DM (1999) Do plant populations purge their genetic load? Effects of population size and mating history on inbreeding depression. *Annual Review of Ecology and Systematics* 30: 479–513. doi: 10.1146/annurev.ecolsys.30.1.479
- Callaway RM, Maron JL (2006) What have exotic plant invasions taught us over the past 20 years? *Trends in Ecology & Evolution* 21: 369–374. doi: 10.1016/j.tree.2006.04.008
- Cano L, Escarré J, Fleck I, Blanco-Moreno JM, Sans FX (2008) Increased fitness and plasticity of an invasive species in its introduced range: a study using *Senecio pterophorus*. *Journal of Ecology* 96: 468–476. doi: 10.1111/j.1365-2745.2008.01363.x
- Cano L, Escarré J, Vrieling K, Sans FX (2009) Palatability to a generalist herbivore, defence and growth of invasive and native *Senecio* species: testing the evolution of increased competitive ability hypothesis. *Oecologia* 159: 95–106. doi: 10.1007/s00442-008-1182-z

- Cipollini D, Mbagwu J, Barto K, Hillstrom C, Enright S (2005) Expression of constitutive and inducible chemical defenses in native and invasive populations of *Alliaria petiolata*. *Journal of Chemical Ecology* 31: 1255–1267. doi: 10.1007/s10886-005-5284-3
- Cody ML, Overton JMC (1996) Short-term evolution of reduced dispersal in island plant populations. *Journal of Ecology* 84: 53–61. doi: 10.2307/2261699
- Colautti RI, Maron JL, Barrett SCH (2009) Common garden comparisons of native and introduced plant populations: latitudinal clines can obscure evolutionary inferences. *Evolutionary Applications* 2: 187–199. doi: 10.1111/j.1752-4571.2008.00053.x
- Crawley MJ (1987) What makes a community invisable? In: Gray AJ, Crawley MJ, Edwards PJ (Eds) *Colonization, succession and stability*. Blackwell Scientific, Oxford, 429–453.
- Cripps MG, Hinz HL, McKenney JL, Price WJ, Schwarzländer M (2009) No evidence for an “evolution of increased competitive ability” for the invasive *Lepidium draba*. *Basic and Applied Ecology* 10: 103–112. doi: 10.1016/j.baae.2008.03.001
- Daehler CC, Denslow JS, Ansari S, Kuo HC (2004) A risk-assessment system for screening out invasive pest plants from Hawaii and other Pacific islands. *Conservation Biology* 18: 360–368. doi: 10.1111/j.1523-1739.2004.00066.x
- Daehler CC, Strong DR (1997) Reduced herbivore resistance in introduced smooth cordgrass (*Spartina alterniflora*) after a century of herbivore-free growth. *Oecologia* 110: 99–108. doi: 10.1007/s004420050138
- Davis MA, Thompson K, Grime JP (2001) Charles S. Elton and the dissociation of invasion ecology from the rest of ecology. *Diversity and Distributions* 7: 97–102. doi: 10.1046/j.1472-4642.2001.00099.x
- DeWalt SJ, Denslow JS, Hamrick JL (2004) Biomass allocation, growth, and photosynthesis of genotypes from native and introduced ranges of the tropical shrub *Clidemia hirta*. *Oecologia* 138: 521–531. doi: 10.1007/s00442-003-1462-6
- Ebeling SK, Hensen I, Auge H (2008) The invasive shrub *Buddleja davidii* performs better in its introduced range. *Diversity and Distributions* 14: 225–233. doi: 10.1111/j.1472-4642.2007.00422.x
- Erfmeier A, Bruelheide H (2005) Invasive and native *Rhododendron ponticum* populations: is there evidence for genotypic differences in germination and growth? *Ecography* 28: 417–428. doi: 10.1111/j.0906-7590.2005.03967.x
- Eigenbrode SD, Andreas JE, Cripps MG, Ding H, Biggam RC, Schwarlander M (2008) Induced chemical defenses in invasive plants: a case study with *Cynoglossum officinale* L. *Biological Invasions* 10: 1373–1379. doi: 10.1007/s10530-007-9212-z
- Fornoni J (2010) Ecological and evolutionary implications of plant tolerance to herbivory. *Functional Ecology* 25: 399–407. doi: 10.1111/j.1365-2435.2010.01805.x
- Fowler SV, Harman HM, Memmott J, Paynter Q, Shaw R, Sheppard AW, Syrett P (1996) Comparing the population dynamics of broom, *Cytisus scoparius*, as a native plant in the United Kingdom and France and as an invasive alien weed in Australia and New Zealand. In: Moran VC, Hoffman JH (Eds) *Proceedings of the IX International Symposium on Biological Control of Weeds*, University of Cape Town, Stellenbosch, South Africa, 19–26.

- Franks SJ, Pratt PD, Dray FA Jr, Simms EL (2008) Selection on herbivory resistance and competitive ability traits in an invasive plant. *The American Naturalist* 171: 678–691. doi: 10.1086/587078
- Genton BJ, Kotanen PM, Cheptou PO, Adolphe C, Shykoff JA (2005) Enemy release but no evolutionary loss of defence in a plant invasion: an inter-continental reciprocal transplant experiment. *Oecologia* 146: 404–414. doi: 10.1007/s00442-005-0234-x
- Gibson DJ, Connolly J, Hartnett DC, Weidenhamer JD (1999) Designs for greenhouse studies of interactions between plants. *Journal of Ecology* 87: 1–16. doi: 10.1046/j.1365-2745.1999.00321.x
- Grime JP (1973) Competition and diversity in herbaceous vegetation: a reply. *Nature* 244: 311. doi: 10.1038/244311a0
- Gurevitch J, Wilson P, Stone JL, Teese P, Stoutenburgh RJ (1990) Competition Among Old-Field Perennials at Different Levels of Soil Fertility and Available Space. *Journal of Ecology* 78: 727–744. doi: 10.2307/2260895
- Güsewell S, Jakobs G, Weber E (2006) Native and introduced populations of *Solidago gigantea* differ in shoot production but not in leaf traits or litter decomposition. *Functional Ecology* 20: 575–584. doi: 10.1111/j.1365-2435.2006.01141.x
- Handley RJ, Steinger T, Treier UA, Muller-Scharer H (2008) Testing the evolution of increased competitive ability hypothesis in a novel framework. *Ecology* 89: 407–417. doi: 10.1890/07-0160.1
- He WM, Feng Y, Ridenour WM, Thelen GC, Pollock JL, Diaconu A, Callaway RM (2009) Novel weapons and invasion: biogeographic differences in the competitive effects of *Centaurea maculosa* and its root exudate (\pm)-catechin. *Oecologia* 159: 803–815. doi: 10.1007/s00442-008-1234-4
- Henery ML, Bowman G, Mráz P, Treier UA, Gex Fabry E, Schaffner U, Müller-Schärer H (2010) Evidence for a combination of pre adapted traits and rapid adaptive change in the invasive plant *Centaurea stoebe*. *Journal of Ecology* 98: 800–813. doi: 10.1111/j.1365-2745.2010.01672.x
- Herms DA, Mattson WJ (1992) The dilemma of plants: to grow or defend. *The Quarterly Review of Biology* 67: 283. doi: 10.1086/417659
- Herrera AM, Carruthers RI, Mills NJ (2011) No evidence for increased performance of a specialist psyllid on invasive French broom. *Acta Oecologica*.
- Huang W, Siemann E, Wheeler GS, Zou J, Carrillo J, Ding J (2010) Resource allocation to defence and growth are driven by different responses to generalist and specialist herbivory in an invasive plant. *Journal of Ecology* 98: 1157–1167. doi: 10.1111/j.1365-2745.2010.01704.x
- Hufbauer RA, Sforza R (2008) Multiple introductions of two invasive *Centaurea* taxa inferred from cpDNA haplotypes. *Diversity and Distributions* 14: 252–261. doi: 10.1111/j.1472-4642.2007.00424.x
- Hull-Sanders HM, Clare R, Johnson RH, Meyer GA (2007) Evaluation of the evolution of increased competitive ability (EICA) hypothesis: loss of defense against generalist but not specialist herbivores. *Journal of Chemical Ecology* 33: 781–799. doi: 10.1007/s10886-007-9252-y

- Johnson RH, Hull-Sanders HM, Meyer GA (2007) Comparison of foliar terpenes between native and invasive *Solidago gigantea*. *Biochemical Systematics and Ecology* 35: 821–830. doi: 10.1016/j.bse.2007.06.005
- Joshi J, Vrieling K (2005) The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. *Ecology Letters* 8: 704–714. doi: 10.1111/j.1461-0248.2005.00769.x
- Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* 17: 164–170. doi: 10.1016/S0169-5347(02)02499-0
- Lambert AM, Casagrande RA (2007) Susceptibility of native and non-native common reed to the non-native mealy plum aphid (Homoptera: Aphididae) in North America. *Environmental Entomology* 36: 451–457. doi: 10.1603/0046-225X(2007)36[451:SONANC]2.0.CO;2
- Lankau RA, Rogers WE, Siemann E (2004) Constraints on the utilisation of the invasive Chinese tallow tree *Sapium sebiferum* by generalist native herbivores in coastal prairies. *Ecological Entomology* 29: 66–75. doi: 10.1111/j.0307-6946.2004.00575.x
- Leger EA, Forister ML (2005) Increased resistance to generalist herbivores in invasive populations of the California poppy (*Eschscholzia californica*). *Diversity and Distributions* 11: 311–317. doi: 10.1111/j.1366-9516.2005.00165.x
- Leger EA, Rice KJ (2003) Invasive California poppies (*Eschscholzia californica* Cham.) grow larger than native individuals under reduced competition. *Ecology Letters* 6: 257–264. doi: 10.1046/j.1461-0248.2003.00423.x
- Lym RG, Carlson RB (2002) Effect of leafy spurge (*Euphorbia esula*) genotype on feeding damage and reproduction of *Aphthona* spp.: implications for biological weed control. *Biological Control* 23: 127–133. doi: 10.1006/bcon.2001.0998
- Maron JL, Vilà M, Bommarco R, Elmendorf S, Beardsley P (2004) Rapid evolution of an invasive plant. *Ecological Monographs* 74: 261–280. doi: 10.1890/03-4027
- McKenney JL, Cripps MG, Price WJ, Hinz HL, Schwarzländer M (2007) No difference in competitive ability between invasive North American and native European *Lepidium draba* populations. *Plant Ecology* 193: 293–303. doi: 10.1007/s11258-007-9268-y
- Meyer G, Clare R, Weber E (2005) An experimental test of the evolution of increased competitive ability hypothesis in goldenrod, *Solidago gigantea*. *Oecologia* 144: 299–307. doi: 10.1007/s00442-005-0046-z
- Meyer GA, Hull-Sanders HM (2008) Altered patterns of growth, physiology and reproduction in invasive genotypes of *Solidago gigantea* (Asteraceae). *Biological Invasions* 10: 303–317. doi: 10.1007/s10530-007-9131-z
- Mitchell CE, Agrawal AA, Bever JD, Gilbert GS, Hufbauer RA, Klironomos JN, Maron JL, Morris WF, Parker IM, Power AG (2006) Biotic interactions and plant invasions. *Ecology Letters* 9: 726–740. doi: 10.1111/j.1461-0248.2006.00908.x
- Müller C, Martens N (2005) Testing predictions of the ‘evolution of increased competitive ability’ hypothesis for an invasive crucifer. *Evolutionary Ecology* 19: 533–550. doi: 10.1007/s10682-005-1022-0
- Ridenour WM, Vivanco JM, Feng Y, Horiuchi J, Callaway RM (2008) No evidence for trade-offs: *Centaurea* plants from America are better competitors and defenders. *Ecological Monographs* 78: 369–386. doi: 10.1890/06-1926.1

- Rogers WE, Siemann E (2004) Invasive ecotypes tolerate herbivory more effectively than native ecotypes of the Chinese tallow tree *Sapium sebiferum*. *Journal of Applied Ecology* 41: 561–570. doi: 10.1111/j.0021-8901.2004.00914.x
- Rogers WE, Siemann E (2005) Herbivory tolerance and compensatory differences in native and invasive ecotypes of Chinese tallow tree (*Sapium sebiferum*). *Plant Ecology* 181: 57–68. doi: 10.1007/s11258-005-3029-6
- Rogers WE, Siemann E, Lankau RA (2003) Damage Induced Production of Extrafloral Nectar-ies in Native and Invasive Seedlings of Chinese Tallow Tree (*Sapium sebiferum*). *The American Midland Naturalist* 149: 413–417. doi: 10.1674/0003-0031(2003)149[0413:DIPO EN]2.0.CO;2
- Roman J (2006) Diluting the founder effect: cryptic invasions expand a marine invader's range. *Proceedings of the Royal Society B: Biological Sciences* 273: 2453–2459. doi: 10.1098/rspb.2006.3597
- Siemann E, Rogers WE (2001) Genetic differences in growth of an invasive tree species. *Ecology Letters* 4:514–518. doi: 10.1046/j.1461-0248.2001.00274.x
- Siemann E, Rogers WE (2003a) Increased competitive ability of an invasive tree may be limited by an invasive beetle. *Ecological Applications* 13: 1503–1507. doi: 10.1890/03-5022
- Siemann E, Rogers WE (2003b) Reduced resistance of invasive varieties of the alien tree *Sapium sebiferum* to a generalist herbivore. *Oecologia* 135: 451–457. PMID:12721836
- Simmons AD, Thomas CD (2004) Changes in dispersal during species' range expansions. *The American Naturalist* 164: 378–395. doi: 10.1086/423430
- Stastny M, Schaffner U, Elle E (2005) Do vigour of introduced populations and escape from specialist herbivores contribute to invasiveness? *Journal of Ecology* 93: 27–37. doi: 10.1111/j.1365-2745.2004.00962.x
- Thebaud C, Simberloff D (2001) Are plants really larger in their introduced ranges? *The American Naturalist* 157: 231–236. doi: 10.1086/318635
- Van Grunsven RHA, Bos F, Ripley BS, Suehs CM, Veenendaal EM (2009) Release from soil pathogens plays an important role in the success of invasive *Carpobrotus* in the Mediterranean. *South African Journal of Botany* 75: 172–175. doi: 10.1016/j.sajb.2008.09.003
- van Kleunen M, Fischer M (2008) Adaptive rather than non-adaptive evolution of *Mimulus guttatus* in its invasive range. *Basic and Applied Ecology* 9: 213–223. doi: 10.1016/j.baae.2007.03.006
- van Kleunen M, Schmid B (2003) No evidence for an evolutionary increased competitive ability in an invasive plant. *Ecology* 84: 2816–2823. doi: 10.1016/j.baae.2007.03.006
- Vilà M, Gimeno I (2006) Potential for higher invasiveness of the alien *Oxalis pes-caprae* on islands than on the mainland. *Plant Ecology* 183: 47–53. doi: 10.1007/s11258-005-9005-3
- Vilà M, Gómez A, Maron JL (2003) Are alien plants more competitive than their native conspecifics? A test using *Hypericum perforatum* L. *Oecologia* 137: 211–215. doi: 10.1007/s00442-003-1342-0
- Whitney KD, Gabler CA (2008) Rapid evolution in introduced species, 'invasive traits' and recipient communities: challenges for predicting invasive potential. *Diversity and Distributions* 14: 569–580. doi: 10.1111/j.1472-4642.2008.00473.x

- Widmer TL, Guermache F, Dolgovskaia MY, Reznik SY (2007) Enhanced growth and seed properties in introduced vs. native populations of yellow starthistle (*Centaurea Solstitialis*). *Weed Science* 55: 465–473. doi: 10.1614/WS-06-211R.1
- Williams JL, Auge H, Maron JL (2008) Different gardens, different results: native and introduced populations exhibit contrasting phenotypes across common gardens. *Oecologia* 157: 239–248. doi: 10.1007/s00442-008-1075-1
- Willis AJ, Blossey B (1999) Benign environments do not explain the increased vigor of non-indigenous plants: a cross-continental transplant experiment. *Biocontrol Science and Technology* 9: 567–577. doi: 10.1080/09583159929523
- Willis AJ, Memmott J, Forrester RI (2000) Is there evidence for the post-invasion evolution of increased size among invasive plant species? *Ecology Letters* 3: 275–283. doi: 10.1046/j.1461-0248.2000.00149.x
- Willis AJ, Thomas MB, Lawton JH (1999) Is the increased vigour of invasive weeds explained by a trade-off between growth and herbivore resistance? *Oecologia* 120: 632–640. doi: 10.1007/s004420050899
- Zou J, Rogers WE, Siemann E (2007) Differences in morphological and physiological traits between native and invasive populations of *Sapium sebiferum*. *Functional Ecology* 21: 721–730. doi: 10.1111/j.1365-2435.2007.01298.x
- Zou J, Rogers WE, Siemann E (2008) Increased competitive ability and herbivory tolerance in the invasive plant *Sapium sebiferum*. *Biological Invasions* 10: 291–302. doi: 10.1007/s10530-007-9130-0
- Zou J, Siemann E, Rogers WE, DeWalt SJ (2008) Decreased resistance and increased tolerance to native herbivores of the invasive plant *Sapium sebiferum*. *Ecography* 31: 663–671. doi: 10.1111/j.0906-7590.2008.05540.x

Alien plants in urban nature reserves: from red-list species to future invaders?

Vojtěch Jarošík^{1,2}, Petr Pyšek^{2,1}, Tomáš Kadlec^{1,3}

1 Department of Ecology, Faculty of Science, Charles University in Prague, CZ-12843 Viničná 7, Prague, Czech Republic **2** Institute of Botany, Academy of Sciences of the Czech Republic, CZ-25243 Průhonice, Czech Republic **3** Department of Ecology, Faculty of Environmental Sciences, Czech University of Life Sciences, Prague, Czech Republic

Corresponding author: Vojtěch Jarošík (jarosik@cesnet.cz)

Academic editor: Ingolf Kühn | Received 16 March 2011 | Accepted 24 April 2011 | Published 5 October 2011

Citation: Jarošík V, Pyšek P, Kadlec T (2011) Alien plants in urban nature reserves: from red-list species to future invaders? NeoBiota 10: 27–46. doi: 10.3897/neobiota.10.1262

Abstract

Urban reserves, like other protected areas, aim to preserve species richness but conservation efforts in these protected areas are complicated by high proportions of alien species. We examined which environmental factors determine alien species presence in 48 city reserves of Prague, Czech Republic. We distinguished between archaeophytes, i.e. alien species introduced since the beginning of Neolithic agriculture up to 1500 A. D., and neophytes, i.e. modern invaders introduced after that date, with the former group separately analysed for endangered archaeophytes (listed as C1 and C2 categories on national red list). Archaeophytes responded positively to the presence of arable land that was in place at the time of the reserve establishment, and to a low altitudinal range. In addition to soil properties, neophytes responded to recent human activities with the current proportion of built-up area in reserves serving as a proxy. Endangered archaeophytes, with the same affinity for past arable land as other archaeophytes, were also supported by the presence of current shrubland in the reserve. This suggests that for endangered archaeophytes it may have been difficult to adapt to changing agricultural practices, and shrublands might act as a refugium for them. Forty-six of the 155 neophytes recorded in the reserves are classified as invasive. The reserves thus harbour 67% of the 69 invasive neophytes recorded in the country, and particularly worrisome is that many of the most invasive species are shrubs and trees, a life form that is known to account for widespread invasions with high impacts. Our results thus strongly suggest that in Prague nature reserves there is a high potential for future invasions.

Keywords

Alien plants, archaeophyte, Czech Republic, nature reserve, neophyte, plant invasions, red list, urban

Introduction

Urbanization is the most dramatic form of natural habitat destruction making cities a rather hostile environment for natural wildlife. Conserving the native biodiversity in urbanized areas is therefore particularly challenging because remnants of natural habitats in urban areas are restricted to small and isolated patches. These often harbour fragmented populations of native plants and animals that face risks associated with small population sizes and pressures from heavily altered urban environments (Raupp et al. 2010, Jarošík et al. 2011). Maintaining biological biodiversity in urban landscapes has recently become a conservation priority and protecting natural remnants within cities is increasingly viewed as important (Celesti-Grapow and Blasi 2003, Turner et al. 2004, Palmer et al. 2008, Toth et al. 2009, Vermonden et al. 2009). Many cities are located in naturally species-rich areas (Kühn et al. 2004) and their heterogeneous environments (Zerbe et al. 2003) have the potential to support high numbers of species.

However, overall species diversity in entire cities has been intensively studied (Klotz 1987, 1988, 1990, Pyšek 1989, Knapp et al. 2008, 2010) and it has been repeatedly documented that urban environments and the associated life styles promote introductions of alien species (Pyšek 1998, Celesti-Grapow et al. 2001, 2006, Chocholoušková and Pyšek 2003, LaSorte et al. 2007, 2008, Ricotta et al. 2009). Plant invasions are strongly dependent on propagule pressure and pathways associated with human activities that are extremely pronounced in urban areas, and also create favourable conditions for the establishment of arriving species via disturbances (Hulme et al. 2008, Pyšek et al. 2010c, Essl et al. 2011). These factors contribute to plant species richness in cities that is higher than surrounding landscapes (Haeupler 1974), and overall alien species contribute to the remarkably high species richness of European cities (Pyšek 1993, 1998).

However, as in other protected areas, the conservation focus in nature reserves in urban areas is on the diversity of native species. Urban areas are where these “two diversities” come into the sharp conflict that results from the mismatch between human efforts to protect natural biodiversity and their activities that create ideal environments for alien species invasions. This matrix of urban development and nature reserves is therefore an appropriate testing ground to explore resistance patterns of natural vegetation against penetration by alien plants. It has been shown for other environments that nature reserves and protected areas possess some resistance against invasions (Pyšek et al. 2003, Foxcroft et al. 2011).

