Cell PRESS

Bias and error in understanding plant invasion impacts

Philip E. Hulme[1], Petr Pyšek[1,2,3], Vojtěch Jarošík[1,2,3], Jan Pergl[2,4], Urs Schaffner[5], and Montserrat Vilà[6]

[1] The Bio-Protection Research Centre, PO Box 84, Lincoln University, Canterbury, New Zealand
[2] Institute of Botany, Department of Invasion Ecology, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic
[3] Department of Ecology, Faculty of Science, Charles University Prague, Viničná 7, CZ-128 44 Prague, Czech Republic
[4] Institute of Ecology and Evolution, University of Bern, CH-3012 Bern, Switzerland
[5] CABI, 1 Rue des Grillons, CH-2800 Delémont, Switzerland
[6] Estación Biológica de Doñana (EBD-CSIC), Avda. Américo Vespucio s/n, Isla de la Cartuja, E-41092 Sevilla, Spain

Quantitative assessments of alien plant impacts are essential to inform management to ensure that resources are prioritized against the most problematic species and that restoration targets the worst-affected ecosystem processes. Here, we present the first detailed critique of quantitative field studies of alien plant impacts and highlight biases in the biogeography and life form of the target species, the responses assessed, and the extent to which spatial variability is addressed. Observed impacts often fail to translate to ecosystem services or evidence of environmental degradation. The absence of overarching hypotheses regarding impacts has reduced the consistency of approaches worldwide and prevented the development of predictive tools. Future studies must ensure that the links between species traits, ecosystem stocks, and ecosystem flows, as well as ecosystem services, are explicitly defined.

Challenging the impact of impact studies

It has long been recognized that if an alien plant species (see Glossary) can significantly alter ecological and/or ecosystem processes, then it could also determine the functioning of a whole ecosystem [1]. Increasing numbers of studies (Box 1) have documented how invasion by a single alien plant species can alter biodiversity [2], hydrology [3], nutrient cycling [4], soil properties [5], disturbance regimes [6], and fire frequency [7], as well as many above- and belowground trophic interactions [8]. The frequent, and often marked, effects observed on these processes highlight that certain alien plants can modify the functioning of whole ecosystems [9,10]. However, although research has progressively characterized and quantified the ecological impacts of alien plants, it is clear that quantitative assessments of comparable invaded and uninvaded ecosystems remain scarce (Box 1). Furthermore, recent analyses reveal that alien plant impacts are strongly context dependent and variable, both in magnitude and direction [11,12]. As a consequence, critics have pointed out that ecological impacts are often assumed rather than proven and cannot yet be predicted, such that current management of alien plants might be poorly targeted or completely unwarranted [13]. It is therefore imperative that ecologists address these shortcomings to deliver a better quantitative evidence base for alien plant management.

Although several recent reviews address the ecological impacts of alien species [14–18], there has not yet been a critical appraisal of current research approaches and their limitations. We use the most comprehensive database on quantitative studies of terrestrial alien vascular plant

Glossary

Alien: an organism occurring outside its natural past or present range and dispersal potential, whose presence and dispersal is due to intentional or unintentional human action.
Ecological impact: a significant change, whether an increase or decrease, in an ecological or ecosystem process that might be perceived as being of positive, negative, or neutral value to humans.
Ecological process: an interaction among organisms, such as herbivory, predation, competition, pollination, and seed dispersal, that frequently regulates the dynamics of ecosystems and the structure of biological communities.
Ecosystem process: the flow of energy and materials through the arrangement of biotic and abiotic components of an ecosystem, including net primary production, trophic transfer from plants to animals, nutrient cycling, water dynamics, and heat transfer.
Ecosystem services: ecosystem processes that provide benefits and value to humans.
Environmental degradation: any change or disturbance to the environment perceived to be deleterious or undesirable as a consequence of changes in ecosystem stocks and/or flows or other interference with the ecological systems of which they are part.
Flow: transfer of materials in an ecosystem from stocks and between pools (e.g., C sequestration or species extinction rate).
Invasion or invasive: refers to established alien organisms that are rapidly extending their range in the new region, usually causing significant harm to biological diversity, ecosystem functioning, socio-economic values, and/or human health in invaded regions.
Invasion chronosequence: a series of locations that share similar ecosystem characteristics but have been invaded by an alien species for different lengths of time.
Plant functional diversity: the value and range of all traits considered relevant to ecosystem processes (e.g., leaf size, toughness and longevity, tissue nutrient content, capacity for symbiotic fixation of N, canopy height, and rooting depth) encompassed by plant species present in a given ecosystem.
Resident species: species present in an ecosystem that might be impacted by an alien plant. Most focus has been on effects on the native biota, but many invaded ecosystems comprise both native and alien species that might respond differently to the alien species that is the focus of study.
Stock: the amount of a material in a given pool in an ecosystem (e.g., soil C content, number of endangered species, etc.).

Corresponding author: Hulme, P.E. (philip.hulme@lincoln.ac.nz)
Keywords: biodiversity; biological invasions; ecosystem processes; functional traits; weeds

 0169-5347/$ – see front matter http://dx.doi.org/10.1016/j.tree.2012.10.010 Trends in Ecology and Evolution, April 2013, Vol. 28, No. 4

Box 1. How well are plant invasion impacts understood?

