Bias and error in understanding plant invasion impacts

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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.).

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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).

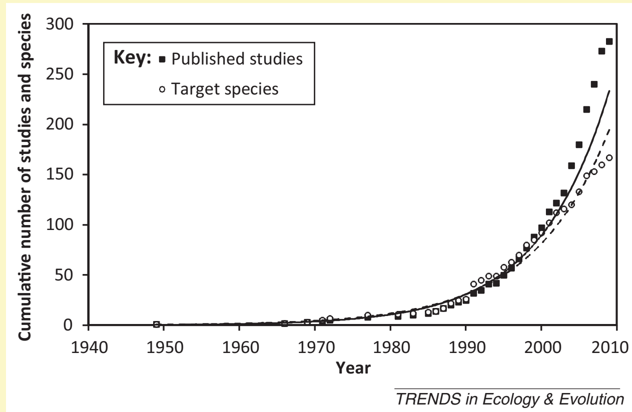

Figure I. Cumulative temporal trend in the number of published quantitative impact studies and target alien plant species.

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