This study analyses patterns of species richness of alien vascular plants in the city of Prague, Czech Republic. Based on the same data set as in Jarošík et al. (2011) where the factors shaping the richness of native, including endangered, butterflies and plants were analysed, this paper focuses on alien plants. It aims to identify the factors that contribute to the levels of reserve invasions (in the sense of Hierro et al. 2005, Richardson and Pyšek 2006, Chytrý et al. 2008a) and that determine the numbers of archaeophytes and neophytes currently observed in nature reserves in Prague.

Methods

Study area

The city of Prague, Czech Republic, contains 88 nature reserves in an area of 496 km² (Kubíková et al. 2005). Complete plant species lists were available for 48 reserves, and resulted from a systematic surveys of flora in the late 1980s/early 1990s (Špryňar and Marek 2001; Appendix 1). The reserves analysed are evenly distributed across the metropolitan area, both in its central and peripheral areas between 14°13'51" and 14°43'80"N and 49°56'33" and 50°12'23"E, and were established between 1953 and 1990. The vegetation protected in the reserves ranges from plant communities of rocky outcrops and unused quarries to thermophilous grasslands and shrublands, and semi-natural woodlands (see Jarošík et al. 2011 for details). Nineteen of the reserves (mainly rocks and unused quarries) were originally established to protect geological or palaeontological sites and 15 to conserve rare plants (Kubíková et al. 2005). At present all of them represent sites protected from human influence other than tourism.

Plant data

For each reserve, the total number of vascular plant species was recorded; only naturally occurring species were considered; planted shrubs and trees were excluded. The total number of plant species in all reserves was 1309 (about a half of the Czech flora; Kubát et al. 2002), mean species number per reserve was 291, ranging from 117 to 683.

Species were classified into native and alien, with archaeophytes and neophytes distinguished among the latter group (e.g. Pyšek et al. 2002b, 2004c, Preston et al. 2004). Archaeophytes are plant species introduced to the Czech Republic since the beginning of Neolithic agriculture up to 1500 A. D., mostly from the Mediterranean region and Western Asia, while neophytes arrived after that date and represent a much more variable group in terms of the areas of origin (Pyšek et al. 2002b, Lambdon et al. 2008). The effect of the time of arrival is still detectable at present and both groups markedly differ in their ecology and habitat affinities in Central Europe (Pyšek et al. 2004b, 2005, 2011, Chytrý et al. 2005, 2008a, b). In total there were 175 archaeophytes and 155 neophytes in the reserves analysed (mean per reserve 14.0 and 20.3, range 4–63 and 6–104, respectively).

Since some archaeophytes appear on national red lists despite their alien origin, (Holub and Procházka 2000, Cheffings et al. 2005, Zajac et al. 2009), we recorded the number of species that are considered endangered in the Czech Republic for each reserve following the red-list classification in Kubát et al. (2002). This group (further referred to as "endangered") included species classified in categories C1 (critically threatened taxa, corresponding to the IUCN category "critically endangered") and C2 (strongly threatened taxa, corresponding to the IUCN category "endangered"; see

Holub and Procházka 2000 for details). In total there were 15 endangered species in the reserves analysed (mean = 0.6, range 0–8).

The numbers of neophytes, archaeophytes and endangered archaeophytes recorded in reserves were used to calculate their proportions among total numbers of species, used in statistical analyses.

Explanatory variables

Explanatory variables describing factors that were assumed to affect the patterns of alien species occurrence in the reserves reflect geography (no. 1–7 below), habitat characteristics (8–9), substrate (10–12) and urbanization (13–16), and included: 1. reserve area (ha); 2. degree of reserve isolation (categorical: isolated, > 1 000 m from the closest reserve; clustered, < 300 m from the closest reserve; neighbouring, adjoining other reserves); 3. reserve age, expressed as years since the establishment; 4. aspect (north to north-east; plain; south-east and west; south and south-west; valley with all aspects present); 5. mid altitude, i.e., the mid value between minimum and maximum altitude; 6. altitudinal range, i.e. the difference between maximum and minimum altitude; 7. presence or absence of railway; 8. past habitat, reflecting the proportional representation of the following habitat types at the time of reserve establishment, with each type treated as an independent variable: forest, arable land, pasture, grassland, orchards, shrubland (including rocky outcrops) and built-up area; 9. present habitat, referring to the current state, using the same classification; 10. soil type (categorical variable with following levels: alluvial; acid; calcareous; neutral; acid and alluvial; acid and neutral; acid and calcareous; acid, neutral and calcareous); 11. presence or absence of bare rock; 12. presence or absence of a quarry; 13. minimum distance to natural habitat; 14. minimum distance to built-up area; 15. built-up perimeter, i.e. length of perimeter formed by built-up area; 16. natural perimeter, i.e. length of perimeter formed by other than built-up area.

The variables are the same as in Jarošík et al. (2011) where further details and means and ranges for continuous variables are given.

Statistical analysis

The response variables were proportional representations of species numbers of archaeophytes (mean 11.8%, range 2.4–21.5%), neophytes (mean 6.0%, range 2.0–17.4%) and endangered archaeophytes (mean 0.2%, range 0–1.3%) within all wild-growing species of vascular plants in each reserve. To prevent these proportions from species-poor reserves having undue influence, the proportions were weighted by the total numbers of species in each reserve (e.g. Pyšek et al. 2010a). The response variables were then analysed as a function of the environmental characteristics of the 48 nature reserves. These analyses were made by boosted trees (Friedman 2002) in a commercial

statistical software TreeNet® v.1 (Friedman 1999, 2001). This data mining technique enables to make predictions and identify the most important predictors by screening a large number of candidate variables, without requiring any assumptions about the form of the relationships between predictors and the response variable, and without a priori formulated hypotheses (Hochachka et al. 2007). The method is more flexible than traditional statistical analyses also because it enables to reveal structures in the dataset that are other than linear, and to solve complex interactions. Importantly, the technique is nonparametric and thus not affected by spatial autocorrelations and by collinearity of the predictor variables (e.g. Jarošík 2011).

Using trees, the data are successively split along coordinate axes of the predictors, represented by the environmental characteristics, so that at any node, the split is selected that maximally distinguishes the response variable, represented by the proportional representation of the species, in the left and the right branches (Breiman et al. 1984, De'ath and Fabricius 2000). This is done using binary recursive partitioning, with a best split made based on Gini impurity measure (e.g. Steinberg and Colla 1995, Cutler et al. 2007). In boosted trees (Friedman 1999, 2001), five hundred six-node classification trees were sequentially built from residual-like measures from previous trees. At each iteration, a tree was built from a default (50%) random subsample of the data set, producing a default incremental improvement in a model (0.01 learning rate at each iteration). The calculations were made with Huber-M regression loss criterion having breakdown 0.9, and minimum number of training observations in terminal nodes equal to three.

Five-fold cross-validation was used to obtain estimate of regression accuracy for each tree, and the best tree, having the smallest cross-validated mean absolute error, was chosen for interpretation. The quality of the best tree was expressed as R^2 value (Friedman 1999, 2001). Predictors of the best tree were ranked based on improvements of all splits associated with a given variable across all trees in the model, with the raw importance scores rescaled so that the most important predictor always got a score of 100. The resulting relative importance scores thus provided a relative measure of each predictor's contribution to the model's predictive power. Partial dependence plots (Friedman 2001, Hastie et al. 2001, Cutler et al. 2007) were used to graphically characterize relationships between the individual predictor variables and predicted probabilities of species presence.

The absolute numbers of archaeophytes, neophytes and endangered archaeophytes closely correlated with their proportional representation in the species pool of each reserve (Spearman's rank: archaeophytes $r_s = 0.76$; neophytes $r_s = 0.70$; endangered archaeophytes $r_s = 0.99$). However, it cannot be a priori excluded that the alien species respond very differently than native species to the predictors; if so, it may not be appropriate to weigh the proportions of alien species by the total number of wild growing species in each reserve, as it could change some of the conclusions presented. To verify that the results on proportions are generic, all analyses were repeated using numbers of alien species as the response variable. Comparing to previous analyses on proportions, there were no changes in conclusions, and thus only the results on proportions are presented.

Results

The most important factors affecting the proportion of archaeophytes among all species in a reserve were mainly the presence of arable land before the reserve was established, but also its altitudinal characteristics (Figure 1A): archaeophytes were more abundant when the reserve had a low altitudinal range (Figure 2). The proportion of neophytes consistently increased with the proportion of present built-up area and depended on soil type: neophytes were more represented on alluvial and neutral to calcareous soils than in reserves with acidic soils (Figure 1B and 3).

As with all archaeophytes, the proportion of endangered archaeophytes among all species in a reserve positively depended on the past presence of arable land (Figure 1C and 4A), but there was also an important effect of shrubland. The proportion of endangered archaeophytes abruptly declined in reserves with less than 30% of currently present shrubland (Figure 4B).

Discussion

Factors that determine the level of invasion of urban nature reserves

Prague nature reserves are important sanctuaries for native plants because they harbour approximately half of the native flora in the Czech Republic (Špryňar and Marek 2001, Kubát et al. 2002, Jarošík et al. 2011). Alien species in the reserves studied, on the other hand, constitute a much lower proportion of the total alien species richness in the country, but the figure differs with respect to the time of arrival: while the 175 archaeophytes represent 53% of all archaeophytes registered in the Czech Republic, the 155 neophytes found in reserves are only 15% of the 1046 neophytes (Pyšek et al. 2002b). On average, 17.8% of reserve floras are formed by alien species; this is much higher proportion than found in a larger set of 302 reserves in the whole of the Czech Republic where alien species make up on average 6.1% of the reserve flora (Pyšek et al. 2002a, 2004a).

Our study shows that the numbers of alien species in urban nature reserves can be predicted by relatively few factors. We used a number of variables that reflected site geography, land-use history and connectivity, and propagule pressure, but only five of them were needed to explain from 54 to 71% of the overall variability. That habitats were the most important factor for archaeophytes corresponds well to the recent results of studies on regional determinants of plant invasions in the Czech Republic and Europe that show habitat identity to play a decisive role, more important than propagule pressure and climate (Chytrý et al. 2008a, b, Pyšek et al. 2010b). For neophytes, the strongest effect of the proportion of built-up area reflects that it is a surrogate for propagule pressure by human activities. The effect of soil type corresponds to the well-known avoidance of acidic soils by neophytes and their affinity to resource-rich habitats (Chytrý et al. 2005, 2008b, Blumenthal et al. 2009). This is consistent with

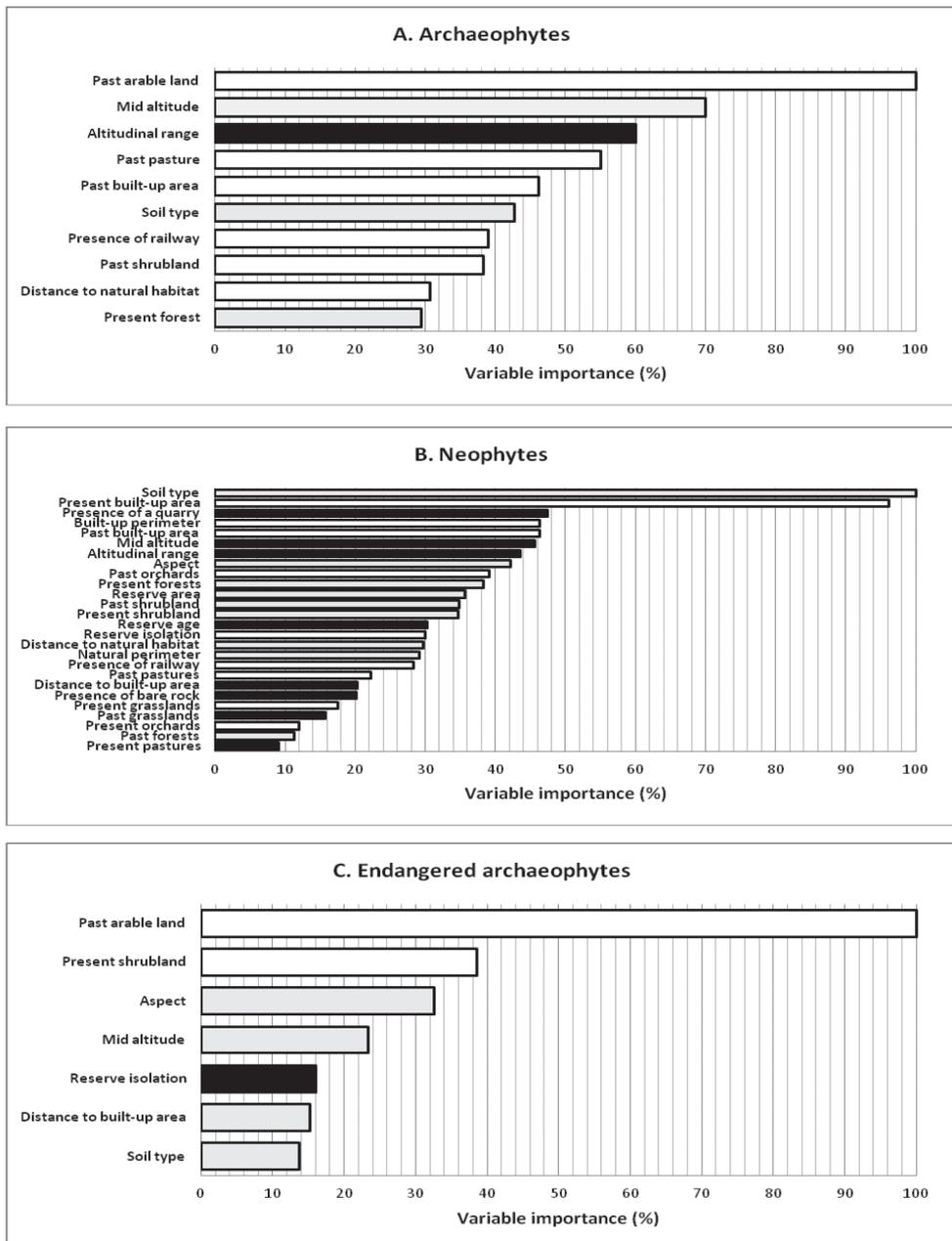


Figure 1. Rank of importance of the individual predictor variables from boosted regression trees for archaeophytes **A** neophytes **B** and endangered archaeophytes **C** Variable importance is scaled to have values between 0 and 100. Results for the best trees with $R^2 = 0.71$ **A** $R^2 = 0.69$ **B** and $R^2 = 0.54$ **C** White bars are predictors in which large values means positive effect, black bars in which large values mean negative effect, and grey bars are predictors with effect varying equivocally.

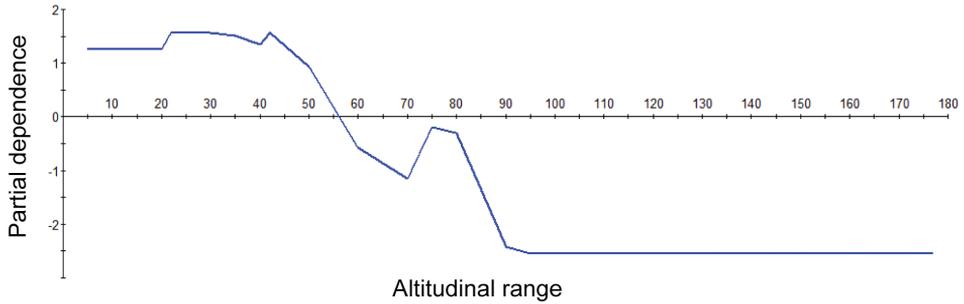


Figure 2. Partial dependence plot of representation of archaeophytes on altitudinal range. The partial dependence describes positive and negative dependences of the representation of archaeophytes on altitudinal range, averaging out the effects of the other predictor variables in the model.

the finding of Chytrý et al. (2008a) that habitat is disproportionately a more important determinant of the level of invasion by archaeophytes than neophytes, with propagule pressure also playing an important role in the latter group.

The results also reflect that the two groups differ in long-term dynamics (Pyšek and Jarošík 2005). Archaeophytes, prehistoric invaders to Central Europe, respond to the presence of arable land that was in place at the time of the reserve establishment; this is in accordance with the results of a previous study from Prague nature reserves that found native plants generally responding to the past factors, unlike butterflies that were more affected by current landscape settings (Jarošík et al. 2011). From the nature conservation perspective this implies that future levels of reserve invasion by archaeophytes were “imprinted” at the time of their establishment. The effect of low altitudinal range that also significantly affected the numbers of archaeophytes may also be related to habitat structure in a reserve since hilly sites were traditionally considered less suitable for agriculture in a lowland region.

Neophyte introductions, however, continue at an accelerating rate in Europe (Lambdon et al. 2008, Hulme et al. 2009), and a substantial proportion of them were introduced when most reserves were already established. Neophytes, therefore, respond to more recent ongoing human activities with the current proportion of built-up area in our study serving as a proxy for this activity. Still, the historical signal, similar to that for archaeophytes, is present and manifested by the effect of soil properties.

Endangered archaeophytes: better not lose them

Though it is questionable whether species of alien origin should be a part of red lists, these species are perceived by botanists as elements of local nature, especially when they are rare, and many of them are typical of traditional cultural landscapes in Europe and considered to be species of cultural and historical importance (Cheffings et al. 2005). From the management perspective, this attitude is justified because rare archaeophytes

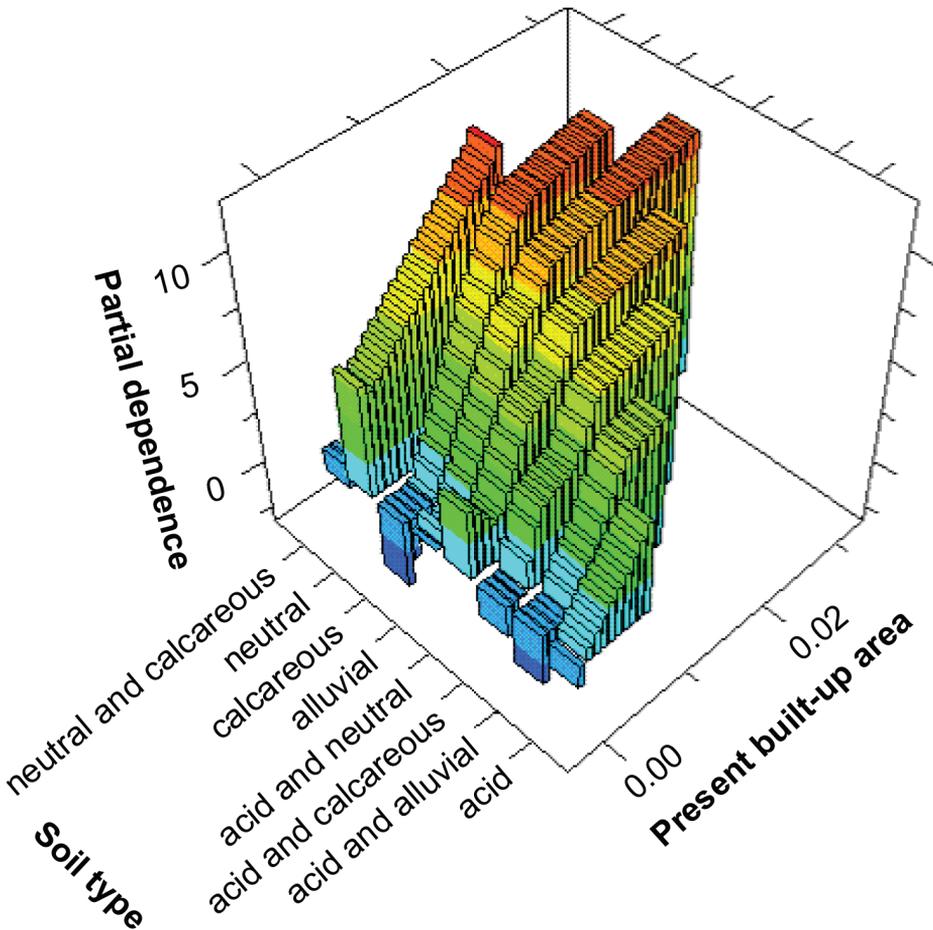


Figure 3. Bivariate partial dependence plots of representation of neophytes on present built-up area and soil type. Otherwise as in Figure 2.

are unlikely to exert any impact. Moreover, it is generally difficult to draw the line between the archaeophyte and native status, resulting sometimes in uncertain labelling (Pyšek et al. 2002b, Lambdon et al. 2008). In some cases the decision to assign a species the archaeophyte rather than native status is based on the fact that native range or habitat of the given species is unknown, and criteria applied are mostly indirect. A strong argument for protecting rare archaeophytes follows from the fact that many archaeophytes have native world ranges which are not known or are highly uncertain, and some archaeophytes are regarded as alien throughout their known global range (so-called anecophytes; Zohary 1962). As pointed by Cheffings et al. (2005), if such species were excluded from conservation efforts on account of their non-native status, it would lead to them being ignored almost everywhere and they would effectively fall through the conservation net.