Meta-analysis has been used to estimate the effect of alien plants on resident species richness [2,37], performance [54], nutrient cycling [29], and pollinator activity [55]. Yet, the power of meta-analyses to detect consistent trends in impacts is limited by the small number of quantitative studies available, with only one meta-analysis to date able to include more than 100 published studies [11]. In addition, alien plant impacts might lead to either increases or decreases in a particular ecosystem variable and there is usually no *a priori* suggestion that any one direction should be of more concern than another. Thus, the calculation of mean effect sizes might fail to detect significant trends where both increases and decreases of a response variable occur, because they might on average cancel themselves out. This arises because the crucial effects of ecological impacts can often appear not as main effects, but in interactions with other effects. Other tools, such as data mining, might be preferable under these circumstances [12].

Using a similar underlying data set, interpretation of alien plant impacts based on meta-analysis [11] and data mining [12] were subtly different. In our assessment of sources of bias in the detection of alien plant impacts, we use the data-mining data set that quantitatively compared the frequencies of significant and non-significant impacts and their directions on a broad range of species and ecological impacts in both invaded (including experimental alien addition) and uninvaded (including experimental alien removal) plots in natural or semi-natural ecosystems. A total of 25 impact responses were assessed that included the abundance, diversity, richness, biomass, fitness (e.g., fecundity), and performance (e.g., survivorship) of resident plant and animal species; animal and microbial activity; soil parameters, such as organic matter content; nutrients (e.g., C, N, and phosphorous pools and fluxes); minerals; pH; soil fauna and microbial richness and diversity; and plant tissue measures, such as litter decomposition rate, nutrient and mineral content, and flammability. The data set comprised 287 studies (representing 1551 case studies across 167 taxa) addressing the impact of alien plant species that statistically tested for its significance. Intriguingly, although the data set highlights the rapid increase in quantitative studies on alien plant impacts in recent years, it also reveals that the diversity of species on which this knowledge is based is increasing at a lower rate (Figure I).

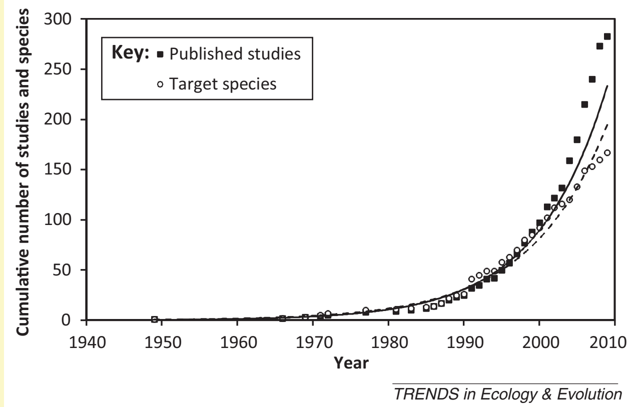

Figure I. Cumulative temporal trend in the number of published quantitative impact studies and target alien plant species.

impacts assembled to date [12] to address three fundamental questions that underpin current knowledge of alien species impacts: (i) is the pool of species for which there is quantitative information on impacts representative of invasive alien plants or biased towards other criteria?; (ii) does a sound ecological basis exist for the choice of response variables examined, or is this driven by convenience or fashion?; and (iii) are quantitative studies adequately addressing the sources of variability in impacts to provide improved understanding of their context dependence? Our findings highlight that the approaches adopted to date in large part fail to deliver predictive and practical insights due to biases in biogeography and life form of the target species, the idiosyncratic choice of responses assessed, and the lack of explicit controls addressing spatial variability. By pointing out research and methodological gaps, we propose a new agenda for impact studies that aims to deliver greater consensus regarding the threat posed by alien plants and to provide a more rigorous basis for their management.

Species biases: are we cheating if we study cheatgrass?

Even the most ardent advocates of controlling alien plants acknowledge that only a fraction of naturalized species, perhaps as few as 10%, ultimately have a noticeable impact on natural ecosystems [17]. However, given that there are at least 3427 naturalized alien plant species in North America [19], 5789 in Europe [20], 2741 in Australia, and 2136 in New Zealand [21] then, even accounting for species naturalized in more than one region, the number causing impacts worldwide will be in the thousands. Yet, robust quantitative assessments of ecological impacts have been undertaken for fewer than 200 alien plants, highlighting a considerable knowledge deficit (Box 1). Are these studies representative of alien plant impacts as a whole? It does not appear so, given that only nine species account for one-third of all quantitative assessments of ecological impacts: cheatgrass (*Bromus tectorum*, 7.6% of studies), Japanese knotweed (*Fallopia japonica*, 6.1%), Port Jackson willow (*Acacia saligna*, 4.0%), giant goldenrod (*Solidago gigantea*, 3.6%), common reed (*Phragmites australis*, 2.6%), boneseed (*Chrysanthemoides monilifera*, 2.4%), giant hogweed (*Heracleum mantegazzianum*, 2.3%), purple loosestrife (*Lythrum salicaria*, 2.2%), and crested wheatgrass (*Agropyron cristatum*, 2.1%). Several high-profile alien plants that are viewed as particularly problematic are either absent from the database [e.g., miconia (*Miconia calvescens*) and kudzu (*Pueraria montana*)] or have been the focus of only a single quantitative study [e.g., strawberry guava (*Psidium cattleianum*) and Brazilian pepper (*Schinus terebinthefolius*)]. By contrast, several species for which quantitative impact studies exist are colonists of highly transformed human landscapes and rarely the target for specific management [e.g., slender wild oat (*Avena barbata*), black mustard (*Brassica nigra*), perennial ryegrass (*Lolium perenne*), and red clover (*Trifolium pratense*)].