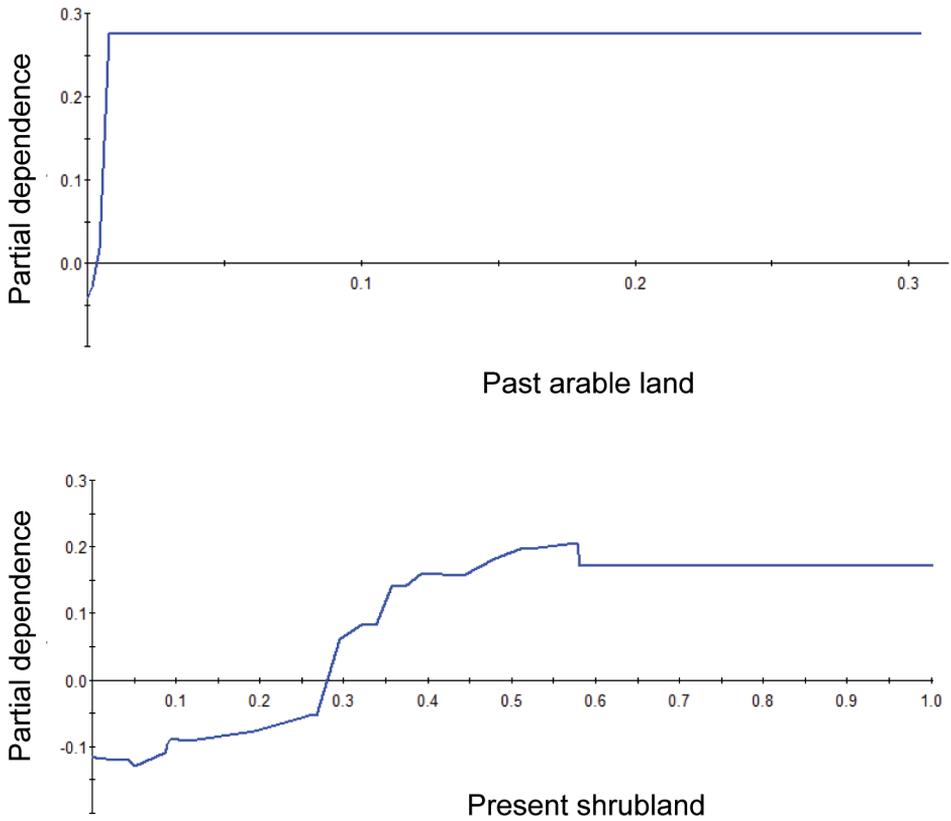


Figure 4. Partial dependence plots of representation of endangered archaeophytes on past arable land (A) and current shrubland (B). Otherwise as in Figure 2.

Endangered archaeophytes, in addition to the same affinity for past arable land as other archaeophytes, are supported by the presence of current shrubland in a reserve. This seems to indicate that there are species among this group for which it might have been difficult in the past to adapt to changing agricultural practices and that new technologies might have negatively impacted their population dynamics (Kropáč 2006). For such species, shrublands serve as refugia. This is further supported by the fact that it is current, not past shrublands that play a role. This finding points out that from the viewpoint of conservation of endangered archaeophytes, nature reserves could be more important than previously thought.

From endangered to endangering: rare archaeophytes and invasive neophytes

Our results support previously raised concerns about studies that analyse patterns of regional plant invasions and lump all aliens regardless of the time of immigration. It

has been repeatedly shown that archaeophytes and neophytes are ecologically distinct groups that differ in habitat affinities, historical dynamics, pollination patterns and response to climate (Pyšek et al. 2004b, 2005, 2011). This is even more pronounced in nature reserves where the categories of alien species stand on opposite sides from the conservation point of view, ranging from threatened species included on red lists to potentially dangerous invaders that are targeted by management efforts. Obviously, species numbers used to infer general patterns that can lead to universal management recommendations (Jarošík et al. 2011) are one side of the coin, but to realize the immediate threat at the local scale, species identities need to be taken into account.

In total, 15 threatened archaeophytes were recorded in nature reserves studied, eight of them considered critically endangered (C1 category): *Conringia orientalis* (occurring in 3 reserves), *Erysimum repandum*, *Marrubium vulgare*, *Torilis arvensis* (2), *Adonis flammea*, *Misopates orontium*, *Polycnemum arvense* and *P. majus* (1). Additional seven species belong to the endangered (C2) category: *Adonis aestivalis* (5), *Veronica triloba* (3), *Anthriscus caucalis*, *Stachys annua*, *Veronica agrestis* (2), *Geranium molle* and *Sclerochloa dura* (1).

On the other hand, 46 of the 155 neophytes recorded in reserves (Appendix 2) are classified as invasive (Pyšek et al. 2002b). Also, the above figure about the percentage of all neophytes recorded in the set of reserves studied among their total number in the Czech Republic, 15%, changes dramatically if expressed for a subgroup of invasive neophytes: Prague reserves harbour 67% of the 69 invasive neophytes recorded in the country (Pyšek et al. 2002b). Therefore, the potential threat to Prague nature reserves by alien plants may be in fact greater than inferred from species numbers. The list from reserves includes the majority of noxious invaders of the Czech flora, species that often exert a high impact on vegetation and species diversity of invaded communities, e.g. *Heracleum mantegazzianum*, *Reynoutria japonica*, *Helianthus tuberosus*, *Lupinus polyphyllus*, *Solidago gigantea*, *S. canadensis* (Hejda et al. 2009). Invasive species in Prague reserves include diverse life forms and it should be seen as warning that there are many species of shrubs and trees, a life form that is known to account for many widespread invaders, often with a high impact (Křivánek and Pyšek 2006, Pyšek et al. 2009): *Robinia pseudoacacia* (recorded in 38 reserves), *Symphoricarpos albus* (24), *Mahonia aquifolium* (21), *Quercus rubra* (18), *Syringa vulgaris* (17), *Lycium barbarum* (10), *Populus ×canadensis* (4), *Ailanthus altissima* (3), *Rhus hirta* (2) and *Amorpha fruticosa* (1). Considering that none of the reserves was free of alien species, that the most invaded reserves harboured up to as much as 17.4% of neophytes and 32.3% of all aliens, and which species are most represented, our results strongly suggest that in Prague nature reserves there is a warning potential for future invasions unless appropriate control measures are imposed by nature conservation authorities. To make targeted practical recommendations specific to particular reserves with distinct environmental and vegetation settings, studies on current status of individual invasive species and their dynamics over time are needed, ideally initiated by state/municipal administration.

Acknowledgements

We thank two anonymous reviewers for their comments, Laura Meyerson for editing our English, and Jan Pergl, Ivan Ostrý and Zuzana Sixtová for technical assistance. The study was funded by grants no. 206/09/0563 from the Czech Science Foundation, and long-term research plans no. AV0Z60050516 (from the Academy of Sciences of the Czech Republic), and no. MSM0021620828, and project no. LC06073 (both from the Ministry of Education, Youth and Sports of the Czech Republic). Petr Pyšek acknowledges support from by the Praemium Academiae award (AV0Z60050516) from the Academy of Sciences of the Czech Republic.

References

- Blumenthal D, Mitchell CE, Pyšek P, Jarošík V (2009) Synergy between pathogen release and resource availability in plant invasion. *Proceedings of the National Academy of Sciences of the United States of America* 106: 7899–7904. doi: 10.1073/pnas.0812607106
- Breiman L, Friedman J, Olshen R, Stone C (1984) *Classification and Regression Trees*. Pacific Grove, Wadsworth.
- Celesti-Grapow L, Blasi C (2003) Archaeological sites as areas for biodiversity conservation in cities: The spontaneous vascular flora of the Caracalla Baths in Rome. *Webbia* 58: 77–102.
- Celesti-Grapow L, Di Marzio P, Blasi C (2001) The importance of alien and native species in the urban flora of Rome (Italy). In: Brundu G, Brock J, Camarda I, Child L, Wade M (Eds) *Plant invasions: Species ecology and ecosystem management*. Backhuys Publ. (The Hague): 209–220.
- Celesti-Grapow L, Pyšek P, Jarošík V, Blasi C (2006) Determinants of native and alien species richness in the flora of Rome. *Diversity and Distributions* 12: 490–501. doi: 10.1111/j.1366-9516.2006.00282.x
- Cheffings CM, Farrell L, Dines, TD, Jones RA, Leach SJ, McKean DR, Pearman DA, Preston CD, Rumsey FJ, Taylor I (2005) The vascular plant red data list for Great Britain. Joint Nature Conservation Committee (Peterborough). *Species Status* 7: 1–116.
- 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.
- Chytrý M, Jarošík V, Pyšek P, Hájek O, Knollová I, Tichý L, Danihelka J (2008a) Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology* 89: 1541–1553. doi: 10.1890/07-0682.1
- Chytrý M, Maskell LC, Pino J, Pyšek P, Vilà M, Font X, Smart SM (2008b) Habitat invasions by alien plants: A quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *Journal of Applied Ecology* 45: 448–458. doi: 10.1890/07-0682.1
- Chytrý M, Pyšek P, Tichý L, Knollová I, Danihelka J (2005) Invasions by alien plants in the Czech Republic: A quantitative assessment across habitats. *Preslia* 77: 339–354.
- Cutler DR, Edwards TC, Beard KH, Cutler A, Hess KT, Gibson J, Lawler JJ (2007) Random forests for classification in ecology. *Ecology* 88: 2783–2792. doi: 10.1890/07-0539.1

- De'ath G, Fabricius KE (2000) Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81: 3178–3192. doi: 10.1890/0012-9658(2000)081[3178:CARTAP]2.0.CO;2
- Essl F, Dullinger S, Rabitsch W, Hulme PE, Hülber K, Jarošík V, Kleinbauer I, Krausmann F, Kühn I, Nentwig W, Vilà M, Genovesi P, Gherardi F, Desprez-Lousteau M-L, Roques A, Pyšek P (2011) Socioeconomic legacy yields an invasion debt. *Proceedings of the National Academy of Sciences of the United States of America* 108: 203–207. doi: 10.1073/pnas.1011728108
- Foxcroft LC, Jarošík V, Pyšek P, Richardson DM, Rouget M (2011) Protected-area boundaries as filters of plant invasions. *Conservation Biology* 25: 400–405.
- Friedman JH (1999) Stochastic Gradient Boosting. Technical report, Dept. of Statistics, Stanford University.
- Friedman JH (2001) Greedy function approximation: A gradient boosting machine. *Annals of Statistics* 29: 1189–1232. doi: 10.1214/aos/1013203451
- Friedman JH (2002) Stochastic gradient boosting. *Computational Statistics and Data Analysis* 38: 367–378. doi: 10.1016/S0167-9473(01)00065-2
- Haeupler H (1974) Statistische Auswertung von Punktrasterkarten der Gefäßpflanzenflora Süd-Niedersachsens. *Scripta Geobotanica* 8: 1–141.
- Hastie TJ, Tibshirani RJ, Friedman JH (2001) *The Elements of Statistical Learning: Data Mining, Inference, and Prediction*. Springer, New York.
- Hejda M, Pyšek P, Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology* 97: 393–403. doi: 10.1111/j.1365-2745.2009.01480.x
- Hierro JL, Maron JL, Callaway RM (2005) A biogeographical approach to plant invasions: The importance of studying exotics in their introduced and native range. *Journal of Ecology* 93: 5–15. doi: 10.1111/j.0022-0477.2004.00953.x
- Hochachka WM, Caruana R, Fink D, Munson A, Riedewald M, Sorokina D, Kelling S (2007) Data-mining discovery of pattern and process in ecological systems. *The Journal of Wildlife Management* 71: 2427–2437. doi: 10.2193/2006-503
- Holub J, Procházka F (2000) Red list of vascular plants of the Czech Republic – 2000. *Preslia* 72: 187–230.
- Hulme PE, Bacher S, Kenis M, Klotz S, Kühn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pyšek P, Roques A, Sol D, Solarz W, Vilà M (2008) Grasping at the routes of biological invasions: A framework for integrating pathways into policy. *Journal of Applied Ecology* 45: 403–414. doi: 10.1111/j.1365-2664.2007.01442.x
- Hulme PE, Pyšek P, Nentwig W, Vilà M (2009) Will threat of biological invasions unite the European Union? *Science* 324: 40–41. doi: 10.1126/science.1171111
- Jarošík V (2011) CART and related methods. In: Simberloff D, Rejmánek M (Eds) *Encyclopedia of Biological Invasions*. University of California Press (Berkeley and Los Angeles): 104–108.
- Jarošík V, Konvička M, Pyšek P, Kadlec T, Beneš J (2011) Conservation in a city: Do the same principles apply to different taxa? *Biological Conservation* 144: 490–499. doi: 10.1016/j.biocon.2010.10.002

- Klotz S (1988) Flora und Vegetation in der Stadt, ihre Spezifik und Indikationsfunktion. *Landchaftsarchitektur* 17: 104–107.
- Klotz S (1990) Species/area and species/inhabitants relations in European cities. In: Sukopp H, Hejný S, Kowarik I (Eds) *Urban ecology: Plants and plant communities in urban environment*. SPB Acad. Publ. (The Hague): 99–104.
- Klotz S (1987) Floristische und vegetationskundliche Untersuchungen in Städten der DDR. *Düsseldorf Geobotanisches Kolloquium* 4: 61–69.
- Knapp S, Kühn I, Stolle J, Klotz S (2010) Changes in the functional composition of a Central European urban flora over three centuries. *Perspectives in Plant Ecology, Evolution and Systematics* 12: 235–244. doi: 10.1016/j.ppees.2009.11.001
- Knapp S, Kühn I, Schweiger O, Klotz S (2008) Challenging urban species diversity: Contrasting phylogenetic patterns across plant functional groups in Germany. *Ecology Letters* 11: 1054–1064. doi: 10.1111/j.1461-0248.2008.01217.x
- Křivánek M, Pyšek P (2006) Predicting invasions by woody species in a temperate zone: A test of three risk assessment schemes in the Czech Republic (Central Europe). *Diversity and Distributions* 12: 319–327. doi: 10.1111/j.1366-9516.2006.00249.x
- Kropáč Z (2006) Segetal vegetation of the Czech Republic: Synthesis and syntaxonomical revision. *Preslia* 78: 123–209.
- Kubát K, Hrouda L, Chrtek jun J, Kaplan Z, Kirschner J, Štěpánek J, Zázvorka J (Eds) (2002) *Klíč ke květeně České republiky* [Key to the Flora of the Czech Republic]. Academia, Praha.
- Kubíková J, Ložek V, Špryňar P, et al. (2005) Praha [Prague]. In: Mackovčín P, Sedláček M (Eds) *Chráněná území ČR XII* [Protected regions of the Czech Republic, volume XII]. Agentura ochrany přírody a krajiny ČR a EkoCentrum (Brno, Praha): 1–304.
- Kühn I, Brandl R, Klotz S (2004) The flora of German cities is naturally species rich. *Evolutionary Ecology Research* 6: 749–764.
- Lambdon PW, Pyšek P, Basnou C, Hejda M, Arianoutsou M, Essl F, Jarošík V, Pergl J, Winter M, Anastasiu P, Andriopoulos P, Bazos I, Brundu G, Celesti-Grapow L, Chassot P, Delipetrou P, Josefsson M, Kark S, Klotz S, Kokkoris Y, Kühn I, Marchante H, Perglová I, Pino J, Vilà M, Zikos A, Roy D, Hulme PE (2008) Alien flora of Europe: Species diversity, temporal trends, geographical patterns and research needs. *Preslia* 80: 101–149.
- La Sorte FA, McKinney ML, Pyšek P (2007) Compositional similarity among urban floras within and across continents: Biogeographical consequences of human mediated biotic interchange. *Global Change Biology* 13: 913–921. doi: 10.1111/j.1365-2486.2007.01329.x
- La Sorte FA, McKinney ML, Pyšek P, Klotz S, Rapson GJ, Celesti-Grapow L, Thompson K (2008) Distance decay of similarity among European urban floras: the impact of anthropogenic activities on β diversity. *Global Ecology and Biogeography* 17: 363–371. doi: 10.1111/j.1466-8238.2007.00369.x
- Palmer GC, Fitzsimons JA, Antos MJ, White JG (2008) Determinants of native avian richness in suburban remnant vegetation: Implications for conservation planning. *Biological Conservation* 141: 2329–2341. doi: 10.1016/j.biocon.2008.06.025
- Preston CD, Pearman DA, Hall AR (2004) Archaeophytes in Britain. *Botanical Journal of the Linnean Society* 145: 257–294. doi: 10.1111/j.1095-8339.2004.00284.x

- Pyšek P (1989) On the richness of Central European urban flora. *Preslia* 61: 329–334.
- Pyšek P (1993) Factors affecting the diversity of flora and vegetation in central European settlements. *Vegetatio* 106: 89–100. doi: 10.1007/BF00044860
- Pyšek P (1998) Alien and native species in Central European urban floras: A quantitative comparison. *Journal of Biogeography* 25: 155–163. doi: 10.1046/j.1365-2699.1998.251177.x
- Pyšek P, Bacher S, Chytrý M, Jarošík V, Wild J, Celesti-Grapow L, Gassó N, Kenis M, Lambdon WP, Nentwig W, Pergl J, Roques A, Sádlo J, Solarz W, Vilà M, Hulme PE (2010a) Contrasting patterns in the invasions of European terrestrial and freshwater habitats by alien plants, insects and vertebrates. *Global Ecology and Biogeography* 19: 317–331. doi: 10.1111/j.1466-8238.2009.00514.x
- Pyšek P, Chytrý M, Jarošík V (2010b) Habitats and land-use as determinants of plant invasions in the temperate zone of Europe. In: Perrings C, Mooney HA, Williamson M (Eds) *Bioinvasions and globalization: Ecology, economics, management and policy*. Oxford University Press (Oxford): 66–79.
- Pyšek P, Jarošík V (2005) Residence time determines the distribution of alien plants. In: Inderjit (Ed.) *Invasive plants: Ecological and agricultural aspects*. Birkhäuser Verlag-AG (Basel): 77–96.
- Pyšek P, Jarošík V, Chytrý M, Danihelka J, Kühn I, Pergl J, Tichý L, Biesmeijer J, Ellis WN, Kunin WE, Settele J (2011) Successful invaders co-opt pollinators of native flora and accumulate insect pollinators with increasing residence time. *Ecological Monographs* 81: 277–293. doi: 10.1890/10-0630.1
- Pyšek P, Jarošík V, Chytrý M, Kropáč Z, Tichý L, Wild J (2005) Alien plants in temperate weed communities: Prehistoric and recent invaders occupy different habitats. *Ecology* 86: 772–785. doi: 10.1890/04-0012
- Pyšek P, Jarošík V, Hulme PE, Kühn I, Wild J, Arianoutsou M, Bacher S, Chiron F, Didžiulis V, Essl F, Genovesi P, Gherardi F, Hejda M, Kark S, Lambdon PW, Desprez-Loustau A-M, Nentwig W, Pergl J, Pobljšaj K, Rabitsch W, Roques A, Roy DB, Shirley S, Solarz W, Vilà M, Winter M (2010c) Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences of the United States of America* 107: 12157–12162. doi: 10.1073/pnas.1002314107
- Pyšek P, Jarošík V, Kučera T (2002a) Patterns of invasion in temperate nature reserves. *Biological Conservation* 104: 13–24. doi: 10.1016/S0006-3207(01)00150-1
- Pyšek P, Jarošík V, Kučera T (2003) Inclusion of native and alien species in temperate nature reserves: an historical study from Central Europe. *Conservation Biology* 17: 1414–1424. doi: 10.1046/j.1523-1739.2003.02248.x
- Pyšek P, Křivánek M, Jarošík V (2009) Planting intensity, residence time, and species traits determine invasion success of alien woody species. *Ecology* 90: 2734–2744. doi: 10.1890/08-0857.1
- Pyšek P, Kučera T, Jarošík V (2004a) Druhov diverzita a rostlinn invaze v eskch rezervacch: Co nm mohou rci poty druh? *Přroda* 21: 63–89.
- Pyšek P, Richardson DM, Williamson M (2004b) Predicting and explaining plant invasions through analysis of source area floras: Some critical considerations. *Diversity and Distributions* 10: 179–187. doi: 10.1111/j.1366-9516.2004.00079.x

- Pyšek P, Richardson DM, Rejmánek M, Webster G, Williamson M, Kirschner J (2004c) Alien plants in checklists and floras: Towards better communication between taxonomists and ecologists. *Taxon* 53: 131–143. doi: 10.2307/4135498
- Pyšek P, Sádlo J, Mandák B (2002b) Catalogue of alien plants of the Czech Republic. *Preslia* 74: 97–186.
- Raupp MJ, Shrewsbury PM, Herms DA (2010) Ecology of herbivorous arthropods in urban landscapes. *Annual Review of Entomology* 55: 19–38. doi: 10.1146/annurev-ento-112408-085351
- Richardson DM, Pyšek P (2006) Plant invasions: Merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography* 30: 409–431. doi: 10.1191/0309133306pp490pr
- Ricotta C, La Sorte FA, Pyšek P, Rapson GL, Celesti-Grapow L, Thompson K (2009) Phylogeography of urban alien floras. *Journal of Ecology* 97: 1243–1251. doi: 10.1111/j.1365-2745.2009.01548.x
- Špryňar M, Marek M (2001) Květena pražských chráněných území [Flora of the Prague protected areas]. In Proceedings of the conference “Praga 2000 natura megalopolis”. EnviTypo (Prague). [CD ROM]
- Steinberg G, Colla P (1995) CART: Tree-structured Non-parametric Data Analysis. Salford Systems, San Diego.
- Toth SF, Haight RG, Snyder SA, George S, Miller JR, Gregory MS, Skibbe AM (2009) Reserve selection with minimum contiguous area restrictions: An application to open space protection planning in suburban Chicago. *Biological Conservation* 142: 1617–1627. doi: 10.1016/j.biocon.2009.02.037
- Turner WR, Nakamura T, Dinetti M (2004) Global urbanization and the separation of humans from nature. *Bioscience* 54: 585–590. doi: 10.1641/0006-3568(2004)054[0585:GUATS O]2.0.CO;2
- Vermonden K, Leuven RSEW, van der Velde G, van Katwijk MM, Roelofs JGM, Hendriks AJ (2009) Urban drainage systems: An undervalued habitat for aquatic macroinvertebrates. *Biological Conservation* 142: 1105–1115. doi: 10.1016/j.biocon.2009.01.026
- Zajac M, Zajac A, Tokarska-Guzik B (2009) Extinct and endangered archaeophytes and the dynamics of their diversity in Poland. *Biodiversity: Research and Conservation* 13: 17–24.
- 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. doi: 10.1016/S0169-2046(02)00145-7
- Zohary M (1962) *Plant Life of Palestine, Israel and Jordan*. The Ronald Press, New York.

Appendix 1. Numbers of species in Prague nature reserves and characteristics of reserves. Total includes both native and alien species. Only characteristics of the reserves that affect the proportion of archaeophytes and neophytes are shown (see Methods for details). Soil types present in a reserve: al – alluvial; ac – acid; ca – calcareous; n – neutral.

Reserve	Species numbers			Reserve characteristics							
	Total	Archaeophytes	Neophytes	Archaeophytes endangered	Age (yrs)	Area (ha)	Altitudinal Range (m)	Past arable (%)	Present shrubland (%)	Present built-up (%)	Soil type
1. Baba	368	67	29	1	21	7.3	80	0.00	97.68	0.00	ac
2. Barrandovské skály	160	14	14	1	21	11.6	100	0.00	51.86	0.05	ca
3. Bažantnice v Satalicích	158	24	17	0	52	15.8	10	0.00	0.00	0.00	ac
4. Bohnické údolí	202	12	10	0	21	4.6	60	0.00	0.00	0.00	ac
5. Podhoří	363	57	30	2	21	8.4	75	0.00	57.86	0.00	ac
6. Zámky	379	64	23	1	21	5.2	60	0.00	51.05	0.00	ac
7. Branické skály	160	21	13	0	35	9.1	50	0.00	48.02	0.00	ca
8. V Hrobech	187	24	6	0	15	1.3	10	0.00	98.46	0.00	ac
9. Šance	225	9	6	0	21	116.8	177	0.00	0.43	0.00	ac
10. Čimické údolí	341	49	23	1	35	11.2	30	9.17	8.90	0.00	ac
11. Dalejský profil	280	46	18	1	21	22.8	50	0.00	19.32	0.00	ac-ca
12. Divoká Šárka	683	104	47	4	39	25.4	105	2.56	32.07	1.58	n
13. Dolní Šárka	248	29	12	1	21	6.2	70	0.00	65.69	0.00	n
14. Homolka	192	11	4	0	21	13.5	60	0.00	33.90	0.00	ca
15. Hrnčířské louky	221	15	10	0	15	29.3	20	0.17	44.27	0.00	ac-al
16. Chuchelský háj	271	21	11	0	21	19.8	90	0.00	0.00	0.00	n-ca
17. Jablonka	158	14	17	0	35	1.3	70	0.00	100.00	0.00	ac-n
18. Jenerálka	357	44	10	2	35	1.5	30	0.00	35.76	0.00	ac
19. Zlatnice	188	12	13	0	35	3.3	50	0.00	0.00	0.00	ac-n
20. Nad mlýnem	266	32	11	0	35	4.0	40	15.66	8.84	0.00	ac
21. Klapice	254	6	6	0	15	16.2	106	0.00	11.63	0.00	ca
22. Královská obora	362	54	63	0	15	104.5	42	0.00	26.78	3.10	al
23. Lochkovský profil	205	16	4	1	15	39.1	95	0.00	29.49	0.00	ca
24. Meandry Botiče	117	16	11	0	35	6.7	15	0.00	93.58	0.60	ac-al

Reserve	Species numbers			Reserve characteristics						Soil type	
	Total	Archaeophytes	Neophytes	Archaeophytes endangered	Age (yrs)	Area (ha)	Altitudinal Range (m)	Past arable (%)	Present shrubland (%)		Present built-up (%)
25. Milčovský les a rybníky	435	33	17	0	15	93.3	30	0.00	10.07	0.20	ac-al
26. Modránská rokle	333	54	29	0	15	124.9	80	0.00	3.13	0.09	ac
27. Okrouhlick	137	23	9	0	21	0.6	20	0.00	0.00	0.00	ac
28. Pitkovická sraň	173	14	4	0	34	0.5	20	0.00	3.92	0.00	ac
29. Počernický rybník	251	38	21	0	15	41.8	5	0.00	69.18	0.00	ac
30. Podbabské skály	264	51	19	1	21	0.8	30	0.00	35.71	0.00	ac
31. Cholupická bažantnice	264	51	19	1	21	13.8	12	0.00	0.00	0.00	ac
32. Obora v Uhlíněvsi	326	52	24	0	21	34.9	22	0.00	4.33	0.34	ac-al
33. Prokopské údolí	606	84	29	8	25	101.5	110	0.78	39.33	0.38	ac-ca
34. Radorinské údolí	552	64	22	3	50	103.3	80	6.90	3.79	0.00	ca
35. Rohožník a lom v Dubči	332	48	18	0	15	3.5	20	0.00	8.70	0.00	n
36. Tiché údolí a Roztocký háj	381	26	15	0	52	114.2	105	0.46	5.12	0.00	n-ca
37. Sedlecké skály	211	22	5	0	21	7.5	70	0.00	37.33	0.00	ac
38. Slavičí údolí	263	16	7	0	15	38.3	105	0.00	0.00	0.00	ac-ca
39. Trojská	195	42	15	0	21	1.3	35	0.00	100.00	0.00	ac
40. Údolí Kunratického potoka	283	21	12	0	15	152.0	80	0.00	10.55	0.13	ac
41. Vizevka	350	33	12	0	15	3.1	40	0.00	25.89	0.00	ac
42. Havránka	401	59	34	0	21	4.2	50	0.00	58.10	0.00	ac-n
43. Zmrzlík	335	46	15	0	15	16.4	80	30.46	10.28	0.01	ac-ca
44. Klánovický les	435	46	35	0	21	225.5	20	0.00	0.00	0.00	ac
45. Obora Hvězda	460	55	29	1	15	84.2	50	0.00	9.40	0.77	ac
46. Staňkovka	171	7	5	0	15	44.5	160	0.00	3.76	0.00	ac
47. Vínořský park	202	27	23	0	21	34.1	20	0.00	0.00	0.00	ac
48. Xaverovský háj	268	27	14	0	21	97.2	30	0.00	3.01	0.00	ac

Appendix 2. List of invasive neophytes recorded in Prague nature reserves. Species are ranked according to the decreasing number of reserves in which they were recorded (n = 48). Plant names according to Kubát et al. (2002).

Species	Family	Life form	Number of reserves invaded
<i>Impatiens parviflora</i>	Balsaminaceae	Annual	40
<i>Robinia pseudacacia</i>	Fabaceae	Tree	38
<i>Symphoricarpos albus</i>	Caprifoliaceae	Shrub	24
<i>Mahonia aquifolium</i>	Berberidaceae	Shrub	21
<i>Quercus rubra</i>	Fagaceae	Tree	18
<i>Sisymbrium loeselii</i>	Brassicaceae	Annual	18
<i>Solidago canadensis</i>	Asteraceae	Perennial	18
<i>Conyza canadensis</i>	Asteraceae	Annual	17
<i>Echinops sphaerocephalus</i>	Asteraceae	Perennial	17
<i>Syringa vulgaris</i>	Oleaceae	Shrub	17
<i>Epilobium ciliatum</i>	Onagraceae	Perennial	16
<i>Geranium pyrenaicum</i>	Geraniaceae	Perennial	14
<i>Solidago gigantea</i>	Asteraceae	Perennial	14
<i>Bidens frondosa</i>	Asteraceae	Annual	13
<i>Galeobdolon argentatum</i>	Lamiaceae	Perennial	13
<i>Galinsoga parviflora</i>	Asteraceae	Annual	12
<i>Galinsoga quadriradiata</i>	Asteraceae	Annual	12
<i>Lycium barbarum</i>	Solanaceae	Shrub	11
<i>Heracleum mantegazzianum</i>	Apiaceae	Monocarpic	10
<i>Cytisus scoparius</i>	Fabaceae	Shrub	10
<i>Veronica persica</i>	Scrophulariaceae	Annual	10
<i>Parthenocissus quinquefolia</i>	Vitaceae	Woody vine	9
<i>Amaranthus retroflexus</i>	Amaranthaceae	Annual	8
<i>Juncus tenuis</i>	Juncaceae	Perennial	8
<i>Matricaria discoidea</i>	Asteraceae	Annual	8
<i>Pinus strobus</i>	Pinaceae	Tree	8
<i>Reynoutria japonica</i>	Polygonaceae	Perennial	7
<i>Bunias orientalis</i>	Brassicaceae	Perennial	5
<i>Rumex thyrsoiflorus</i>	Polygonaceae	Perennial	4
<i>Aster novi-belgii</i> agg.	Asteraceae	Perennial	4
<i>Digitalis purpurea</i>	Scrophulariaceae	Monocarpic	4
<i>Populus ×canadensis</i>	Salicaceae	Tree	4
<i>Virga strigosa</i>	Dipsacaceae	Monocarpic	4
<i>Ailanthus altissima</i>	Simaroubaceae	Tree	3
<i>Telekia speciosa</i>	Asteraceae	Perennial	3
<i>Aster lanceolatus</i>	Asteraceae	Perennial	2
<i>Elodea canadensis</i>	Hydrocharitaceae	Aquatic	2
<i>Helianthus tuberosus</i>	Asteraceae	Perennial	2
<i>Impatiens glandulifera</i>	Balsaminaceae	Annual	2
<i>Oenothera biennis</i>	Onagraceae	Monocarpic	2
<i>Rhus hirta</i>	Anacardiaceae	Shrub	2

Species	Family	Life form	Number of reserves invaded
<i>Amorpha fruticosa</i>	Fabaceae	Shrub	1
<i>Aster ×salignus</i>	Asteraceae	Perennial	1
<i>Lupinus polyphyllus</i>	Fabaceae	Perennial	1
<i>Sedum hispanicum</i>	Crassulaceae	Perennial	1
<i>Veronica filiformis</i>	Scrophulariaceae	Perennial	1

Characteristics of exotic ants in North America

Daniela Wittenborn¹, Jonathan M. Jeschke^{1,2}

1 Ludwig-Maximilians-University Munich, Department of Biology II, Grosshaderner Str. 2, 82152 Planegg-Martinsried, Germany **2** Cary Institute of Ecosystem Studies, P.O. Box AB, Millbrook, NY 12545, USA

Corresponding author: *Jonathan M. Jeschke* (jonathan.jeschke@gmx.net)

Academic editor: *Sven Bacher* | Received 2 February 2011 | Accepted 27 June 2011 | Published 5 October 2011

Citation: Wittenborn D, Jeschke JM (2011) Characteristics of exotic ants in North America. *NeoBiota* 10: 47–64. doi: 10.3897/neobiota.10.1047

Abstract

The worldwide transport of species beyond their native range is an increasing problem, e.g. for global biodiversity. Many introduced species are able to establish in new environments and some even become invasive. However, we do not know which traits enable them to survive and reproduce in new environments. This study aims to identify the characteristics of exotic ants, and to quantitatively test previously postulated but insufficiently tested assumptions. We collected data on nine traits of 93 exotic ant species (42 of them being invasive) and 323 native ant species in North America. The dataset includes 2536 entries from over 300 different sources; data on worker head width were mostly measured ourselves. We analyzed the data with three complementary analyses: univariate and multivariate analyses of the raw data, and multivariate analyses of phylogenetically independent contrasts. These analyses revealed significant differences between the traits of native and exotic ant species. In the multivariate analyses, only one trait was consistently included in the best models, estimated with AIC_c values: colony size. Thus, of the nine investigated traits, the most important characteristic of exotic ants as compared to native ants appears to be their large colony size. Other traits are also important, however, indicating that native and exotic ants differ by a suite of traits.

Keywords

alien species, Formicidae, Hymenoptera, insects, invasions, invasives, North America, tramp ants

Introduction

Due to globalization, more and more species are being transported across the globe and introduced to regions where they did not occur before. Such species have taken step

1 of the invasion process (Kolar and Lodge 2001; Jeschke and Strayer 2005, 2006). Species that have also established one or more self-sustaining populations in the wild in their exotic range (step 2) are called exotic established species here. Those species that have additionally spread substantially from their point of introduction (step 3) are called exotic invasive species here. Although the term “invasive” is sometimes reserved for species with clear negative impacts, we are not restricting our definition of invasive species in this way. Certainly, however, many exotic invasive species do have devastating effects, e.g. on biodiversity or ecosystem services (Pimentel et al. 2005; Kettunen et al. 2009).

A central question of invasion biology has been which species with which characteristics are the ones that establish themselves and become invasive. What separates such species from those that have not established populations in exotic ranges? Most studies focusing on this question investigated plants and vertebrates (reviewed in Kolar and Lodge 2001; Jeschke and Strayer 2006; Richardson and Pyšek 2006), whereas only a few studies have looked at invertebrates (Mondor et al. 2007; Statzner et al. 2008; Šefrová and Laštůvka 2009). Here, we investigate this question for ants (Hymenoptera: Formicidae).

Most countries and regions of the world are now populated by numerous exotic ant species. Hawaii, for instance, has no native ants but 51 exotic established ant species (Starr et al. 2008). McGlynn (1999a) listed 147 ant species that have established themselves beyond their native range. Despite the existence of many invasive ants, most studies have focused on a few invasive ant species, e.g. the Argentine ant *Linepithema humile*, the big-headed ant *Pheidole megacephala*, or the red imported fire ant *Solenopsis invicta* (Holway et al. 2002). These species are also included in the Global Invasive Species Database's (2011) list of *100 of the World's Worst Invasive Alien Species*. As most studies on invasive ant species have focused on a few species, quantitative studies that compare many species have been largely lacking (but see McGlynn 1999b; Lester 2005; King and Porter 2007).

Despite this lack of formal quantitative analyses, exotic established and invasive ants are often assumed to have the following characteristics (Passera 1994; McGlynn 1999b; Holway et al. 2002; Tsutsui and Suarez 2003): their colonies have (1) more reproducing queens (polygyny) and (2) more workers than the colonies of native species; (3) they form new nests more frequently via budding than native species; and their workers are (4) more frequently monomorphic, (5) smaller, and (6) more frequently sterile than the workers of native or unsuccessfully introduced species. There are only few previous studies that quantitatively tested any of these six assumptions by comparing many ant species. With respect to assumption 5 that exotic ant species have smaller workers than native species, McGlynn (1999b) compared worker head width – a standard measure of body size in ants (Wilson 1980; Hölldobler and Wilson 1990; Kaspari 1993) – between 78 exotic and 233 native ants, finding that the workers of exotic ants are smaller than their native relatives. Lester (2005) similarly found for 66 species introduced to New Zealand that smaller species are better able to establish themselves than larger species. By contrast, King and Porter (2007) found no obvious

difference in body size between 94 native and 13 exotic ant species in Florida. Their results also do not support assumption 2 that exotic ant species form larger colonies than native species. In conclusion, quantitative tests of the six mentioned assumptions have been largely lacking, and the few tests that do exist had mixed results.

Using a dataset with more than 400 species, we quantitatively tested the six assumptions about the characteristics of exotic ants by comparing traits of exotic and native ant species in North America. These comparisons were done twice: once between exotic established ants and native ants, and once between exotic invasive ants and native ants. We expected that differences will be more pronounced for the latter comparison, as exotic invasive ants are the subset of exotic established ants that have successfully completed the full invasion process. If our analysis identifies traits that are related to the success of ant species in new environments, these traits should be more pronounced in the subset of invasive species.

Methods

Geographic Focus

We focused on regions that are particularly well investigated with respect to exotic ants: 14 states of the U.S. (Alabama, Arizona, Arkansas, California, Florida, Georgia, Illinois, Louisiana, Mississippi, Missouri, North Carolina, Ohio, South Carolina, and Tennessee) and one state of Mexico (Baja California). This study area has definite and naturally given borders (e.g. coastlines) and is part of the Nearctic and Neotropic bioregion, with mean annual temperatures from 10° C in northern Illinois and northern California, to 25° C in southern Baja California and southern Florida (Geodata 2011). The area includes not only a wide range of temperatures but also a diversity of biomes, thus covering a broad range of conditions.

Species List

Our species list is based on the database AntWeb (2009) which is hosted by the California Academy of Sciences and lists native as well as exotic ant species. We added further exotic species from literature sources (given in Appendix 1) and based on personal communications with other researchers (see Acknowledgements), giving a total of 416 ant species. The category Exo (exotic established ant species; $n = 93$ species) includes all species that were reported as exotic, introduced, alien, non-indigenous, or non-native in at least one of the above mentioned 15 states. Since the discovery and determination of an ant colony requires a certain amount of persistence of that colony, it seems likely that such exotic species have established at least one colony in the relevant state(s) and have thus completed the first two steps of the invasion process (see above). The category Inv (exotic invasive ant species; $n = 42$) is a sub-category of Exo and includes those

species of this category that were given as exotic, introduced, alien, non-indigenous, or non-native in at least two of the above mentioned 15 states. Due to their occurrence in at least two states, it seems likely that they have spread and have thus completed all three steps of the invasion process, even if this cannot be fully revealed. Ants can spread either by human transport over short to large distances (jump dispersal) or naturally over short distances by themselves. Given that 86% of the species in this category were reported as present in directly neighboring states, many of them have probably spread naturally. Independently of whether or not the species in this category really completed the full invasion process, most of them have been more successful in their exotic range than the other species in the category Exo which were only reported to be present in one state. We thus expect stronger differences between ants of this category Inv and native ants (Nat; $n = 323$ species) than between all exotic (category Exo) and native ants. Our complete species list is given in Appendix 2.

Traits

In a literature search until July 2009, we collected data on traits of the 416 ant species in our species list. The sources included scientific papers, books, websites, and personal communications with researchers (Appendix 1 and Acknowledgements). Synonyms and antiquated names of species were noticed. Tools for searching were Google, Google Scholar, Google Books, and the ISI Web of Science. The complete dataset with references for all data points is provided as Appendix 3. It includes 2536 data points from over 300 different sources; data on worker head width of 414 ant species were measured ourselves. The nine specific traits we analyzed are as follows:

A) Gyny – the degree of gyny, i.e. the number of reproductive queens (corresponding to assumption 1 mentioned in the Introduction; $n = 226$ species). We differentiated between obligate monogyny (only one functional queen; $n = 103$), obligate polygyny (two or more functional queens; $n = 67$), and facultative monogyny/polygyny ($n = 56$).

B) Colony size – the mean colony size, defined as the average number of workers in a colony (corresponding to assumption 2; $n = 227$). For exotic species, it is the average number of workers in colonies in both the native and exotic range. Since this trait only relates to the workers of each species, we excluded the two parasitic species *Pogonomyrmex colei* (Snelling) and *Anergatus atratulus* (Schenk) that do not have a worker caste.

C) Founding – how new nests are founded ($n = 190$), either by the queen alone (independent; $n = 144$), with the help of accompanying workers (dependent; $n = 35$), or a mix of these strategies ($n = 11$). The category “independent” includes claustral, semiclaustral, and pleometrotic founding strategies. The category “dependent” is applicable to species that found new nests via budding, splitting, sociotomy, or fission. This trait corresponds to assumption 3 in the Introduction, but to an extended version of this assumption, as only budding as a characteristic of exotic ants has been previously assumed and has thus been mentioned in the Introduction. We consequently extended assumption 3 to assumption 3a: Exotic ants form new nests more frequently

in a dependent way than native ants. With respect to forming new nests, we additionally included information on social parasitism in our dataset:

D) Parasitism ($n = 225$) – we differentiated between facultatively or obligately parasitic species ($n = 35$; e.g. optional slaveholders, dulotic ants, orinquilines) and non-parasitic species ($n = 190$). We assumed that parasites, which depend on their host species being present in the exotic range, are found less frequently among exotic than among native species (assumption 3b).

The remaining traits only concern the workers of each species. As for colony size, we again excluded the two species *Pogonomyrmex colei* and *Anergatus atratulus* that do not have a worker caste.

E) Morphs – the morphology of the workers ($n = 386$) with the following categories: monomorphic ($n = 265$), dimorphic ($n = 44$), or polymorphic ($n = 77$) worker caste. This trait corresponds to assumption 4 in the Introduction. For testing assumption 5 on worker body size, we used data on head width and total body length. For simplicity, no differentiation was made between monomorphic, dimorphic, and polymorphic ant species here.

F) HW (head width; $n = 414$) – since literature values were only available for less than half of the species in our dataset (HW1; $n = 178$), we measured head width for all species ourselves, using the software ImageJ (2009). These measurements (HW2; $n = 414$) were carried out with digital photographs, showing the frontal view of workers. Following Hölldobler and Wilson (1990), we measured maximum head width without the workers' eyes. We measured five individuals of each species (except where this was not possible due to lacking photos) and then calculated average head width. Photos were acquired from authoritative websites (AntWeb 2009; Discover Life 2009; Mississippi Entomological Museum 2009). As the data from the literature (HW1) were highly correlated with the data we measured ourselves (HW2) ($r = 0.954$; analysis performed for species where we had both HW1 and HW2; $n = 178$), we merged these two variables to HW, using the mean of HW1 and HW2 for species where both data were available.

G) TL (total body length) – an alternative measure of body size in ants is total body length ($n = 313$). We collected these data from the literature, thereby not discriminating between different methods to measure body length, as such information was often not provided.

H) Reproduction – the reproductive ability of workers ($n = 179$), discriminating workers that are sterile ($n = 90$; without ovarioles) from those that are potentially fertile ($n = 89$; able to produce males, trophic eggs, or are thelytoke, i.e. produce females). This trait corresponds to assumption 6.