Over 80% of impact studies only examine a single species of alien plant and this limits the options for comparative studies of different species to test for phylogenetic, dominant versus subordinate, or functional trait signals. Most invaded ecosystems contain several species of alien plant and a focus of just one, albeit the most abundant, might miss more subtle effects of rare aliens in the ecosystem [22]. In addition, removal of the most abundant alien plant can often result in subordinate alien species becoming dominant [23]. Quantitative impact studies tend to show a bias towards species classed as being invasive in America and Europe, whereas Africa and

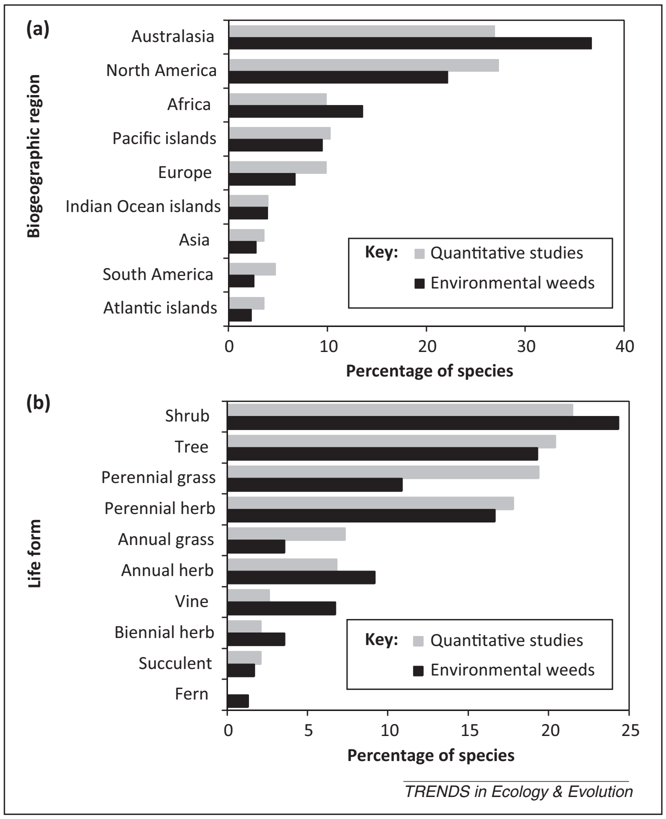

Figure 1. Biogeographic and life-form biases in the representation of alien plant species for which ecological impacts have been quantitatively assessed. Comparisons between the proportion of alien plants for which the statistical significance of impacts has been assessed and the representation of 435 terrestrial environmental weeds [24] in relation to **(a)** the biogeographic region in which a focal species was classed as invasive (χ^2 = 16.09, df 8, P = 0.031) and **(b)** plant life form (χ^2 = 26.99, df 10, P = 0.003).

Australasia are under-represented (Figure 1a). Similarly, perennial herbs and grasses, as well as annual grasses, are over-represented, whereas ferns or vines are under-represented in impact studies (Figure 1b). Although it is unrealistic to assume comprehensive coverage of all species that might cause impacts, it might be expected that those perceived as posing the greatest threat to ecosystems would be the focus of more effort. Yet, quantitative impact studies have been undertaken for only a quarter (115) of the 435 terrestrial species listed in a major compendium of the worst alien environmental weeds in the world [24]. Thus, the scientific evidence base for the impacts of many species perceived as among the worst invasive alien plants remains weak. Furthermore, for those 115 species listed in the global compendium of alien environmental weeds [24], no relation exists between the frequency with which the impact of a species has been quantitatively assessed and the number of global regions in which it was classed as either naturalized or invasive (Figure S1 in the supplementary material online). For example, although more quantitative studies have been undertaken on cheatgrass than on any other species, it is only classed as invasive in the natural areas of western USA. Thus, neither the perceived magnitude of impact to natural ecosystems nor species global prevalence is the primary criterion in species selection.

There are sound reasons to study species with negligible impacts to understand factors that might structure plant community assembly [25,26], but the considerable effort expended on a few species does not seem effective unless these taxa represent particularly good model systems. Clearly, there are also benefits in examining a species for which ecological impacts are already known, either to extend the range of ecological variables examined or increase the number of study locations. However, it might also be true that researchers tend to hedge their bets and focus on species for which quantitative data from other studies on impacts have already been published. This probably underlies the recent profusion of publications examining the impact of the alien Himalayan balsam (*Impatiens glandulifera*) on plant–pollinator interactions in Europe [27]. It might also explain why the recent increase in the cumulative number of quantitative studies examining alien plant impacts has, at least in recent years, not been matched by a similar increase in the number of species examined (Box 1).