I) Stinger ($n = 388$) – we discriminated workers with a functional stinger ($n = 232$) from those without a stinger or a rudimental or non-functional stinger ($n = 156$). This trait does not belong to an assumption mentioned in the Introduction. In fact, no clear assumption with respect to the frequency of a functional stinger in exotic as compared to native ant species can be found in the literature, possibly because two intuitively reasonable lines of thought lead to opposite expectations. On the one hand,

a functional stinger represents a weapon that might be beneficial to survive in an exotic environment, hence one could expect that workers of exotic ants are more frequently equipped with a stinger than those of native ants. On the other hand, the stinger is a phylogenetically primary trait that has been secondarily lost in many ant species of derived clades (Hölldobler and Wilson 1990), questioning the adaptive advantage of having a stinger under at least some environmental conditions. Analyzing our data on stinger presence may help assess which of these two conflicting lines of thought is more applicable to exotic ants in North America.

For all metric literature data (colony size, HW1, and TL), we adopted means reported in the literature for a given species. If no mean but only an interval was reported (minimal and maximal limits for di- or polymorphic species; colony sizes for different colony ages), we calculated the mean by averaging the minimal and maximal value of each interval. If data for a given trait and species were available from more than one source, we calculated the mean by averaging across sources.

Analyses

Comparisons were done between native (Nat) and exotic established (Exo) ants, and between native and exotic invasive (Inv) ants. We applied univariate analyses, multivariate analyses of the raw data, and multivariate analyses of phylogenetically corrected data. For the univariate analyses, we performed two different two-sample tests for each of our nine traits. In these tests, one sample consisted of Nat species; the other sample consisted of Exo species for the first test and of Inv species for the second test. In the multivariate analyses, the independent variables were the traits, and the dependent variable was the species category: Nat/Exo for the first comparison and Nat/Inv for the second comparison. In our analyses, we followed the approach taken by Jeschke and Strayer (2006, 2008) and Jeschke and Kokko (2008) to combine the strengths of univariate and multivariate analyses by performing both types of analysis and interpreting them jointly. Univariate analyses have the advantage that all species can be considered for which data on a certain trait are available. In multivariate analyses, however, only those species can be considered for which data on all traits are available. As our dataset includes empty cells, multivariate analyses will have a smaller sample size than univariate analyses. On the other hand, the species being lost in the multivariate analyses will be those that are not as well investigated as species for which data on all traits are available. The data on the latter species are thus probably more reliable, and some data of species additionally included in univariate analyses might not be reliable. An additional drawback of univariate analyses is that their results have to be interpreted with caution, as spurious correlations cannot be detected, and the relative importance of different variables for explaining observed variations cannot be inferred. The latter can only be achieved with multivariate analyses. As Jeschke and Strayer (2006, 2008) and Jeschke and Kokko (2008), we performed two types of multivariate analyses: one with the raw data and one with phylogenetically corrected data. Details of these three com-

plementary analyses – (A) univariate analyses of the raw data, (B) multivariate analyses of the raw data, and (C) multivariate analyses of phylogenetically independent contrasts – follow in the next paragraphs. Their complexity increases from A to C, while their sample size decreases. When interpreting the results, we consider all three analyses jointly. For the reasons given above, however, we put most weight on the multivariate analyses of phylogenetically independent contrasts. If not stated otherwise, statistical analyses were performed with PASW Statistics version 17.0.

A) For the univariate analyses, we ran two-tailed binomial tests for the binary variables parasitic, reproduction, and stinger; *U*-tests were done for the ordinal variables gyny, founding, and morphs; and *t*-tests for unequal variances were run for the metric variables HW, TL, and colony size.

B) As mentioned above, multivariate analyses can only consider those species for which data on all included variables are available. As our dataset includes empty cells, reducing the number of variables in the multivariate analysis increases the number of species in the analysis and thus the sample size. This is one reason why it is necessary to consider *a priori* knowledge and thoroughly think about which variables should be included in a multivariate analysis and which should be excluded; further reasons are given in Burnham and Anderson (2002). We excluded the variable TL (total body length), as it was available for fewer species than HW (head width), the other variable quantifying body size. We also excluded the variable parasitism from the multivariate analyses, as it was uninformative in the reduced dataset of the multivariate analyses: all species in the reduced dataset were non-parasitic. The remaining seven traits were included as independent variables in the multivariate analyses: gyny, colony size, founding, HW, morphs, reproduction, and stinger. The species list decreased to $n = 70$ for the comparison of native and exotic established ants, and to $n = 60$ for the comparison of native and exotic invasive ants. For all combinations of traits, but excluding interactions, we calculated multiple logistic regressions (due to our binary dependent variables: Nat, Exo, and Inv). For each of the two comparisons, we thus calculated $2^7 - 1 = 127$ regression models. We evaluated the models by means of AIC_c values (Akaike's information criterion corrected for small sample size, Burnham and Anderson 2002).

C) As our data quantify traits of species that are phylogenetically related to each other, they are not independent of each other. To correct for this phylogenetic dependence, we calculated phylogenetically independent contrasts (Felsenstein 1985; Garland et al. 1992, 1999, 2005; Pagel 1992), using Mesquite version 2.71 (Maddison and Maddison 2009) and the PDAP module version 1.14 (Midford et al. 2008). Branch lengths were set according to Pagel's (1992) method. The phylogeny was taken from the literature and is freely available from the authors upon request (sources are provided in Appendix 1). A drawback is that phylogenetic relationships among ant species are not fully resolved, which is one reason why the results of raw-data multivariate analyses should be considered as well. Another reason is that similarities and differences between both types of analyses are informative (Garland et al. 1999). Independent contrasts are not binary, so we ran linear regressions in this case that were forced through the origin, which is necessary when analyzing independent contrasts (Garland et al. 1992). The same traits and reduced datasets were used as for multivariate analyses of the raw data.

Results

The above mentioned existing assumptions on differences between exotic and native ant species are supported by the univariate analyses. As expected, ant species that are exotic in North America (Exo and Inv) are more often polygynous than native (Nat) species (assumption 1; Fig. 1a; for both comparisons, Nat vs. Exo and Nat vs. Inv, $p < 0.001$) and form new nests more frequently in a dependent way (assumption 3a; Fig. 1b; both $p < 0.001$). Social parasitism is infrequent among all ant species but especially rare among exotic established (3%) and invasive (0%) species (native species: 20%; assumption 3b; Fig. 1c; both $p < 0.001$). Workers of exotic ants are mostly monomorphic, whereas those of native species tend to be more polymorphic (assumption 4; Fig. 1d; $p < 0.001$ and $p < 0.05$, respectively). Furthermore, head widths of exotic established (mean = 0.725 mm; SE = 0.037) and invasive species (mean = 0.699 mm; SE = 0.050) are significantly smaller than those of native species (mean = 1.051 mm; SE = 0.032) (assumption 5; Fig. 2a; both $p < 0.001$). As expected, the differences for total body length (TL) are similar to those of head width: workers of exotic established (mean = 2.99 mm; SE = 0.17) and invasive species (mean = 2.81 mm; SE = 0.24) have significantly shorter bodies than those of native species (mean = 4.22 mm; SE = 0.13) (both $p < 0.001$). Sterility is more frequent among workers of exotic established (78%) and invasive (93%) species than among natives (40%) (assumption 6; Fig. 1e; both $p < 0.001$). Finally, colonies of exotic established (mean \approx 123037; SE \approx 63591) and invasive species (mean \approx 136777; SE \approx 87659) are larger than those of native species (mean \approx 6265; SE \approx 1688) (assumption 2; Fig. 2b), but differences are not significant here. Please note that colony size is highly variable, however, ranging from five individuals to millions of workers for the species analyzed here. Thus, all assumed trait differences (assumptions 1–6) are shown by the data and are significant in the univariate analyses except for colony size which is highly variable. Still, the trend shown by the data for colony size is in the assumed direction. Also as expected, differences between exotic and native species are usually more pronounced if only exotic invasive species are compared with the native species. With respect to the presence of a functional stinger, workers of exotic established (72%) and invasive (76%) ants are significantly more frequently equipped with a functional stinger than those of native species (56%) (Fig. 1f; both $p < 0.01$).

Only multivariate analyses can reveal the relative importance of traits to differentiate between exotic and native ant species. In the four types of multivariate analyses that we performed, the only variable that is included in all models with substantial empirical support (Akaike weight $\omega_i \geq 0.05$, Table 1) is colony size, suggesting that a large colony size is the most important characteristic of exotic ants as compared to native ants in North America. The mode of colony founding and the reproductive ability of workers also appear to be particularly important variables to differentiate between exotic and native ant species, as they are included in many models with substantial empirical support. The remaining variables seem less important.

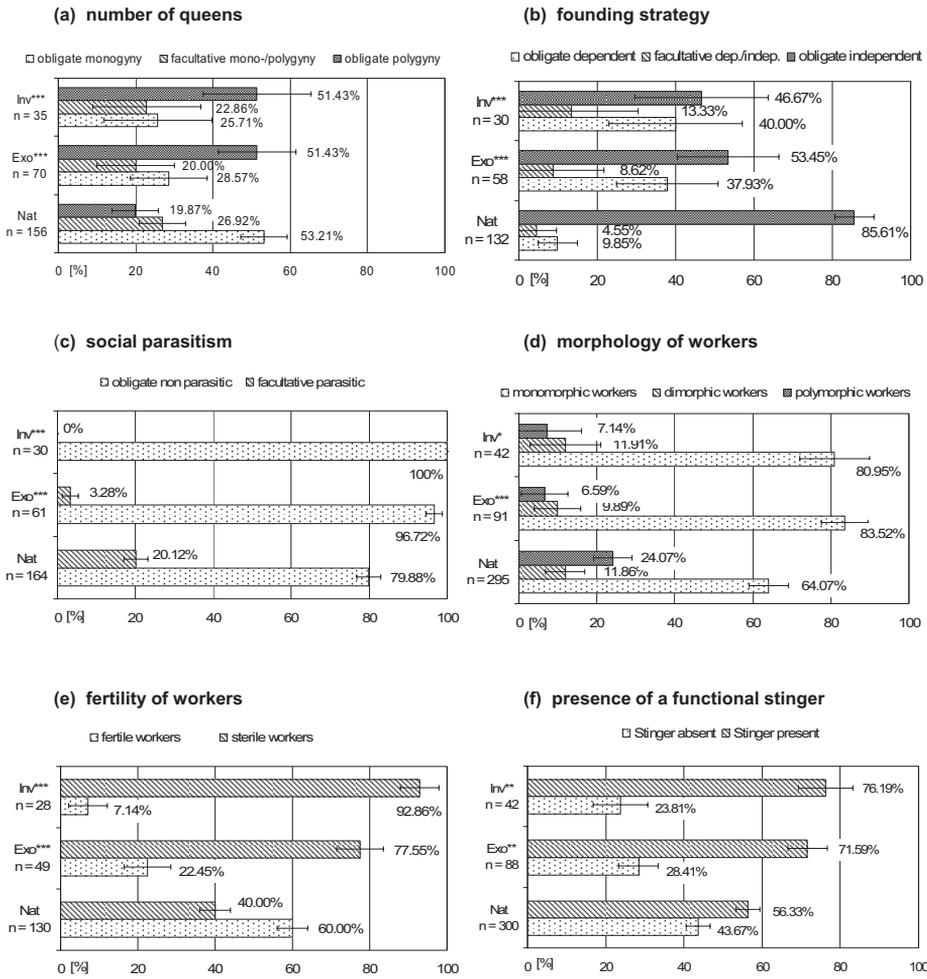


Figure 1. Results of univariate analyses, categorical traits. Differences among native (Nat), exotic established (Exo), and exotic invasive (Inv) ants in North America. Illustrated are means \pm SE. Asterisks indicate significant differences between native and exotic established species, and between native and exotic invasive species: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Discussion

We examined traits of exotic and native ant species in North America in order to test previously postulated but insufficiently tested assumptions on the characteristics of exotic ant species. Our results support all investigated assumptions. Thus indeed, colonies of exotic ant species have more reproducing queens (polygyny; assumption 1) and more workers (assumption 2) than colonies of native species; they form new nests more frequently in a dependent way than native species (assumption 3a); parasites

Table 1. Results of multivariate analyses. Shown are multivariate regression models with substantial empirical support, i.e. with Akaike weights $\omega_i \geq 0.05$, calculated on the basis of $\Delta_i AIC_c$ values which are shown as well. Models with low empirical support, i.e. with Akaike weights $\omega_i < 0.05$, are not shown. Each regression model compared native ants with either exotic established or exotic invasive ants, as indicated. Model inputs were either raw data or phylogenetically independent contrasts, also as indicated. Each model included the given variables' main effects.

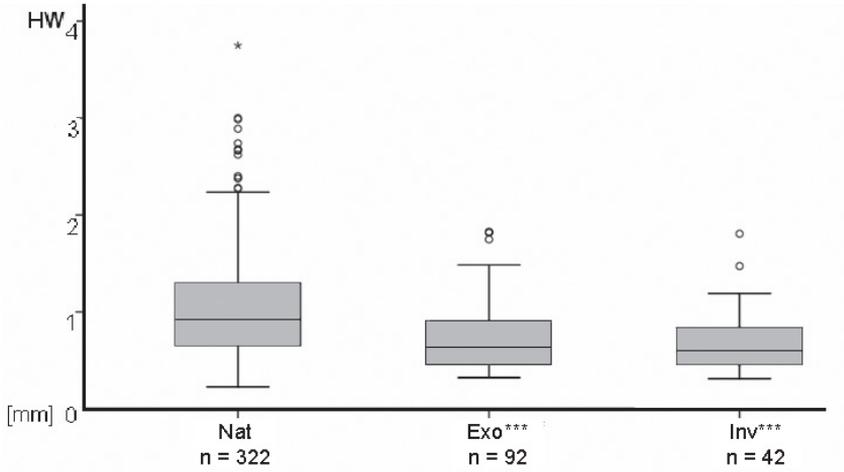
Model (variables included)	$\Delta_i AIC_c$	ω_i
<i>Exotic established ants, raw data</i>		
Colony size, founding, reproduction, morphs	0	0.203
Colony size, founding, reproduction, morphs, gyny	0.267	0.178
Colony size, founding, reproduction, morphs, HW	0.686	0.144
Colony size, founding, reproduction, morphs, gyny, HW	1.879	0.079
Colony size, founding, reproduction, morphs, stinger	2.467	0.059
Colony size, founding, reproduction, morphs, gyny, stinger	2.568	0.056
<i>Exotic established ants, independent contrasts</i>		
Colony size, founding	0	0.089
Colony size, founding, reproduction	0.983	0.055
Colony size, founding, stinger	1.011	0.054
<i>Exotic invasive ants, raw data</i>		
Colony size, founding, reproduction, morphs, gyny	0	0.428
Colony size, founding, reproduction, morphs, gyny, stinger	1.268	0.227
Colony size, founding, reproduction, morphs, gyny, HW	2.350	0.132
Colony size, founding, reproduction, morphs, gyny, HW, stinger	3.752	0.066
<i>Exotic invasive ants, independent contrasts</i>		
Colony size, reproduction	0	0.202
Colony size, reproduction, HW	1.264	0.107
Colony size, reproduction, founding	1.762	0.084
Colony size, reproduction, morphs	2.267	0.065
Colony size, reproduction, gyny	2.295	0.064
Colony size, reproduction, stinger	2.300	0.064

are found less frequently among exotic than among native species (assumption 3b); and the workers of exotic species are more frequently monomorphic (assumption 4), smaller (assumption 5), and more frequently sterile than the workers of native species (assumption 6). As expected, differences between exotic invasive and native species are more pronounced and in the same direction than differences between exotic established and native species.

Of the six assumptions, only assumptions 2 and 5 were, to our knowledge, previously tested (see Introduction). Assumption 2, which says that exotic ant species tend to form larger colonies than native species, has been previously tested by King and Porter (2007) who had mixed results depending on the inclusion or exclusion of the red imported fire ant *Solenopsis invicta* in their analysis. Our results are based on a much larger dataset and support assumption 2.

Our results also support assumption 5, which says that the workers of exotic ant species are smaller than those of native species, and are in line with previous tests of this

(a) head width of workers



(b) colony size

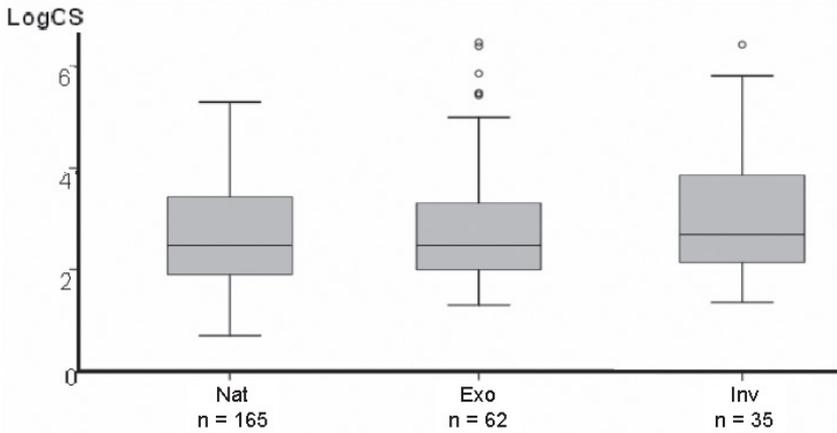


Figure 2. Results of univariate analyses, metric traits. Differences among native (Nat), exotic established (Exo), and exotic invasive (Inv) ants in North America. Asterisks indicate significant differences between native and exotic established species, and between native and exotic invasive species: *** $p < 0.001$ **a** Nat: median = 0.923 (range: 0.227 to 3.750), mean = 1.051 (SE = 0.032); Exo: median = 0.633 (range: 0.322 to 1.828), mean = 0.725 (SE = 0.037); Inv: median = 0.609 (range: 0.323 to 1.818), mean = 0.699 (SE = 0.050) **b** Nat: median = 296 (range: 5 to 200000), mean = 6265 (SE = 1688); Exo: median = 300 (range: 20 to 3000000), mean = 123037 (SE = 63591); Inv: median = 550 (range: 25 to 3000000), mean = 136777 (SE = 87659); differences between Nat and Exo ($p = 0.071$) and Nat and Inv ($p = 0.146$) were not significant here. Please note that the y -axis is \log_{10} -scaled here.

assumption by McGlynn (1999b) and Lester (2005), whereas King and Porter (2007) did not find an obvious difference in body size between exotic and native ant species. As mentioned above (Methods), we did not differentiate between monomorphic, dimorphic, and polymorphic ant species when measuring body size but simply used the average of five individuals. This approach was also used by King and Porter (2007), thus it cannot explain different results between their and our study. McGlynn (1999b) only used monomorphic species to avoid this problem. Using this approach for our dataset, thus restricting the analysis to monomorphic species, does not change our finding that workers of exotic ant species are typically smaller than workers of native ant species: Nat ($n = 189$): median = 0.781 (range: 0.227 to 2.380), mean = 0.829 (SE = 0.030); Exo ($n = 76$): median = 0.599 (range: 0.322 to 1.828), mean = 0.671 (SE = 0.039); Inv ($n = 34$): median = 0.564 (range: 0.323 to 1.818), mean = 0.653 (SE = 0.056). Both differences, between native and exotic species ($p < 0.01$) and between native and invasive species ($p < 0.01$), also remain significant for the restricted dataset. Another approach to correct body size for polymorphism was applied by Lester (2005) who measured the smallest and largest available ant for each species. Neither approach – taking the average of measured individuals, restricting the analysis to monomorphic species, or measuring the smallest and largest available ant – is perfect, and this point demands further attention in future studies. Given currently available evidence, however, it seems that the workers of exotic ant species really are often smaller than the workers of native species.

Our results show that exotic ants have a suite of characteristics that separate them from the native ant fauna of North America (Table 2). The most important of these characteristics is, according to our multivariate analyses, colony size, followed by the founding strategy and reproductive ability of workers. Indeed, the univariate tests for differences in colony size were not significant, whereas the multivariate analyses identified this variable as the most important characteristic of exotic ants in North America. The non-significant results of the univariate analyses are less surprising when considering the huge variation in this trait, ranging from five individuals to several millions. Still, the trend shown by the univariate analyses was consistent with the multivariate analyses that exotic ant species have larger colonies than native species. Also, more weight should be put on the multivariate analyses, for the reasons given above in the Methods section. Within exotic species, there was a trend that exotic invasive species have larger colonies than exotic established species. It is reasonable that larger colonies have an advantage over smaller ones, especially when they are competing or even fighting with each other. A challenge with colony size is data availability: as the size of a colony depends on its stage (founding stage, ergonomic stage, or reproductive stage; Hölldobler and Wilson 1990), it would be desirable to compare colony size by correcting for colony stage. This was not possible for the current study due to lack of data. Another question is whether colony size of exotic species should be measured only in the native range, only in the exotic range, or in both ranges. We decided to take the average colony size in both ranges, as this measure best represents a species' overall average colony size. Other approaches are possible as well, but any approach currently suffers from the shortage of data on colony size. Once more data are available, it should be tested if colony size remains the most important characteristic of exotic ants.

Table 2. Summary of the combined results. Listed is the suite of traits that characterize exotic as compared to native ants, based on this study's results.

Characteristics of exotic ants
Large colony size
New nests founded by queen with workers [†] rather than queen alone
Not socially parasitic on other ants
Sterile workers
Monomorphic workers
More than one queen per colony (polygyny)
Small body size
Equipped with a functional stinger

[†]Dependent nest founding, either via budding, splitting, sociotomy, or fission.

In addition to colony size, the sterility of workers is an important characteristic of exotic ant species in North America, which is in line with the literature (Passera 1994; Holway et al. 2002). Species with large colonies consisting of sterile workers have a high probability to spread and thus to become invasive. Sterile workers do not invest their resources and those of their colony in their own reproduction, hence reproductive rivalries with the queen(s) or other workers are avoided (e.g. worker policing). Besides a large colony size and worker sterility, our results also show that exotic ants form new nests more frequently in a dependent way than native species, either via budding, splitting, sociotomy, or fission. Such a nest-founding strategy reduces the risk of the queen to die of starvation or predation. The queen can dedicate her resources to reproduction while the accompanying workers take care of foraging, defense, brood care, and other tasks.