Made to measure: time to tailor response variables to hypotheses

A considerable number of plant, animal, microbial, and soil variables might be impacted by an alien plant, with consequences for ecosystem processes and the services that they provide (Box 1). Consistent, significant impacts have been found on some response variables (e.g., survival of resident biota, activity of resident animals, resident community productivity, mineral and nutrient content in native plant tissues, and fire frequency and intensity), whereas for others (species richness, diversity, and soil resources) the significance of impacts appears determined by interactions between species traits and the biome invaded [12]. A key question is why certain responses are more likely to change in direction and magnitude following invasion than are others, and this would entail examining a larger set of responses on a small number of alien species identified as suitable model systems. Researchers appear no closer to answering this question given that many studies only examine one or two response variables at most (mean = 2.00 ± 0.06, Figure 2a), usually soil nutrients (16.2%), plant biomass (9.8%), or plant richness (8.6%). Few studies have examined impacts on the abundance or richness of soil fauna and microbes (both <1%), despite biotic belowground processes gaining importance in current understanding of the drivers and impacts of plant invasions [10,28]. Do differences in the extent to which individual responses have been studied reflect *a priori* hypotheses regarding impacts? Unfortunately not; rather, these differences indicate that the most frequently studied responses are simply those that have been studied the longest (Figure S2 in the supplementary material online), probably because they are technically simpler to measure and more conspicuous to the eye. A general pattern is that ecological stocks, such as species abundance and diversity, and soil nutrient and mineral pools, were among the first impacts to have been studied, whereas ecological processes, such as fecundity, animal behavior microbial activity, and decomposition, came later.

The increasing variety of different responses examined over time has resulted in some complementarity in that the more studies undertaken on a species, the greater number

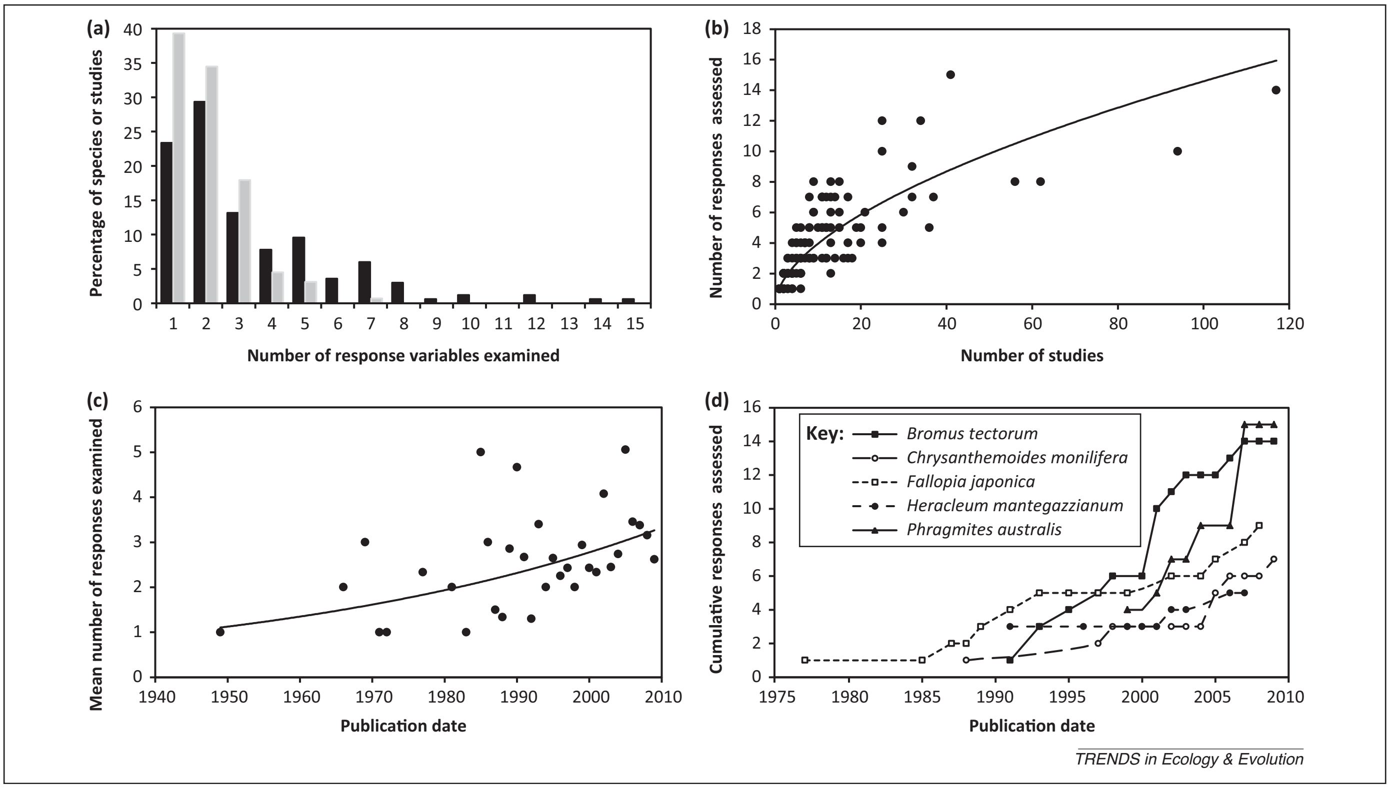

Figure 2. Biases in the number, timing, and combination of response variables assessed to measure the impacts of alien plants. The frequency with which different impact responses have been examined in relation to **(a)** individual quantitative impact studies (black bars) and alien plant species (gray bars), **(b)** overall number of studies undertaken per species (Pearson r = 0.752, df 165 $P < 0.001$), **(c)** as a function of publication date (r = 0.464, df 31 $P = 0.006$), and **(d)** over time for five of the most frequently studied alien plant species.

of responses examined (Figure 2b). Indeed, the mean number of responses examined per study has tended to increase over time (Figure 2c), but even accounting for this increase, the number of responses examined per species is still low (mean 3.37 ± 0.20, Figure 2a). Furthermore, for the most frequently studied species, the incremental gain in knowledge per additional study is small, with on average one new response per species added per annum (Figure 2d). Overall, the rationale for which response variables have been included in a study does not appear clear and there are no obvious suites of variables that consistently co-occur.

The large number of variables that might change following plant invasion demands a systematic approach and a mechanism for prioritization. Although there are recent calls for new response variables to be assessed [14,15,29], researchers still need to make better use of those that are currently studied before embarking on yet more measures. Indeed, it may be sufficient to assess only a few responses if this triggers management action. A potential way forward is to ensure that the following four key considerations are addressed in impact studies (Table 1).

First, the choice of which impact responses to measure should be hypothesis led and more strongly linked to the existing body of evidence relating plant functional traits to ecosystem processes [30], particularly in relation to trait differences between the alien and resident plant species in the community. Second, response variables should not be assessed in isolation but viewed as inter-related components of ecosystems that might be directly or indirectly

Table 1. Representative ecosystem services and their underpinning stocks and flows, with examples of associated alien plant species traits that might impact upon them

Ecosystem service	Stock	Flow	Plant trait
Aesthetic appeal	Species richness	Species turnover	Resource use efficiency
Productivity	Plant biomass	ANPP	Canopy height and growth rate
Heat transfer	Canopy structure	Evapotranspiration	Canopy reflectance
Soil formation	Soil organic matter	Litter decomposition and root turnover	Leaf C:N:P content and rooting depth
C storage	Soil C pool	Soil respiration	Leaf lifespan
Soil fertility	Soil available N	N mineralization and nitrification	N fixation
Water cycling	Soil moisture content	Evapotranspiration and infiltration	Water use efficiency and root:shoot ratio
Soil or water quality	Soil or water conductivity and pH	Salinization and sodification	Salt tolerance and root activity and/or exudates
Low fire risk	Vegetation flammability	Water stress	Leaf moisture content
Pollination	Connectance	Visitation rate	Flowering phenology

impacted by an alien plant [31,32]. Thus, response variables need to be integrated, such that studies on the impacts of alien plants on particular ecosystem stocks should also assess changes to their corresponding ecosystem flows (Table 1). For example, rather than study the impacts of an alien plant on three different ecosystem stocks [e.g., plant species richness, soil carbon (C) pool, and pH], it would be better to focus on the impacts on one particular stock (e.g., soil C pool) and several of its respective flows (e.g., soil respiration and litter decomposition). An increased focus on mechanisms will help distinguish direct from indirect effects of alien plants on ecosystems [33] and identify which response variables might be strongly context dependent. Such an approach could also identify where stocks have changed, but there is no clear link to the alien plant, indicating that the species is responding to, rather than driving, the stock change [34].

Third, the magnitude of a response should be quantified along a gradient of alien plant abundance [35,36]. It is neither surprising nor important to quantify that an alien plant with close to 100% cover reduces resident floristic richness. Unless the species always occurs at such high densities, it will be more instructive to examine a representative range of plant abundances and establish whether impacts scale non-linearly with abundance. Fourth, if the aim of quantifying impacts is to assist management prioritization, then any change should relate to potential effects on ecosystem services (Table 1). Many quantitative studies examine changes in plant species richness or diversity [2,11,37] but are insufficiently detailed to assess the consequences of these changes on ecosystem functioning and services [38,39].

Now you see it, now you don't: variability and context dependence of alien plant impacts

One of the challenges in prioritizing the management of alien plants is that their impacts can be perceived differently and this often depends on the particular response variable considered and the ecosystem invaded. Two measures might provide useful insights into the variability of impacts: impact frequency (the proportion of cases where a significant change in the response variable was found) and impact reliability (the proportion of significant changes that were in the most frequently observed direction). For example, saltcedar (*Tamarix ramosissima*) and purple loosestrife have impact frequencies (0.56 and 0.50, respectively) and reliabilities (0.57 and 0.64, respectively) that indicate that significant impacts have been recorded in only approximately 50% of the studies and they are just as likely to lead to increases as much as decreases in response variables. This variability undoubtedly fuels the ongoing debate regarding whether these species pose significant ecological problems, but these differences in perspective are dependent upon the response assessed [40,41]. Intriguingly, the source of variation differs for these species: purple loosestrife has variable impacts across a wide range of response variables, whereas the variation in saltcedar arises because it has a significant impact on some responses but not others.