Besides testing previously postulated assumptions, we also investigated if workers of exotic ant species differ from those of native ant species in the presence of a functional stinger. Our analyses revealed such a difference, showing that workers of exotic ant species are more frequently equipped with a functional stinger than workers of native ant species. Within exotic species, a functional stinger is more frequent in exotic invasive than exotic established species. These findings support the line of thought mentioned above that a functional stinger is a weapon that helps to survive in an exotic environment. Our dataset also showed a significant relationship of stinger presence with worker body size: workers of species with a functional stinger are smaller (mean head width in mm = 0.788, SE = 0.026, $n = 232$) than those of species without a functional stinger (mean = 1.259, SE = 0.052, $n = 156$) ($p < 0.001$, two-tailed t -test for unequal variances). Thus, species with large workers appear to often have lost their stinger in the course of evolution, probably because their large size is sufficient to be competitive. In species with small workers, on the other hand, the stinger may at least partly compensate for the size disadvantage.

A weakness of our dataset is that it does not include information on ant species that were introduced to North America but did not establish there. Even although sub-samples of ant species introduced to North America exist (Suarez et al. 2005), it is impossible to know all ant species that were introduced to North America and all that were not. We can, however, speculate to which extend observed differences between ex-

otic and native ant species are influenced by an introduction bias (Blackburn and Duncan 2001; Cassey et al. 2004; Jeschke and Strayer 2006; Blackburn and Jeschke 2009; van Kleunen et al. 2010). An introduction bias with respect to body size seems likely: Introductions of ants and other invertebrates are typically unintentional (Hulme et al. 2008), and since it is easier for small organisms than for large ones to remain undetected by the human eye, small ant species are probably more frequently introduced to North America than large species (see Mondor et al. (2007) and Šefrová and Laštůvka (2009) for similar arguments on aphids and lepidopterans, respectively). It is thus possible that observed differences between exotic and native ant species in body size are at least partly attributable to an introduction bias. There might be introduction biases with respect to other investigated traits as well, but they are less obvious and possibly less pronounced.

Another weakness of this study is that it can only provide correlative patterns rather than causative findings. For example, our finding that exotic ants have larger colonies than native ants does not necessarily imply that they successfully established *because* they form larger colonies. Despite limitations of this study, it may nonetheless contribute to a better understanding of exotic ant species. Together with a few other studies, this study also sheds light on differences between native and exotic invertebrates. Combining these differences with those found for vertebrates and plants will substantially improve our understanding of the general characteristics of exotic as compared to native species.

Acknowledgements

We thank S. Foitzik, K. Ivanov, R.A. Johnson, L. Keller, J.T. Longino, T. McGlynn, J. Ness, G.C. Snelling, P.S. Ward, and V. Witte for providing us with important advice and information. J.D. Olden, V. Witte, and two anonymous reviewers provided comments on the manuscript. Financial support was received from the Deutsche Forschungsgemeinschaft (JE 288/2-1, JE 288/4-1).

References

- AntWeb (2009) <http://www.antweb.org> (last access: August 2009).
- Blackburn TM, Duncan RP (2001) Establishment patterns of exotic birds are constrained by non-random patterns in introduction. *Journal of Biogeography* 28: 927–939. doi: 10.1046/j.1365-2699.2001.00597.x
- Blackburn TM, Jeschke JM (2009) Invasion success and threat status: two sides of a different coin? *Ecography* 32: 83–88. doi: 10.1111/j.1600-0587.2008.05661.x
- Burnham KP, Anderson DR (2002) *Model selection and multimodel inference*. 2nd edition. Springer (New York): 1–488.
- Cassey P, Blackburn T, Russell GJ, Jones KE, Lockwood JL (2004) Influences on the transport and establishment of exotic bird species: an analysis of the parrots (Psittaciformes) of the world. *Global Change Biology* 10: 417–426. doi: 10.1111/j.1529-8817.2003.00748.x

- Discover Life (2009) <http://www.discoverlife.org> (last access: May 2009).
- Felsenstein J (1985) Phylogenies and the comparative method. *American Naturalist* 125: 1–15. doi: 10.1086/284325
- Garland T Jr, Bennett AF, Rezende EL (2005) Phylogenetic approaches in comparative physiology. *Journal of Experimental Biology* 208: 3015–3035. doi: 10.1242/jeb.01745
- Garland T Jr, Harvey PH, Ives AR (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* 41: 18–32.
- Garland T Jr, Midford PE, Ives AR (1999) An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. *American Zoologist* 39: 374–388.
- Geodata (2011) <http://gos2.geodata.gov/wps/portal/gos> (last access: January 2011).
- Global Invasive Species Database (2011) <http://www.issg.org/database> (last access: January 2011).
- Hölldobler B, Wilson EO (1990) *The ants*. Harvard University Press (Cambridge): 1–745.
- Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ (2002) The causes and consequences of ant invasions. *Annual Review of Ecology and Systematics* 33: 181–233. doi: 10.1146/annurev.ecolsys.33.010802.150444
- Hulme PE, Bacher S, Kenis M, Klotz S, Kühn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pyšek P, Roques A, Sol D, Solarz W, Vilà M (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *Journal of Applied Ecology* 45: 403–414. doi: 10.1111/j.1365-2664.2007.01442.x
- Jeschke JM, Kokko H (2008) Mortality and other determinants of bird divorce rate. *Behavioral Ecology and Sociobiology* 63: 1–9. doi: 10.1007/s00265-008-0646-9
- Jeschke JM, Strayer DL (2005) Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences USA* 102: 7198–7202. doi: 10.1073/pnas.0501271102
- Jeschke JM, Strayer DL (2006) Determinants of vertebrate invasion success in Europe and North America. *Global Change Biology* 12: 1608–1619. doi: 10.1111/j.1365-2486.2006.01213.x
- Jeschke JM, Strayer DL (2008) Are threat status and invasion success two sides of the same coin? *Ecography* 31: 124–130. doi: 10.1111/j.2007.0906-7590.05343.x
- Kaspari M (1993) Body size and microclimate use in neotropical granivorous ants. *Oecologia* 96: 500–507. doi: 10.1007/BF00320507
- Kettunen M, Genovesi P, Gollasch S, Pagad S, Starfinger U, ten Brink P, Shine C (2009) Technical support to EU strategy on invasive alien species (IAS) – Assessment of the impacts of IAS in Europe and the EU. Institute for European Environmental Policy (Brussels, Belgium): 1–44 + Annexes.
- King JR, Porter SD (2007) Body size, colony size, abundance, and ecological impact of exotic ants in Florida's upland ecosystems. *Evolutionary Ecology Research* 9: 757–774.
- Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* 16: 199–204. doi: 10.1016/S0169-5347(01)02101-2
- Lester PJ (2005) Determinants for the successful establishment of exotic ants in New Zealand. *Diversity and Distributions* 11: 279–288. doi: 10.1111/j.1366-9516.2005.00169.x

- Maddison WP, Maddison DR (2009) Mesquite: a modular system for evolutionary analysis. Version 2.71. <http://mesquiteproject.org>.
- McGlynn TP (1999a) The worldwide transfer of ants: geographical distribution and ecological invasions. *Journal of Biogeography* 26: 535–548. doi: 10.1046/j.1365-2699.1999.00310.x
- McGlynn TP (1999b) Non-native ants are smaller than related native ants. *American Naturalist* 154: 690–699. doi: 10.1086/303270
- Midford PE, Garland T Jr, Maddison WP (2008) PDAP Package of Mesquite. Version 1.14. http://mesquiteproject.org/pdap_mesquite.
- Mississippi Entomological Museum (2009) <http://mississippientomologicalmuseum.org.msstate.edu/index.html> (last access: June 2009).
- Mondor EB, Tremblay MN, Messing RH (2007) Morphological and ecological traits promoting aphid colonization of the Hawaiian Islands. *Biological Invasions* 9: 87–100. doi: 10.1007/s10530-006-9010-z
- Pagel MD (1992) A method for the analysis of comparative data. *Journal of Theoretical Biology* 156: 431–442. doi: 10.1016/S0022-5193(05)80637-X
- Passera L (1994) Characteristics of tramp species. In: Williams DF (Ed) *Exotic ants – biology, impact and control of introduced species*. Westview Press (Oxford): 23–43.
- 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. doi: 10.1016/j.ecolecon.2004.10.002
- Rasband WS (2009) ImageJ. U.S. National Institutes of Health, Bethesda, Maryland.
- Richardson DM, Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invisibility. *Progress in Physical Geography* 30: 409–431. doi: 10.1191/0309133306pp490pr
- Šefrová H, Laštůvka Z (2009) Do invasive species of Lepidoptera in the Czech Republic share traits favouring introduction and invasion? *Neobiota* 8: 87–100.
- Starr F, Starr K, Loop LL (2008) Survey for ants on the island of Maui, Hawaii, with emphasis on the little fire ant (*Wasmannia auropunctata*). Technical Report 156, University of Hawai'i (Manoa, Hawai'i): 1–47.
- Statzner B, Bonada N, Dolédec S (2008) Biological attributes discriminating invasive from native European stream macroinvertebrates. *Biological Invasions* 10: 517–530. doi: 10.1007/s10530-007-9148-3
- Suarez AV, Holway DA, Ward PS (2005) The role of opportunity in the unintentional introduction of nonnative ants. *Proceedings of the National Academy of Sciences USA* 102: 17032–17035. doi: 10.1073/pnas.0506119102
- Tsutsui ND, Suarez AV (2003) The colony structure and population biology of invasive ants. *Conservation Biology* 17: 48–58. doi: 10.1046/j.1523-1739.2003.02018.x
- van Kleunen M, Dawson W, Schlaepfer D, Jeschke JM, Fischer M (2010) Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecology Letters* 13: 947–958. doi: 10.1111/j.1461-0248.2009.01418.x
- Wilson EO (1980) Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*). I. The overall pattern in *A. sexdens*. *Behavioral Ecology and Sociobiology* 7: 143–156. doi: 10.1007/BF00299520

Appendix 1

Literature sources. (doi: 10.3897/neobiota.10.1047.app1) File format: PDF.

Explanation note: This file lists all literature sources for our dataset, phylogeny, and species list.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Citation: Wittenborn D, Jeschke JM (2011) Characteristics of exotic ants in North America. *NeoBiota* 10: 47–64. doi: 10.3897/neobiota.10.1047.app1

Appendix 2

Species list. (doi: 10.3897/neobiota.10.1047.app2) File format: PDF.

Explanation note: This file lists all species included in our analyses. The species are subdivided into native, exotic established, and exotic invasive ant species.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Citation: Wittenborn D, Jeschke JM (2011) Characteristics of exotic ants in North America. *NeoBiota* 10: 47–64. doi: 10.3897/neobiota.10.1047.app2

Appendix 3

Dataset. (doi: 10.3897/neobiota.10.1047.app3) File format: Excel spreadsheet (xls).

Explanation note: This file provides our complete dataset with references for all data points.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL)

is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Citation: Wittenborn D, Jeschke JM (2011) Characteristics of exotic ants in North America. *NeoBiota* 10: 47–64. doi: 10.3897/neobiota.10.1047.app3

Impact scores of invasive plants are biased by disregard of environmental co-variation and non-linearity

Jan Thiele¹, Maike Isermann², Johannes Kollmann³, Annette Otte⁴

1 University of Münster, Institute of Landscape Ecology, Robert-Koch-Strasse 28, 48149 Münster, Germany
2 University of Bremen, Vegetation Ecology and Conservation Biology, Leobener Strasse, NW 2, 28359 Bremen, Germany
3 Technische Universität München, Restoration Ecology, Emil-Ramann-Strasse 6, 85354 Freising, Germany
4 University of Giessen, Division of Landscape Ecology and Landscape Planning, Heinrich-Buff-Ring 26, 35392 Giessen, Germany

Corresponding author: Jan Thiele (jan.thiele@uni-muenster.de)

Academic editor: Franz Essl | Received 2 March 2011 | Accepted 18 May 2011 | Published 5 October 2011

Citation: Thiele J, Isermann M, Kollmann J, Otte A (2011) Impact scores of invasive plants are biased by disregard of environmental co-variation and non-linearity. NeoBiota 10: 65–79. doi: 10.3897/neobiota.10.1191

Abstract

Prioritisation of high-impact species is becoming increasingly important for management of introduced species ('neobiota') because of their growing number of which, however, only a small fraction has substantial impacts. Impact scores for prioritising species may be affected by the type of effect model used. Recent studies have shown that environmental co-variation and non-linearity may be significant for effect models of biological invasions. Here, we test for differences in impact scores between simple and complex effect models of three invasive plant species (*Heracleum mantegazzianum*, *Lupinus polyphyllus*, *Rosa rugosa*).

We investigated the effects of cover percentages of the invasive plants on species richness of invaded communities using both simple linear effect models ('basic models') and more complex linear or non-linear models including environmental co-factors ('full models'). Then, we calculated impact scores for each invasive species as the average reduction of species richness predicted by basic and full effect models.

All three non-native species had negative effects on species richness, but the full effect models also indicated significant influence of habitat types. *Heracleum mantegazzianum* had uniform linear effects in all habitats, while effects of *L. polyphyllus* interacted strongly with habitat type, and *R. rugosa* showed a marked non-linear relationship. Impact scores were overestimated by basic effect models for *H. mantegazzianum* and *R. rugosa* due to disregard of habitat effects and non-linearity, respectively. In contrast, impact of *L. polyphyllus* was underestimated by the basic model that did not account for the strong interaction of invader cover and habitat type.

We conclude that simple linear models will often yield inaccurate impact scores of non-native species. Hence, effect models should consider environmental co-variation and, if necessary, non-linearity of the effects of biological invasions on native ecosystems.

Keywords

effect model, *Heracleum mantegazzianum*, impact assessment, *Lupinus polyphyllus*, management, non-native, prioritisation, *Rosa rugosa*

Introduction

Impacts differ in quality and quantity among introduced species ('neobiota'). Many non-indigenous species can be considered neutral, but some have severe implications for native biodiversity, ecosystems, human health and economy (Gaertner et al. 2009, Hejda et al. 2009, Goodenough 2010). Globally, roughly 1% of the introduced species have become invasive with substantial impacts (i.e. invaders sensu Davis and Thompson 2000), but this proportion varies among regions and is likely to increase with longer residence times (Williamson 1996, Richardson and Pysek 2006). The human and financial resources available for management of biological invasions do not allow controlling all invasive species. Hence, it is increasingly necessary to prioritise management of neobiota according to rankings of their impacts (Parker et al. 1999, Byers et al. 2002, Thiele et al. 2010a).

Different approaches have been taken to study the impact of invasive species. Regarding species richness of invaded communities, for instance, removal or seed-addition experiments have been used (Meffin et al. 2010), as well as comparisons of invaded and uninvaded sites (Adams and Engelhardt 2009, Hejda et al. 2009, Flory and Clay 2010, Maurel et al. 2010), multi-year studies of expanding margins of invasive stands (Brewer 2008), comparisons of different stages of invasion (Prévosto et al. 2006), and correlational studies of gradients of invader abundance (Isermann et al. 2007, Gooden et al. 2009). All these approaches have their pros and cons concerning inference about invader impacts (cf. Adams and Engelhardt 2009, Meffin et al. 2010).

For impact assessment, according to the framework provided by Parker et al. (1999), and expanded by Thiele et al. (2010a), it is advantageous to relate invader effects to direct measures of invader abundance or equivalent measures, because the density of stands of a specific invasive species and the consequent impacts may vary among invaded sites, forming continuous gradients. Further, the relationship of effect and invader abundance may be non-linear which may affect impact estimates and also management decisions (Yokomizo et al. 2009).

Relationships of invader abundance and ecosystem traits may be modified by environmental factors (Houlihan and Findlay 2004, Surrrette and Brewer 2008), so that one actually has to deal with a triangular relationship. A negative correlation may partly be the result of environmental conditions facilitating the invasion, while constraining the ecosystem trait. For instance, disturbance events that destroy most biomass of a given plant community may reduce species numbers, but could increase the abundance of invasive plant species. So, a negative relationship of invader abundance and species richness among sites with different disturbance regimes may be caused by environmental factors, instead of being a genuine effect of the invader. Moreover, effects of

an invasive species on a particular ecosystem trait often vary among habitat types. For example, invasion of a tree species may decrease the cover of native herbaceous plants in a formerly treeless habitat, whereas it even could facilitate native species in forests, as has been shown for *Cinchona* spp. (Fischer et al. 2009, Jäger et al. 2009). Different or contrasting effects can be modelled as interactions of invader abundance and habitat type. Although it is important to include environmental variables into effect models of invasive species, the potential strength of the influence of environmental variation on impact scores has rarely been tested.

The aim of the present study was to assess to which extent impact scores of invasive species are affected by environmental variation, and by choice of a linear vs. non-linear effect model. We used empirical data of three invasive plant species for model building and calculation of impact scores. Richness of vascular plant species of invaded communities was chosen as response variable.

Methods

Study species and field data

We used three plant species, *Heracleum mantegazzianum*, *Lupinus polyphyllus* and *Rosa rugosa*, that are invasive and widespread in Europe; all three are able to form dominant stands with >90% cover (Thiele et al. 2010b).

Heracleum mantegazzianum (Apiaceae) is a monocarpic tall herb native to the Western Greater Caucasus. It invades mesic grasslands, waste ground, riverbanks, roadsides and forest edges where it forms tall-herb stands (Tiley et al. 1996, Pyšek et al. 2007).

Lupinus polyphyllus (Fabaceae) is a nitrogen-fixing perennial tall herb from Pacific North America that spreads by seeds and rhizomes. In Central Europe, it mainly invades unimproved and mesic grasslands in mountain areas and transforms them into tall-herb stands, especially when grassland management is abandoned (Otte et al. 2002, Otte and Maul 2005).

Rosa rugosa (Rosaceae) is a shrub originating from the Pacific coasts of East Asia. In Europe, it mainly invades coastal habitats, but it can also become invasive on inland habitats, such as *Calluna* heath (Bruun 2005, Kollmann et al. 2007, Isermann 2008, Thiele et al. 2009).

We estimated cover percentages of the invasive study species and recorded all vascular plant species on plots of 16, 25 or 100 m² (see Table 1) that were established in different communities invaded by the study species. In *H. mantegazzianum* all plots were situated inside of invaded areas, while in *L. polyphyllus* and *R. rugosa*, sampling also included areas adjacent to invaded stands, but still inside of the same plant community. Cover percentages of the invaders ranged between zero and (almost) 100% percent. Details on the datasets are given in Table 1.

The plots were assigned to habitat types based on plant communities of Central Europe (see Ellenberg 2009) or, in few cases, based on physiognomy, land use and

Table 1. Characteristics of the datasets used for effect modelling and for calculating impact scores.

	<i>Heracleum mantegazzianum</i>	<i>Lupinus polyphyllus</i>	<i>Rosa rugosa</i>
Plot size (m ²)	25	25, 100	16
No. of plots	202	80	63
Sampling years	2002, 2003	1998, 2001	2001
Invader cover (%)			
Minimum	1	0	0
Mean	37	22	44
Maximum	95	90	100
Study regions	Western, central and southern Germany (22 areas)	Central Germany (Rhön mountains)	Northwestern Germany (Spiekeroog, Norderney, Juist)

disturbance regime where assignment to plant communities by floristic composition was not feasible. Definitions of habitat types are given in the Supplement (Table A1).

Effect modelling

First, we calculated ‘basic’ effect models that only contained invader cover as predictor of species richness. For all three invaders, species counts within the plots clearly deviated from normal distributions. Thus, we used Generalized Linear Models (GLM) with (quasi-)Poisson distribution and log-link which fitted the data well.

Next, we looked for the best models of species richness considering invader cover, habitat type, squared invader cover and interactions of (squared) invader cover with habitat type, as potential predictor variables. We tested the significance of predictor variables with likelihood ratio tests, starting with the basic model (‘invader cover’) and adding one additional predictor variable at a time, in the aforementioned sequence. Only variables that significantly improved the model fit were included in the final effect model (‘full model’). All effect models were calculated with R 2.10.1 (R Development Core Team 2009).

The models of *L. polyphyllus* included plot size as an additional predictor variable to account for the possibility that 100-m² plots contained more species than 25-m² plots because of species-area relationships. For *R. rugosa*, we calculated Generalized Linear Mixed Models (GLMM) that included a random site effect to account for nest-ness of the plots. The GLMM were calculated with ‘lmer’ of the ‘lme4’ package in R.

Calculation of impact scores

We calculated impact scores by averaging predicted species loss over all sample sites using the basic and full models, thus yielding two impact scores per invasive species.

Impact scores were calculated as the difference between predicted species richness at zero invader cover and predicted richness given the actual cover of the invader, averaged over all plots for each invasive species (see Equ. 1).

$$\text{Equ. 1: } \frac{1}{n} \sum_{i=1}^n (\hat{y}_0 - \hat{y}_{x_i})$$

where \hat{y} = predicted species richness, x_i = invader cover of site i , and n = number of sample plots per invasive species.

For calculation of the predicted species richness, we used estimates of all predictor variables in the model. If habitat type was a significant predictor, we used estimates of all habitat categories in the calculations, even if the estimates of some categories did not differ significantly from zero according to the GLM t test or z test.

We calculated percentile (2.5–97.5%) confidence intervals for impact scores with bootstrapping using 10,000 resamples with replacement of same size as the original sample.

Results

We found different effect models for the three invasive species (Table 2, Figure 1). Models of *H. mantegazzianum* and *R. rugosa* contained main effects of habitat types, indicating that habitat types differed in species richness. Among habitat types invaded by *L. polyphyllus*, i.e. ruderal and managed grasslands, species richness differed not per se, but the relationship of invader cover and species richness interacted with habitat type (Figure 1c).