Although impact frequency and reliability are uncorrelated (Figure S3 in the supplementary material online), across all species, they are both a decreasing function of the number of studies undertaken (Figure 3a,b). Thus, the more studies that are undertaken on the impacts of a particular species, the smaller the proportion of significant results found and the larger the likelihood of these being of a different sign (increase or decrease). Two methodological aspects shape this relation. First, species of alien plant that have only been examined once are more likely to reveal a significant impact than are species that are examined more frequently, whether examined across all response types or separately for each plant, animal, or soil component (Table S1 in the supplementary material online). This is understandable if researchers focus initial

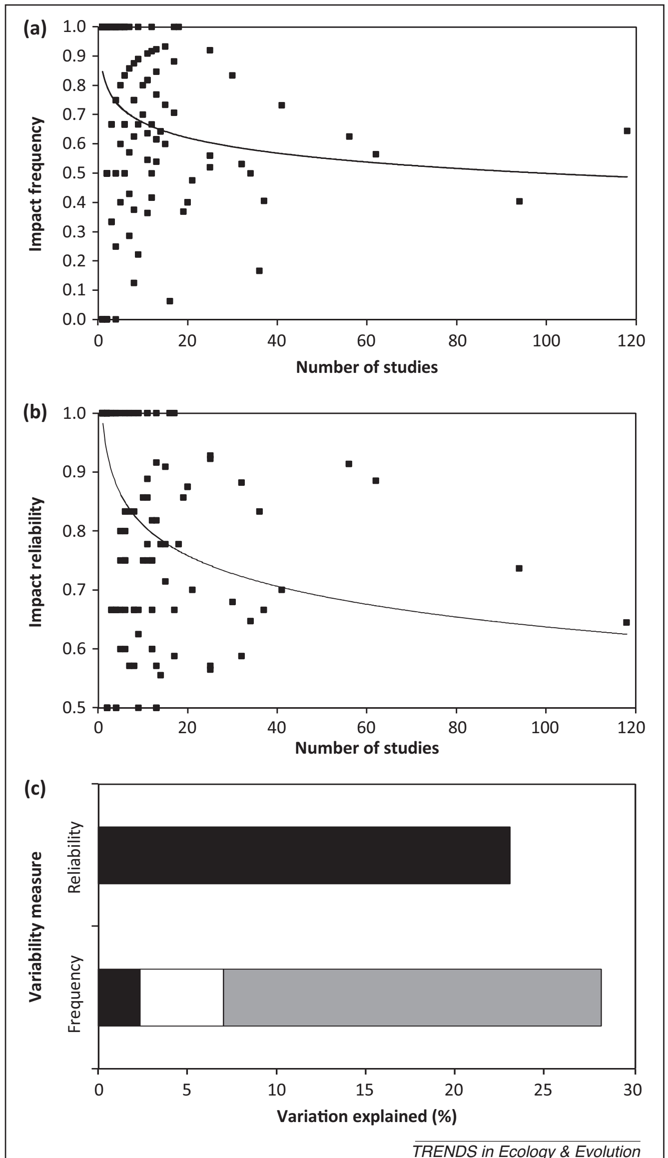

Figure 3. Sources of variability in alien plant impacts as described by impact frequency (the proportion of all cases where a significant change in the response variable was found) and impact reliability (the proportion of all significant changes that were in the most frequently observed direction). There was a negative relation between sample size and **(a)** impact frequency [$y = -0.075\ln(x) + 0.8476$, $R^2 = 0.0847$, $P = 0.006$] and **(b)** impact reliability [$y = -0.075\ln(x) + 0.9834$, $R^2 = 0.2394$, $P < 0.001$]. These relations persist even without the outlier (cheatgrass). In **(c)**, the contribution of three random effects [sample size (black bar), alien plant species (white bar), and response variable (gray bar)] to overall variation in impact frequency and reliability was derived from a maximum likelihood variance partitioning procedure [56].

efforts towards the potentially most impacted study sites and response variables. Second, further studies extend results to less impacted sites or responses either deliberately as a form of contrast or simply as a result of sampling variation. However, this emphasizes that results from single studies at single locations or years might not be widely generalizable. Variance partitioning highlights that impact frequency is primarily a function of the response variable examined (as discussed above) and, to a lesser extent, species identity and the number of cases (i.e., between-study variation). By contrast, variation in impact reliability is entirely a function of the number of cases (Figure 3c). These patterns indicate that the likelihood that an alien plant will have a significant impact is largely down to what response is measured, but whether it results in an increase or a decrease in the variable examined is dependent on its location.

Even for the same response variable, the impacts of an alien plant are context dependent and shaped by the ecological setting. At least six sources of variability can influence alien plant impacts: (i) the spatial scale of the study, with impacts more likely significant at small scales [2,15]; (ii) the length of time an alien has been at a site [42]; (iii) intraspecific phenotypic or genotypic variation in plant performance [43,44]; (iv) differences in local alien abundance [36]; (v) methodological differences, such as where experimental species additions and removals result in different outcomes [35]; and (vi) attributes of the location. The role of location in influencing the impact reliability is illustrated by precipitation gradients that shape whether alien plants increase or decrease soil nutrient dynamics. For example, in the USA, nitrogen (N) cycling rates are increased following cheatgrass invasion in cool deserts, but are decreased in arid grasslands [4]; in New Zealand, hawkweed (*Hieracium pilosella*) increased nutrient cycling in warm, dry tussock grassland but decreased it in cooler, wetter sites [45]; whereas, in the Mediterranean, soil N and C content are decreased by iceplant (*Carpobrotus edulis)* on the more mesic island of Menorca, but are increased on the more xeric island of Crete [46]. Moreover, spatial variation in impacts can depend on the presence of other potential drivers of ecosystem change. Along the Colorado river, salt concentration in soils increases at a faster rate under saltcedar-dominated stands than under native stands along the free-flowing upper sections but not the heavily regulated lower sections [47]. Variation in impacts attributable to location is probably the norm but most studies assess only a few different locations (median = 4) when attempting to quantify impacts. The explicit assessment of how the effects of alien plants vary along climate, productivity, or anthropogenic gradients (grazing, N deposition, etc.) would help better understand the context dependence of impacts and inform management so that it can be tailored to local environmental conditions.

Concluding remarks

Considerable effort and cost are expended in attempts to control alien plants [48,49]. A precautionary approach implies that managers need not wait for quantitative impact data before acting. However, ill-informed management runs the risk that resources will not be prioritized against the most problematic species, and restoration efforts will fail to target the ecosystem processes that have been most affected. Thus, quantitative assessments of alien plant impacts are essential because several studies have shown alien plants targeted for management to have almost no impact on the invaded ecosystem [50,51]. Yet, the targets for scientific assessment often do not meet the needs of those responsible for prioritizing the management of alien plants [52].

Unfortunately, as a result of taxonomic, biogeographic, and life-form biases, it is impossible to assess adequately the frequency with which aliens impact upon ecosystems or how many ecosystems they might substantially affect. Current knowledge of impacts is drawn largely from a relatively small number of herbaceous species in the temperate environments of the northern hemisphere, which more than likely reflects the coincidence of research effort and the tractability of these systems for study rather than management priorities [53]. This knowledge is also limited to a few, easily measured sets of responses and the changes observed often do not translate easily to measures of ecosystem services or evidence of environmental degradation. Logical integration of the set of response variables examined in relation to the attributes of the alien plant and resident community, as well as the consequences upon ecosystem services (Table 1), would reduce the considerable intraspecific heterogeneity in observed impacts. This would also be the key to better management prioritization. Variation in impacts should be expected and researchers must try to incorporate such variation in their designs by specifically examining impacts across explicit environmental gradients or invasion chronosequences. Recognizing that researchers might only have the resources to measure a few responses, pragmatic approaches must be implemented that ensure that the links are defined between species traits, ecosystem stocks and flows, as well as services.

Acknowledgments

The authors would like to thank two anonymous referees for constructive comments on a previous version of this manuscript. P.P., V.J., and J.P. acknowledge the support from long-term research development project no. RVO 67985939 (Academy of Sciences of the Czech Republic), grant no. P504/11/1028 (Czech Science Foundation) and institutional resources of Ministry of Education, Youth and Sports of the Czech Republic. P.P. acknowledges the support by the Praemium Academiae award from the Academy of Sciences of the Czech Republic and J.P. from SCIEX (project ALIEN). M.V. was supported by the Spanish Ministry of Science projects CGL2009-7515 and CSD2008-00040 and the Junta de Andalucía RNM-4031. U.S. was supported by the Swiss National Science Foundation (NCCR project 'Plant Survival').

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.tree.2012.10.010.

References

1 Vitousek, P.M. (1990) Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57, 7–13

2 Powell, K.I. *et al.* (2011) A synthesis of plant invasion effects on biodiversity across spatial scales. *Am. J. Bot.* 98, 539–548