The three invaders had negative effects on vascular plant species richness of invaded communities, but the shapes of the relationships differed. *Heracleum mantegazzianum* had uniform linear effects in all habitat types, while the effects of *L. polyphyllus* were much stronger in ruderal than in managed grasslands. *Rosa rugosa* showed a non-linear relationship, so that species richness only was reduced at high cover percentages (Figure 1e). The details of the basic and full models (estimates etc.) are given in the Supplement (Tables A2–4).

Impact scores differed markedly between basic and full models (Figure 1). For the basic and full model of *H. mantegazzianum*, confidence intervals of impacts scores did not overlap, indicating that part of the apparent effect on species richness predicted by the basic model was, indeed, due to general differences in species richness between invaded habitat types. For *L. polyphyllus* and *R. rugosa*, impact scores calculated with full models were just outside the confidence intervals of the basic models, suggesting significant differences between model variants, but the confidence intervals overlapped by roughly 50%. Impact scores of *L. polyphyllus* tended to be higher when taking the stronger effect in ruderal grasslands into account, whereas impact scores of *R. rugosa* tended to be lower when considering non-linear effects and general differences in species richness between invaded habitat types.

Table 2. Components of ‘full’ effect models. P-values are taken from sequential Likelihood Ratio tests. Signs (–, +) indicate the relationship of (squared) invader cover with species richness; NS, not significant.

Variable	<i>Heracleum mantegazzianum</i>	<i>Lupinus polyphyllus</i>	<i>Rosa rugosa</i>
Invader cover	(–) < 0.001	(–) 0.018	(+) < 0.001
Habitat type	< 0.001	†NS	0.021
Squared invader cover	NS	NS	(–) 0.015
Habitat type x invader cover	NS	0.004	NS
Hab. type x squared inv. cover	NS	NS	NS

† Habitat type was marginally significant in sequential likelihood ratio tests when added after *L. polyphyllus* cover and before squared *L. polyphyllus* cover and the interaction terms ($p = 0.033$), but the main effect of habitat type did not improve the ‘full’ model that contained *Lupinus* cover and the interaction of cover and habitat type ($p = 0.833$).

Discussion

The case studies presented here show that effect models of invasive species may take various forms. Concerning impacts on biodiversity, models should consider environmental variation, because general biodiversity trends along ecological gradients may lead us to believe that impacts are higher than they actually are. However, underestimation of impacts may happen as well.

For instance, *H. mantegazzianum* invades managed grasslands, ruderal (abandoned) grasslands and tall-herb stands – these habitat types resemble, and quite often are, a successional sere (Thiele and Otte 2006). Along this sere, species richness generally decreases, while average cover of *H. mantegazzianum* increases. Only part of the decline in species richness is attributable to *H. mantegazzianum* that shades out lower growing grassland plants (Thiele et al. 2010b), while another part is due to generally lower species numbers in tall-herb stands compared to the grasslands that they replace during succession (Neuhäusl and Neuhäuslova-Novotna 1985). In other words, species numbers of tall-herb stands are low even if *H. mantegazzianum* covers only a minor proportion of the area. In contrast, impact of *L. polyphyllus* was underestimated using a simple model that included no potential interactions of invader cover and habitat type. In fact, reduction of species richness was much stronger in ruderal than managed grasslands. Hence, inclusion of the interaction term increased the impact score, although ruderal grasslands represented only 25% of the plots sampled.

Several recent studies have found that inclusion of environmental variables into effect models changed predictions of invader effects on biodiversity: apparent negative effects of *Lythrum salicaria* L. and *Rhamnus frangula* L. on richness of rare native species disappeared (Houlahan and Findlay 2004), negative correlation of *Lonicera japonica* Thunb. with species richness became less strong (Surrette and Brewer 2008), but on the other side, effect estimates of (native) *Hippophaë rhamnoides* increased, i.e. became

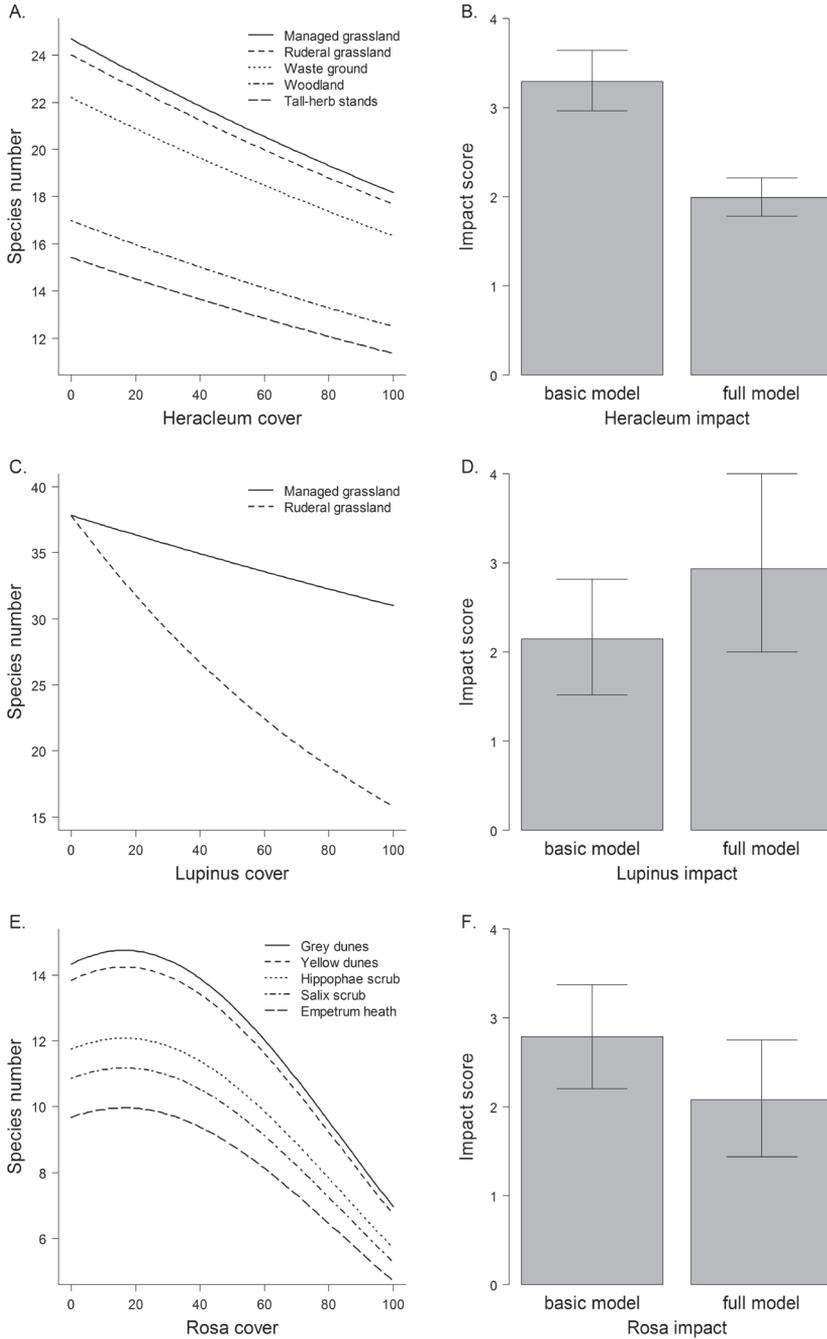


Figure 1. Effect models and impact scores. Left panels show the ‘full’ effect models of *Heracleum mantegazzianum* (A), *Lupinus polyphyllus* (C) and *Rosa rugosa* (E) that included habitat type as a co-factor and, if significant, non-linear terms of cover percentages of the invasive species. Right panels (B, D, F) show the corresponding impact scores calculated with ‘full’ models and with ‘basic’ models that only included a linear term of invader cover.

more negative, by up to 50% when including environmental co-variables (Isermann et al. 2007). Further, *Spartina anglica* C.E. Hubb. reduces native species richness in low-salinity marshes, while facilitating richness in mudflats (Hacker and Dethier 2006), and differences in impact on species richness among sites (Mediterranean islands) have been found for *Ailanthus altissima* (Mill.) Swingle and *Oxalis pes-caprae* L. (Vilá et al. 2006). Hence, it is the rule rather than an exception that disregarding environmental co-variation leads to biased estimates of invader effects on species richness.

Also non-linear relationships between invader abundance and biodiversity can substantially influence impact assessments. In the case of *R. rugosa*, the impact score was lower when introducing a quadratic term into the effect model, while inclusion of habitat type did not change the score much (basic model, 2.8; habitat model, 2.9; quadratic model, 2.1). A non-linear increase of effect with invader abundance will commonly lead to higher impact scores compared to a linear model (Thiele et al. 2010a), but the model of *R. rugosa* included both a negative quadratic and a positive linear term, so that in fact the non-linear model predicted a lesser effect. Non-linear effects on species richness were also found for the shrubs *Lantana camara* L. (Gooden et al. 2009) and *Hippophaë rhamnoides* (Isermann et al. 2007). These results suggest that non-linearity of abundance-effect relationships of invasive species should be considered in future impact studies.

Further advances of impact assessment and a deeper understanding of invader-diversity relationships could be expected from studies that take traits of the resident species into account, e.g. by modelling richness of functional plant groups or of species of high-conservation value. For the invaders studied here, it has been shown that different plant types – size classes, life forms, sociological groups – are affected differently (Thiele et al. 2010b). Regarding theory of biological invasions it would be interesting to investigate whether or not impact models could be generalised within groups of invasive species (e.g. life forms or strategy types). Another question is how to represent environmental variation in effect models. Here, we used habitat type as a co-factor which appears practical and useful, but might not be the optimal solution. The suitability of environmental properties and scaling of the variables (metric, categorical) will depend on both the invasive species and the ecosystem trait under study. Finally, multiple regression models, as applied here, account for main effects and interactions of invader and environment, but do not consider possible correlations among them. Thus, effect estimates may still be affected by spurious correlations. Further improvements could be achieved by more advanced models using, e.g., corrected path coefficients instead of regression coefficients.

Besides scientific approaches, impact assessment is grounded in normative definitions of impact or ecological damage. Not all negative relationships of invasive species with ecosystem traits necessarily have to be considered as damage, but definitions might focus on legal conservation resources or set thresholds discerning minor adverse effects from ‘significant’ damage (Bartz et al. 2010). In a normative sense, changes in species numbers may not directly quantify the ensuing damage (Ingo Kowarik, pers. comm.). Merging scientific and normative approaches into practical implementations

of impact assessment of invasive species remains a challenge for applied invasion biology and environmental planning.

Conclusions

Simple linear effect models may often yield inaccurate impact scores of invasive species. Hence, it appears to be advisable to consider somewhat more complex models that include environmental co-variables and, if applicable, non-linear effect terms. Models should preferentially be based on samples representing the full environmental gradient of invaded habitats and the full range of equilibrium abundances or cover percentages of the invasive species.

Acknowledgements

The study on *Heracleum mantegazzianum* by JT and AO was funded by the European Union within the project 'Giant Alien' (EVK2-CT-2001-00128). Research by JK benefited from a grant by the University of Copenhagen ('Centre for Invasive Species'). We thank Franz Essl and Ingo Kowarik for helpful comments on an earlier version of the manuscript.

References

- Adams SN, Engelhardt KAM (2009) Diversity declines in *Microstegium vimineum* (Japanese stiltgrass) patches. *Biological Conservation* 142: 1003–1010. doi: 10.1016/j.biocon.2009.01.009.
- Bartz R, Heink U, Kowarik I (2010) Proposed definition of environmental damage illustrated by the cases of genetically modified crops and invasive species. *Conservation Biology* 24: 675–681. doi: 10.1111/j.1523-1739.2009.01385.x.
- Brewer S (2008) Declines in plant species richness and endemic plant species in longleaf pine savannas invaded by *Imperata cylindrica*. *Biological Invasions* 10: 1257–1264. doi: 10.1007/s10530-007-9200-3.
- Bruun HH (2005) *Rosa rugosa* Thunb. ex Murray. *Journal of Ecology* 93: 441–470. doi: 10.1111/j.1365-2745.2005.01002.x.
- Byers JE, Reichard S, Randall JM, Parker IM, Smith CS, Lonsdale WM, Atkinson IAE, Seastedt TR, Williamson M, Chornesky E, Hayes D (2002) Directing research to reduce the impacts of nonindigenous species. *Conservation Biology* 16: 630–640. doi: 10.1046/j.1523-1739.2002.01057.x.
- Davis MA, Thompson K (2000) Eight ways to be a colonizer; two ways to be an invader: A proposed nomenclature scheme for invasion ecology. *Bulletin of the Ecological Society of America* 81: 226–230.

- Ellenberg H (2009) *Vegetation ecology of Central Europe*. Cambridge University Press, Cambridge, 731pp.
- Fischer LK, von der Lippe M, Kowarik I (2009) Tree invasion in managed tropical forests facilitates endemic species. *Journal of Biogeography* 36: 2251–2263. doi: 10.1111/j.1365-2699.2009.02173.x.
- Flory SL, Clay K (2010) Non-native grass invasion alters native plant composition in experimental communities. *Biological Invasions* 12: 1285–1294. doi: 10.1007/s10530-009-9546-9.
- Gaertner M, Den Breeyen A, Hui C, Richardson DM (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Progress in Physical Geography* 33: 319–338. doi: 10.1177/0309133309341607.
- Gooden B, French K, Turner PJ, Downey PO (2009) Impact threshold for an alien plant invader, *Lantana camara* L., on native plant communities. *Biological Conservation* 142: 2631–2641. doi: 10.1016/j.biocon.2009.06.012.
- Goodenough AE (2010) Are the ecological impacts of alien species misrepresented? A review of the 'native good, alien bad' philosophy. *Community Ecology* 11: 13–21. doi: 10.1556/ComEc.11.2010.1.3.
- Hacker S, Dethier M (2006) Community modification by a grass invader has differing impacts for marine habitats. *Oikos* 113: 279–286. doi: 10.1111/j.2006.0030-1299.14436.x.
- Hejda M, Pyšek P, Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology* 97: 393–403. doi: 10.1111/j.1365-2745.2009.01480.x.
- Houlahan JE, Findlay CS (2004) Effect of invasive plant species on temperate wetland plant diversity. *Conservation Biology* 18: 1132–1138. doi: 10.1111/j.1523-1739.2004.00391.x.
- Isermann M (2008) Classification and habitat characteristics of plant communities invaded by the non-native *Rosa rugosa* Thunb. in NW Europe. *Phytocoenologia* 38: 133–150. doi: 10.1127/0340-269X/2008/0038-0133.
- Isermann M, Diekmann M, Heemann S (2007) Effects of the expansion by *Hippophaë rhamnoides* on plant species richness in coastal dunes. *Applied Vegetation Science* 10: 33–42. doi: 10.1111/j.1654-109X.2007.tb00501.x.
- Jäger H, Kowarik I, Tye A (2009) Destruction without extinction: long-term impacts of an invasive tree species on Galapagos highland vegetation. *Journal of Biogeography* 36: 1252–1263. doi: 10.1111/j.1365-2745.2009.01578.x.
- Kollmann J, Frederiksen L, Vestergaard P, Bruun HH (2007) Limiting factors for seedling emergence and establishment of the invasive non-native *Rosa rugosa* in a coastal dune system. *Biological Invasions* 9: 31–42. doi: 10.1007/s10530-006-9003-y.
- Maurel N, Salmon S, Ponge J-F, Machon N, Moret J, Muratet A (2010) Does the invasive species *Reynoutria japonica* have an impact on soil and flora in urban wastelands? *Biological Invasions* 12: 1709–1719. doi: 10.1007/s10530-009-9583-4.
- Meffin R, Miller AL, Hulme PE, Duncan RP (2010) Experimental introduction of the alien plant *Hieracium lepidulum* reveals no significant impact on montane plant communities in New Zealand. *Diversity and Distributions* 16: 804–815. doi: 10.1111/j.1472-4642.2010.00684.x.

- Neuhäusl R, Neuhäuslova-Novotna Z (1985) Verstaudung von aufgelassenen Rasen am Beispiel von Arrhenatherion-Gesellschaften. *Tuexenia* 5: 249–258.
- Otte A, Maul P (2005) Verbreitungsschwerpunkte und strukturelle Einnischung der Stauden-Lupine (*Lupinus polyphyllus* Lindl.) in Bergwiesen der Rhön. *Tuexenia* 25: 151–182.
- Otte A, Obert S, Volz H, Weigand E (2002) Effekte von Beweidung auf *Lupinus polyphyllus* Lindl. in Bergwiesen des Biosphärenreservates Rhön. *Neobiota* 1: 101–133.
- Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1: 3–19.
- Prévosto B, Dambrine E, Coquillard P, Robert A (2006) Broom (*Cytisus scoparius*) colonization after grazing abandonment in the French Massif Central: impact on vegetation composition and resource availability. *Acta Oecologica* 30: 258–268. doi: 10.1016/j.actao.2006.05.001.
- Pyšek P, Cock MJW, Nentwig W, Ravn HP (2007) Ecology and Management of Giant Hogweed (*Heracleum mantegazzianum*). CAB International, Wallingford, 352pp.
- R Development Core Team (2009) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Richardson DM, Pyšek P (2006) Plant invasions: Merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography* 30: 409–431. doi: 10.1191/0309133306pp490pr.
- Surrette SB, Brewer JS (2008) Inferring relationships between native plant diversity and *Lonicera japonica* in upland forests in north Mississippi, USA. *Applied Vegetation Science* 11: 205–214. doi: 10.3170/2008-7-18355.
- Thiele J, Otte A (2006) Analysis of habitats and communities invaded by *Heracleum mantegazzianum* Somm. et Lev. (Giant Hogweed) in Germany. *Phytocoenologia* 36: 281–320. doi: 10.1127/0340-269X/2006/0036-0281.
- Thiele J, Kollmann J, Rose-Andersen U (2009) Ecological and socio-economic correlates of plant invasions in Denmark: the utility of environmental assessment data. *Ambio* 38: 89–94. doi: 10.1579/0044-7447-38.2.89.
- Thiele J, Kollmann J, Markussen B, Otte A (2010a) Impact assessment revisited: improving the theoretical basis for management of invasive alien species. *Biological Invasions* 12: 2025–2035. doi: 10.1007/s10530-009-9605-2.
- Thiele J, Isermann M, Otte A, Kollmann J (2010b) Competitive displacement or biotic resistance? Disentangling relationships between community diversity and invasion success of tall herbs and shrubs. *Journal of Vegetation Science* 21: 213–220. doi: 10.1111/j.1654-1103.2009.01139.x.
- Tiley GED, Dodd FS, Wade PM (1996) *Heracleum mantegazzianum* Sommier & Levier. *Journal of Ecology* 84: 297–319.
- Vilà M, Tessier M, Suehs CM, Brundu G, Carta L, Galanidis A, Lambdon P, Manca M, Médail F, Moragues E, Traveset A, Troumbis AY, Hulme PE (2006) Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. *Journal of Biogeography* 33: 853–861. doi: 10.1111/j.1365-2699.2005.01430.x.
- Williamson MH (1996) *Biological invasions*. Chapman & Hall, London, 256pp.

Yokomizo H, Possingham HP, Thomas MB, Buckley YM (2009) Managing the impact of invasive species: the value of knowing the density–impact curve. *Ecological Applications* 19: 376–386. doi: 10.1890/08-0442.1.

Appendix

Table A1. Definitions of habitat types. For descriptions of plant communities (syntaxa) see Ellenberg (2009).

Species	Habitat type	Definition
<i>Heracleum mantegazzianum</i>	Managed grassland	Pastures and meadows of well drained, fertile soils (typical Arrhenatheretalia communities)
	Ruderal grassland	Abandoned grassland, field margins, road verges and embankments (Arrhenatheretalia communities containing characteristic species of Galio-Urticetea and Artemisietea)
	Tall-herb communities	Tall-herb communities of fertile soils (Galio-Urticetea)
	Waste ground	Open communities of disturbed, non-agricultural sites (e.g. abandoned sand pits); floristic composition not matching any particular syntaxon
	Woodland	Communities dominated by trees; alluvial woodland (Alnion-glutinosa incanae, Salicion eleagni), copses and anthropogenic (semi-open) forests
<i>Lupinus polyphyllus</i>	Managed grassland	Unimproved Nardus grassland (Violion caninae) and montane grassland of more fertile soils (Polygono-Trisetion) with current or recent grassland management (mowing, grazing)
	Ruderal grassland	Unimproved Nardus grassland (Violion caninae) and montane grassland of more fertile soils (Polygono-Trisetion) without current land use containing characteristic species of tall-herb communities (Galio-Urticetea); subordinately sedge fens (Caricetum nigrae)
<i>Rosa rugosa</i>	Yellow dune	Mobile yellow dunes dominated by <i>Ammophila arenaria</i> (Ammophiletea: Elymo-Ammophiletum)
	Grey dune	Semi-fixed and fixed grey dunes with short, open grasslands (Koelerio-Corynephoretea), especially Corynephorion canescentis, Violo-Corynephoretum as well as herb-rich communities of the Tortulo-Koelerion
	<i>Hippophaë</i> scrub	<i>Hippophaë rhamnoides</i> scrub on semi-fixed grey dunes (Rhamno-Prunetea: Hippophao-Sambucetum)
	<i>Salix</i> scrub	<i>Salix repens</i> dominated scrub on dry fixed dunes (mainly brown dunes) mostly belonging to the Salici repentis-Empetretum (Empetrium nigri)
	<i>Empetrum</i> heath	<i>Empetrum nigrum</i> dominated heathlands on brown dunes (Empetrium nigri: Carici arenariae-Empetretum and Polypodio-Empetretum)

Table A2. Effect models of *Heracleum mantegazzianum* (Generalized Linear Models with quasi-Poisson distribution and log-link).