3 Le Maitre, D.C. (2004) Predicting invasive species impacts on hydrological processes: the consequences of plant physiology for landscape processes. *Weed Technol.* 18, 1408–1410
4 Ehrenfeld, J.G. (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6, 503–523
5 Ehrenfeld, J.G. (2010) Ecosystem consequences of biological invasions. *Annu. Rev. Ecol. Evol. Syst.* 41, 59–80
6 Mack, M.C. and D'Antonio, C.M. (1998) Impacts of biological invasions on disturbance regimes. *Trends Ecol. Evol.* 13, 195–198
7 Brooks, M.L. *et al.* (2004) Effects of invasive alien plants on fire regimes. *Bioscience* 54, 677–688
8 Levine, J.M. *et al.* (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proc. R. Soc. Lond. B: Biol. Sci.* 270, 775–781
9 Pyšek, P. and Richardson, D.M. (2010) Invasive species, environmental change and management, and health. *Annu. Rev. Environ. Resour.* 35, 25–55
10 Wardle, D.A. *et al.* (2011) Terrestrial ecosystem responses to species gains and losses. *Science* 332, 1273–1277
11 Vilà, M. *et al.* (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.* 14, 702–708
12 Pyšek, P. *et al.* (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biol.* 18, 1725–1737
13 Davis, M. *et al.* (2011) Don't judge species on their origins. *Nature* 474, 153–154
14 Drenovsky, R.E. *et al.* (2012) A functional trait perspective on plant invasion. *Ann. Bot.* 110, 141–153
15 Eviner, V.T. *et al.* (2012) Measuring the effects of invasive plants on ecosystem services: challenges and prospects. *Invasive Plant Sci. Manage.* 5, 125–136
16 Strayer, D.L. (2012) Eight questions about invasions and ecosystem functioning. *Ecol. Lett.* 15, 1199–1210
17 Simberloff, D. (2011) How common are invasion-induced ecosystem impacts? *Biol. Invasions* 13, 1255–1268
18 Simberloff, D. *et al.* (2013) Impacts of biological invasions: what's what and the way forward. *Trends Ecol. Evol.* 28, 58–66
19 Qian, H. and Ricklefs, R.E. (2006) The role of exotic species in homogenizing the North American flora. *Ecol. Lett.* 9, 1293–1298
20 Lambdon, P.W. *et al.* (2008) Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. *Preslia* 80, 101–149
21 Diez, J.M. *et al.* (2009) Learning from failures: testing broad taxonomic hypotheses about plant naturalization. *Ecol. Lett.* 12, 1174–1183
22 Peltzer, D.A. *et al.* (2009) Punching above their weight: low-biomass non-native plant species alter soil properties during primary succession. *Oikos* 118, 1001–1014
23 Hulme, P.E. and Bremner, E.T. (2006) Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. *J. Appl. Ecol.* 43, 43–50
24 Weber, E. (2003) *Invasive Plant Species of the World: a Reference Guide to Environmental Weeds*, CABI
25 MacDougall, A.S. *et al.* (2009) Plant invasions and the niche. *J. Ecol.* 97, 609–615
26 Sax, D.F. *et al.* (2007) Ecological and evolutionary insights from species invasions. *Trends Ecol. Evol.* 22, 465–471
27 Schweiger, O. *et al.* (2010) Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. *Biol. Rev.* 85, 777–795
28 Kardol, P. and Wardle, D.A. (2010) How understanding aboveground–belowground linkages can assist restoration ecology. *Trends Ecol. Evol.* 25, 670–679
29 Liao, C.Z. *et al.* (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytol.* 177, 706–714
30 Westoby, M. and Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends Ecol. Evol.* 21, 261–268
31 Reiss, J. *et al.* (2009) Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol. Evol.* 24, 505–514
32 Shea, K. and Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* 17, 170–176
33 Hulme, P.E. (2006) Beyond control: wider implications for the management of biological invasions. *J. Appl. Ecol.* 43, 835–847
34 Didham, R.K. *et al.* (2005) Are invasive species the drivers of ecological change? *Trends Ecol. Evol.* 20, 470–474
35 Truscott, A-M. *et al.* (2008) Consequences of invasion by the alien plant *Mimulus guttatus* on the species composition and soil properties of riparian plant communities in Scotland. *Perspect. Plant Ecol.* 10, 231–240
36 Maron, J.L. and Marler, M. (2008) Effects of native species diversity and resource additions on invader impact. *Am. Nat.* 172, S18–S33
37 Gaertner, M. *et al.* (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Prog. Phys. Geogr.* 33, 319–338
38 Pejchar, L. and Mooney, H.A. (2009) Invasive species, ecosystem services and human well-being. *Trends Ecol. Evol.* 24, 497–504
39 Mace, G.M. *et al.* (2012) Biodiversity and ecosystem services: a multilayered relationship. *Trends Ecol. Evol.* 27, 19–26
40 Stromberg, J.C. *et al.* (2009) Changing perceptions of change: the role of scientists in *Tamarix* and river management. *Restor. Ecol.* 17, 177–186
41 Lavoie, C. (2010) Should we care about purple loosestrife? The history of an invasive plant in North America. *Biol. Invasions* 12, 1967–1999
42 Strayer, D.L. *et al.* (2006) Understanding the long-term effects of species invasions. *Trends Ecol. Evol.* 21, 645–651
43 Lankau, R.A. *et al.* (2009) Evolutionary limits ameliorate the negative impact of an invasive plant. *Proc. Natl. Acad. Sci. U.S.A.* 106, 15362–15367
44 Saltonstall, K. (2002) Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *Proc. Natl. Acad. Sci. U.S.A.* 99, 2445–2449
45 Scott, N.A. *et al.* (2001) Biogeochemical impact of *Hieracium* invasion in New Zealand's grazed tussock grasslands: sustainability implications. *Ecol. Appl.* 11, 1311–1322
46 Vilà, M. *et al.* (2006) Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. *J. Biogeogr.* 33, 853–861
47 Merritt, D. and Shafroth, P. (2012) Edaphic, salinity, and stand structural trends in chronosequences of native and non-native dominated riparian forests along the Colorado River, USA. *Biol. Invasions* 14, 2665–2685
48 Vilà, M. *et al.* (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Front. Ecol. Environ.* 8, 135–144
49 Hulme, P.E. (2012) Weed risk assessment: a way forward or a waste of time? *J. Appl. Ecol.* 49, 10–19
50 Hejda, M. and Pyšek, P. (2006) What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? *Biol. Conserv.* 132, 143–152
51 Meffin, R. *et al.* (2010) Experimental introduction of the alien plant *Hieracium lepidulum* reveals no significant impact on montane plant communities in New Zealand. *Divers. Distrib.* 16, 804–815
52 Andreu, J. *et al.* (2009) An assessment of stakeholder perceptions and management of noxious alien plants in Spain. *Environ. Manage.* 43, 1244–1255
53 Pyšek, P. *et al.* (2008) Geographical and taxonomic biases in invasion ecology. *Trends Ecol. Evol.* 23, 237–244
54 Thomsen, M.S. *et al.* (2009) Evidence for impacts of nonindigenous macroalgae: a meta-analysis of experimental field studies. *J. Phycol.* 45, 812–819
55 Morales, C.L. and Traveset, A. (2009) A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecol. Lett.* 12, 716–728
56 Norušis, M. (2011) *IBM SPSS Statistics 19 Guide to Data Analysis*, Addison Wesley