A. Basic model

Model component	Estimate	Std. Error	t value	Pr(> t)
Intercept	3.0596	0.0496	61.7	< 0.001
<i>H. mantegazzianum</i> cover	-0.0048	0.0011	-4.2	< 0.001

Null deviance: 842.0 on 201 degrees of freedom

Residual deviance: 771.7 on 200 degrees of freedom

B. Full model

Model component	Estimate	Std. Error	t value	Pr(> t)
Intercept	3.2064	0.0632	50.7	< 0.001
<i>H. mantegazzianum</i> cover	-0.0031	0.0012	-2.6	0.009
Habitat: ruderal grassland	-0.0276	0.0857	-0.3	0.748
Habitat: tall-herb stands	-0.4701	0.0888	-5.3	< 0.001
Habitat: waste ground	-0.1062	0.1132	-0.9	0.349
Habitat: woodland	-0.3745	0.1183	-3.2	0.002

Null deviance: 842.0 on 201 degrees of freedom

Residual deviance: 622.0 on 196 degrees of freedom

Table A3. Effect models of *Lupinus polyphyllus* (Generalized Linear Models with quasi-Poisson distribution and log-link).

A. Basic model

Model component	Estimate	Std. Error	t value	Pr(> t)
Intercept	3.5844	0.0765	46.9	< 0.001
<i>L. polyphyllus</i> cover	-0.0028	0.0012	-2.3	0.024
Plot size (25/ 100 m ²)	0.0017	0.0009	1.8	0.077

Null deviance: 282.8 on 79 degrees of freedom

Residual deviance: 234.3 on 77 degrees of freedom

B. Full model

Model component	Estimate	Std. Error	t value	Pr(> t)
Intercept	3.6334	0.0744	48.9	< 0.001
Plot size (25/ 100 m ²)	0.0012	0.0009	1.3	0.201
<i>L. polyphyllus</i> cover	-0.0020	0.0012	-1.7	0.089
Habitat: ruderal grassland	-0.0067	0.0023	-2.9	0.005

Null deviance: 282.8 on 79 degrees of freedom

Residual deviance: 210.6 on 76 degrees of freedom

Table A4. Effect models of *Rosa rugosa* (Generalized Linear Mixed Models with Poisson distribution and log-link, calculated with “lmer” of the “lme4” package in R).

A. Basic model

Model component	Estimate	Std. Error	z value	Pr(> z)
Intercept	2.5547	0.0659	38.8	< 0.001
<i>R. rugosa</i> cover	-0.0061	0.0011	-5.8	< 0.001

Null deviance: 113.6

Residual deviance: 79.3

B. Full model

Model component	Estimate	Std. Error	z value	Pr(> z)
Intercept	2.2515	0.2209	10.2	< 0.001
<i>R. rugosa</i> cover	0.0035	0.0041	0.9	0.391
Habitat: grey dunes	0.0348	0.1316	0.3	0.791
Habitat: <i>Empetrum</i> heath	-0.3572	0.1463	-2.4	0.015
Habitat: <i>Hippophaë</i> scrub	-0.1643	0.1486	-1.1	0.269
Habitat: <i>Salix</i> scrub	-0.2423	0.1907	-1.3	0.204
Squared <i>R. rugosa</i> cover	-0.4155	0.1684	-2.5	0.014

Null deviance: 113.6

Residual deviance: 61.8

Knowing what we count: a comment on Guo

Petr Pyšek

Institute of Botany, Department of Invasion Ecology, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic & Department of Ecology, Faculty of Science, Charles University Prague, Viničná 7, CZ-128 01 Prague, Czech Republic

Corresponding author: Petr Pyšek (pysek@ibot.cas.cz)

Academic editor: *Ingolf Kühn* | Received 28 August 2011 | Accepted 8 September 2011 | Published 5 October 2011

Citation: Pyšek P (2011) Knowing what we count: a comment on Guo. NeoBiota 10: 81–88. doi: 10.3897/neobiota.10.1976

Guo (2011) points to problems arising from different approaches to estimating the proportions of floras that are native or alien, specifically those across and within various regions. This results in inconsistency of numbers reported from internal administrative units by underestimating the numbers of species that are alien to the region and overestimating native species richness. Resulting species numbers and proportions for smaller units within large countries, or whole continents, can be seriously biased if only species alien to the larger unit as a whole are considered alien, while all other species are considered native.

Alien species databases for large regions need to be built bottom-up

This issue has been dealt with in detail in some invasion biology literature from other regions of the world, a fact that is not acknowledged in Guo (2011). Moreover, even for the US it is not true that previously published plant richness data for each state were always based on species either native or exotic to the entire country, as stated by Guo (2011). The issue has been thoroughly considered in some US state floras, such as California, where species with their origin in other parts of the US were consistently counted as aliens (Rejmánek et al. 1991; Rejmánek and Randall 1994). The analysis by these authors was based on detailed data from the Jepson Manual (Hickman 1993) which represents an excellent regional dataset collated through intensive historical research. However, this is not only true for California; across the US the nativity concept

has been consistently applied at the regional level. Rejmánek and Randall (1994, their Table 2) give the numbers of native and naturalized alien plant species for 37 regions in North America and Hawaii, both at the state level or smaller. They derived the lists from regional or state botanical floras and carefully re-checked each species in terms of their status and origin. For North America there is good coverage of the territory generally; Palmer (2005) reports data from 1870 floras, ranging in size from local checklists to states, provinces and countries. A survey conducted to determine what data currently exists for alien species in the US identified 319 datasets. These datasets ranged from county to national and global scales, with most of them related to plants (Crall et al. 2006). Therefore the data from which native vs alien status can be correctly assessed does exist, it just needs to be searched for in appropriate sources.

The above indicates that the problem may be more political/management related, rather than scientific, i.e. rather related to large databases covering the whole country and built for practical purposes, such as USDA and NRCS, referred to by Guo (2011). Despite biases in the literature on biological invasions, resulting from varying research intensity and regional differences in the level of knowledge (Pyšek et al. 2008), for many regions with a botanical tradition the data can be found in basic botanical works. Floras and checklists of individual regions are generally more precise, for obvious reasons, than if regional information is derived from continental-scale summary floral works or checklists, where the level of inaccuracy, especially when it comes to origin of species and treatment of aliens, can be quite high (Pyšek 2003). The difference between a database of alien species built from the bottom-up and country data downscaled from a continental-wide account, can be illustrated by a comparison of European situation as reported by Lambdon et al. (2008) and Weber (1997). Generally, the bottom-up approach of building alien species databases is scientifically more rigorous and provides more exact information than that resulting from application of nationwide or continental checklists to regional situations.

Illustrating the magnitude of bias on European data

European data (based on the DAISIE project; DAISIE 2009) provide additional and more systematic illustration of the problem pointed by Guo (2011), as well as of its magnitude. The treatment of European alien flora was based on compiling regional checklists and accurately distinguishing between alien species with their native range entirely outside the continental boundaries (termed “alien to” Europe) and alien species of European origin, including those that are native in a part of Europe but alien to another. Both subgroups together formed the “alien in” Europe category, comprising species alien across all regions (Lambdon et al. 2008; Pyšek et al. 2009b). This approach, previously used also by Weber (1997) in his analysis of the continental flora based on *Flora Europaea*, represents a rare case in studies on biological invasions when administrative boundaries are an advantage because the history and tradition of botan-

ical research relates to individual nations. Therefore, country-based research is ideally suited to reliably distinguish native and alien species at this scale.

On the continent as a whole there are 3749 naturalized (*sensu* Richardson et al. 2000; Blackburn et al. 2011) aliens in Europe, of which 1780 are alien to Europe. Therefore 47% of alien species are of extra-European origin (Lambdon et al. 2008). To estimate total alien species richness and its contribution to the total plant diversity in Europe, only species with extra-European origin are relevant. The 1780 naturalized aliens in this group add to 10,928 native species (as given in Winter et al. 2009), resulting in 14% of plant species in Europe being alien.

At the scale of individual countries, for example considering incorrectly only those aliens with their region of origin entirely outside of Europe would move 522 of the neophytes (alien species introduced since the beginning of the 16th century) in the Czech Republic (49.9% of the total number of neophytes) into the “native” category. This would reduce the number of neophytes recorded from 1046 to 524, and their proportional contribution to the country’s entire flora from 25.3% to 12.7% (based on data in Pyšek et al. 2002). The difference between figures obtained by applying the two approaches is of similar magnitude for other countries in Europe (www.europe-alien.org).

Reconciling ecological and biogeographical approaches

The problem is essentially one of scale. There is no specific scale at which invasions should be studied, and the patterns and processes found by researchers differ according to the grain of the study (e.g., Hamilton et al. 2005; Pyšek and Hulme 2005). As pointed by Guo (2011), the concept of nativity/origin status depends on the size of the unit examined. It needs to be emphasized that with an increase in scale, the approach changes from an ecological one (with focus on colonization and evaluation of nativity at the level of a community or habitat), to a biogeographical one (addressing the issue of origin at the level of a region, country or continent). This reflects the differences in perceiving new species through ecological, biogeographical and anthropocentric approaches, and also in the definitions used (e.g. colonizers, invaders and weeds; Rejmánek 2000). As the scale of study decreases, the boundary between the concepts of “native” and “alien” becomes more blurred; biogeographical delimitation works with arbitrarily defined regions to which species are traditionally assigned as native or alien, and the definition of an alien is bound to introduction and dispersal resulting from human activities (Richardson et al. 2000; Blackburn et al. 2011). However, at the ecological scale, the application of the principle “the species would not be present had not been for the activities of humans” (Pyšek et al. 2004) becomes more vague. When classifying species as alien, authors generally do not consider the effect of land-use changes and global environmental change on the spread of native species through landscapes transformed by human activities (Chytrý et al. 2012). Such species would not be present in some of their locales without the influence of humans either, but are

considered native to the region as a whole, mostly due to lack of information needed to make such distinctions. This can be illustrated for the British Isles; the New Atlas of the British and Irish Flora (Preston et al. 2002) is probably the only available source that distinguishes between native and alien occurrences of species that are native to the British Isles as a whole, thereby consistently applying the principles normally used at the biogeographical scale to an ecological grain of study. Using such information reveals species that are good dispersers in their native geographical range and are not confined to their native habitats, exhibiting thus potential to spread (Fig. 1).

Our results are only as good as our data

As pointed by Guo (2011), not distinguishing between the two groups according to origin (or ignoring the “internal” introductions) can have serious consequences for management since these species impact on ecosystems in the same way as “true exotics”. Some continental-scale analyses of invasive species impacts indeed restrict the assessment to invasive species originating from overseas (e.g., Nentwig et al. 2009; Kumschick et al. 2011; but see Vilà et al. 2011) and data to separate the effects of both origin-based groups are not available. There is however one piece of evidence from the United States. Paine et al. (2010) showed that immediate present-day threat from known invasive insect pests is greater from within the United States than from the outside and advocate for invasive species policy paying increased awareness of state-level post-border biosecurity.

In terms of science, lumping both groups of origin together may obscure ecological analyses since the groups differ in many respects; the data gathered for Europe again allow for a more detailed insight. Besides the fact that biased species richness complicates comparisons between regions for which the data was collected by one approach or the other (Guo 2011), there are differences in historical dynamics and rates of introduction. Aliens of European origin for example tended to start spreading earlier in Europe than those from overseas (Lambdon et al. 2008). Similarly, comparison of the alien flora of California from different time periods shows that species of within-continental origin increased their percentage contribution over the period of 50 years from about 8 to 15% (Rejmánek and Randall 1994). European data further show that both groups differ in terms of distribution (almost all among the 15 most widely distributed species in terms of the number of region have their native ranges outside Europe), taxonomy (only a few large genera which have successfully invaded are predominantly non-European), hybridization rate (European natives hybridize more frequently) or habitat affiliation (aliens of European origin tend to occur in a wider range of habitats, most likely profiting from a better habitat match and longer residence times) (Lambdon et al. 2008; Pyšek et al. 2009b).

Moreover, comparisons seeking for determinants of regional invasibility based on floras of whole states or groups of states can be misleading. This is because high environmental heterogeneity across a large area may hide the patterns that could be seen if comparing alien species richness within smaller, more homogeneous areas that are more

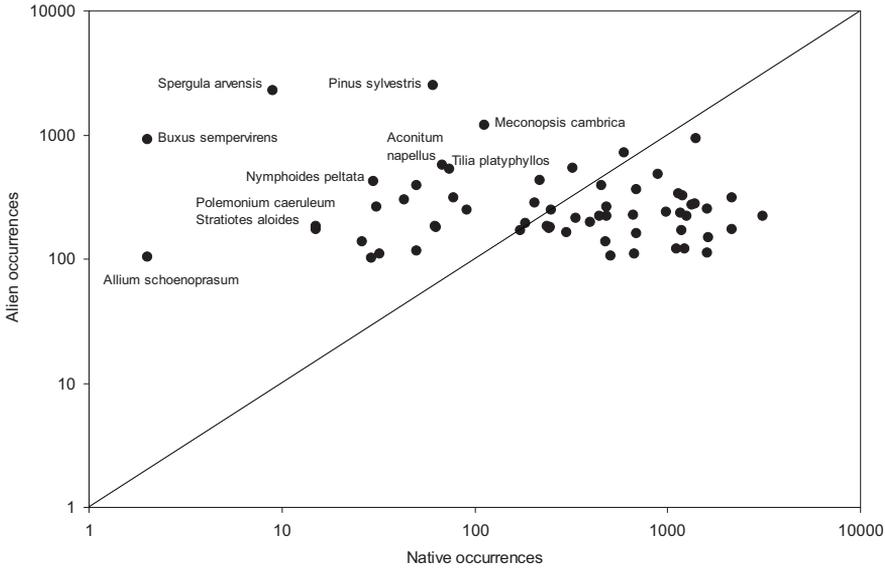


Figure 1. Number of 10 × 10 km grid cells in which species native to the British Isles, that also occur in localities where their occurrence is considered alien, were mapped in 1987–1999. Species above and below the unity line are recorded more frequently as “aliens” and “natives”, respectively. Based on data from Preston et al. (2002), using species with at least 100 “alien” occurrences and excluding hybrids. For species in the top left part of the plot, more than 90% of records refer to alien occurrences, those with the greatest disproportions towards the “alien” occurrences are labelled. Note the log scale.

suitable for revealing causal connections between environmental factors, anthropic disturbance, history, and numbers of alien species (Rejmánek and Randall 1994).

In invasion biology, it is becoming increasingly important to synthesize existing data on alien species abundances and distributions (Crall et al. 2006; Richardson and Pyšek 2006; Pyšek et al. 2009a, 2010; Stohlgren et al. 2011). The important issue raised by Guo (2011) points to that in invasion biology, a field currently enjoying intensive research but relying heavily, for theory, on data collected in different parts of the world by varying means and approaches, it is essential that assumptions of each study are clearly defined and stated. Our results are only as good as our data, and comparability of results drawn from different regions is a necessary step towards building a general framework and synthesis of the field.

Acknowledgments

The author was supported by long-term institutional research plans no. AV0Z60050516 (Academy of Sciences of the Czech Republic), no. MSM0021620828 (Ministry of Education of the Czech Republic), and by the Praemium Academiae award from the Academy of Sciences of the Czech Republic.

References

- 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. doi: 10.1016/j.tree.2011.03.023
- Chytrý M, Wild J, Pyšek P, Jarošík V, Dendoncker N, Reginster I, Pino J, Maskell L, Vilà M, Pergl J, Kühn I, Spangenberg J, Settele J (2012) Projecting trends in plant invasions in Europe under different scenarios of future land-use change. *Global Ecology and Biogeography*, in press. doi: 10.1111/j.1466-8238.2010.00573.x
- Crall AW, Meyerson LA, Stohlgren TJ, Jarnevich CS, Newman GJ, Graham J (2006) Show me the numbers: what data currently exist for non-native species in the USA? *Frontiers in Ecology and the Environment* 4: 414–418. doi: 10.1890/1540-9295(2006)4[414:SMTNWD]2.0.CO;2
- DAISIE (2009) *Handbook of Alien Species in Europe*. Springer, Berlin.
- Guo Q (2011) Counting “exotics”. *Neobiota* 9: 71–73.
- Hamilton MA, Murray BR, Cadotte MW, Hose GC, Baker AC, Harris CJ, Licari D (2005) Life-history correlates of plant invasiveness at regional and continental scales. *Ecology Letters* 8: 1066–1074. doi: 10.1111/j.1461-0248.2005.00809.x
- Hickman JC (Ed) (1993) *The Jepson Manual*. University of California Press, Berkeley.
- Kumschick S, Alba C, Hufbauer RA, Nentwig W (2011) Weak or strong invaders? A comparison of impact between the native and invaded ranges of mammals and birds alien to Europe. *Diversity and Distributions* 17: 663–672. doi: 10.1111/j.1472-4642.2011.00775.x
- Lambdon PW, Pyšek P, Basnou C, Hejda M, Arianoutsou M, Essl F, Jarošík V, Pergl J, Winter M, Anastasiu P, Andriopoulos P, Bazos I, Brundu G, Celesti-Grapow L, Chassot P, Delipetrou P, Josefsson M, Kark S, Klotz S, Kokkoris Y, Kühn I, Marchante H, Perglová I, Pino J, Vilà M, Zikos A, Roy D, Hulme PE (2008) Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. *Preslia* 80: 101–149.
- Nentwig W, Kühnel E, Bacher S (2009) A generic impact-scoring system applied to alien mammals in Europe. *Conservation Biology* 24: 302–311. doi: 10.1111/j.1523-1739.2009.01289.x
- Paini DR, Worner SP, Cook DC, De Barro PJ, Thomas MB (2010) Threat of invasive pests from within national borders. *Nature Communications* 1: 115. doi: 10.1038/ncomms1118
- Palmer MW (2005) Temporal trends of exotic species richness in North American floras: an overview. *Ecoscience* 12: 386–390. doi: 10.2980/i1195-6860-12-3-386.1
- Preston CD, Pearman DA, Dines TD (2002) *New Atlas of the British and Irish Flora*. Oxford University Press, Oxford.
- Pyšek P (2003) How reliable are data on alien species in Flora Europaea? *Flora* 198: 499–507. doi: 10.1078/0367-2530-00122
- Pyšek P, Hulme PE (2005) Spatio-temporal dynamics of plant invasions: linking pattern to process. *Ecoscience* 12: 302–315. doi: 10.2980/i1195-6860-12-3-302.1
- Pyšek P, Jarošík V, Hulme PE, Kühn I, Wild J, Arianoutsou M, Bacher S, Chiron F, Didžiulis V, Essl F, Genovesi P, Gherardi F, Hejda M, Kark S, Lambdon PW, Desprez-Loustau AM,

- Nentwig W, Pergl J, Poboljšaj K, Rabitsch W, Roques A, Roy DB, Shirley S, Solarz W, Vilà M, Winter M (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences of the United States of America* 107: 12157–12162. doi: 10.1073/pnas.1002314107
- Pyšek P, Jarošík V, Pergl J, Randall R, Chytrý M, Kühn I, Tichý L, Danihelka J, Chrtek J jun, Sádlo J (2009a) The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. *Diversity and Distributions* 15: 891–903. doi: 10.1111/j.1472-4642.2009.00602.x
- Pyšek P, Lambdon P, Arianoutsou M, Kühn I, Pino J, Winter M (2009b) Alien vascular plants of Europe. In: DAISIE (Eds) *Handbook of Alien Species in Europe*. Springer, Berlin, 43–61.
- Pyšek P, Richardson DM, Pergl J, Jarošík V, Sixtová Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. *Trends in Ecology and Evolution* 23: 237–244. doi: 10.1016/j.tree.2008.02.002
- Pyšek P, Richardson DM, 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. doi: 10.2307/4135498
- Pyšek P, Sádlo J, Mandák B (2002) Catalogue of alien plants of the Czech Republic. *Preslia* 74: 97–186.
- Rejmánek M (2000) Invasive plants: approaches and predictions. *Austral Ecology* 25: 497–506. doi: 10.1046/j.1442-9993.2000.01080.x
- Rejmánek M, Randall R (1994) Invasive alien plants in California: 1993 summary and comparison with other areas in North America. *Madrono* 41: 161–177.
- Rejmánek M, Thomsen CD, Peters ID (1991) Invasive vascular plants of California. In: Groves RH, di Castri F (Eds) *Biogeography of Mediterranean Invasions*. Cambridge University Press, Cambridge, 81–101.
- Richardson DM, Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography* 30: 409–431. doi: 10.1191/0309133306pp490pr
- 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. doi: 10.1046/j.1472-4642.2000.00083.x
- Stohlgren TJ, Pyšek P, Kartesz J, Nishino M, Pauchard A, Winter M, Pino J, Richardson DM, Wilson JRU, Murray BR, Phillips ML, Ming-yang L, Celesti-Grapow L, Font X (2011) Widespread plant species: natives versus aliens in our changing world. *Biological Invasions* 13: 1931–1944. doi: 10.1007/s10530-011-0024-9
- Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14: 702–708. doi: 10.1111/j.1461-0248.2011.01628.x
- Weber EF (1997) The alien flora of Europe: a taxonomic and biogeographic overview. *Journal of Vegetation Science* 8: 565–572. doi: 10.2307/3237208

Winter M, Schweiger O, Klotz S, Nentwig W, Andriopoulos P, Arianoutsou M, Basnou C, Delipetrou P, Didžiulis V, Hejda M, Hulme PE, Lambdon PW, Pergl J, Pyšek P, Roy DB, Kühn I (2009) Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proceedings of the National Academy of Sciences of the United States of America* 106: 21721–21725. doi: 10.1073/pnas.0907088106