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COMMENTARY

# The biodiversity impacts of non-native species should not be extrapolated from biased single-species studies

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**Abstract** The presence, diversity and abundance of non-native plant species in natural vegetation are common condition indicators used to determine conservation status, with consequences for management strategies and investment. The rationale behind non-native species metrics as condition indicators is the assumption that non-natives have negative consequences on native biodiversity and habitat condition. The case against non-native species is not so clear-cut, with some studies reporting neutral or even facilitative interactions, often depending on spatial scale. Observational and experimental evaluations of the impact of particular non-native species on biodiversity provide a vital evidence-base for general conservation management strategies. Unintentionally though, many studies that quantify the impacts of non-native species have resulted in a publication bias in which species with known impacts are selected for investigation far more often than benign species. Here we argue that meta-analyses of the impacts of individual non-native species on natives, no matter how meticulous or objective, should not be generalized beyond the set of 'training' species. The likelihood of such extrapolation is increased when meta-analyses are reported with little qualification as to the skewed sampling towards problematic species, and because alternative findings such as non-native assemblages having

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positive interactions with native biodiversity, are under-reported. To illustrate, we discuss two meta-analyses that make general conclusions from impact studies skewed towards 'transformers', the most extreme invaders. We warn that if generic non-native species management strategies were to be based on these conclusions, they could not only fail to meet objectives but in some instances harm native biodiversity.

**Keywords** Invasive species · Weeds · Publication bias · Biodiversity conservation · Condition indicators

## Introduction

Non-native plant species are considered to cause negative impacts on biodiversity so pervasively that their presence is used as a general indicator of biodiversity condition (Gibbons and Freudenberger 2006; Turner 2012). Deleterious aspects of biological invasions are the most frequently cited. The assumptions that non-native species pose a general threat to ecosystems, and that invasiveness is a proxy for impact, are often treated as basic tenets of biodiversity conservation (Gaertner et al. 2009). In particular cases, such generalizations appear to hold. For example, Marcantonio et al. (2014) found that the presence of any of 18 non-native species recorded in a coastal dune system significantly reduced native plant species abundance. Nevertheless, reports of positive interactions between non-native species and native biodiversity can be found in the literature (Sax 2002; Schlaepfer et al. 2011; Martín-Forés et al. 2017; Ward-Fear et al. 2017). Additionally, there is agreement that the direction and magnitude of effects are somewhat ecosystem and scale dependent. For example, a common finding is that interactions are negative at very small spatial scales but less dire, even tending towards positive, in terms of overall diversity at regional scales (Sax 2002; Fridley et al. 2007; Gaertner et al. 2009; Powell et al. 2011).

Recent attempts have been made to address the 'invasion paradox' (Fridley et al. 2007) and to find an emergent pattern from biological invasion literature that contains contradictory findings of positive, negative, neutral or mixed effects. One such approach is the systematic review of many case studies combined with formal meta-analysis. This typically involves analytical means to look for overall patterns in the effects of non-native species on native biodiversity, based on many separate studies on the impacts of particular species (Gaertner et al. 2009; Vilà et al. 2011; Kuebbing and Nuñez 2016). Studies on the impacts of individual non-native species are more frequently reported and often more detailed in their measurement of responses than studies on the emergent effects of non-native species assemblages (Marcantonio et al. 2014). These meta-analyses consistently find a majority of negative impacts on native species and diversity. For example, Gaertner et al. (2009) concluded from such a meta-analysis that non-native plant species negatively affect native plant species richness. In principal, this approach should provide the most thorough, objective evidence from which to draw general conclusions that can be further extrapolated to a suite of uninvestigated species and ecosystems.

However, the ability to extrapolate from meta-analyses of non-native species impacts is limited by selection bias. We argue that the conclusions of meta-analyses of this ilk cannot be generalized beyond the case studies considered due to an underlying bias in the ecological literature in which studies tend to target individual species identified a priori as problematic in terms of control or impacts to biodiversity (e.g. Badgery et al. 2005; Atwater et al. 2011; Davis et al. 2011; Rodríguez-Echeverría et al. 2013), while investigation into positive interactions or benign species is rare (Rodríguez 2006; Schlaepfer et al.

2011). A related issue is that impact metrics are also biased towards known negative impacts (such as on native plant diversity) and may not capture other positive impacts (such as provision of fauna habitat). Broad review of papers reporting the effects of individual non-native species reveals that researchers typically make such investigations to quantify known or assumed deleterious effects (Pattison et al. 2017). The studies included by Gaertner et al. (2009) were restricted further to cases where the focal invasive species was dominant. To explore the limitations of meta-analyzing the impacts of non-native species on biodiversity, we examine two examples in more detail, to highlight how the general conclusions made by these studies are skewed by selection bias towards species with extreme impacts.

## Kuebbing and Nuñez

Kuebbing and Nuñez (2016) reported a meta-analysis of pairwise interactions among non-native and native plant species, which led them to conclude that invasions may lead to more invasions. They arrived at this 'melt-down' scenario because non-natives had more negative impacts on natives than other non-natives across a set of compiled studies. In the literature cited therein, however, many non-natives are identified (and indeed deliberately targeted) as problematic for biodiversity, rendering them a biased representation of non-native species, which are diverse in taxonomy and function. In the literature contributing to the meta-analysis, Atwater et al. (2011) describe their focal weed as "one of North America's most problematic invasive plants" that "reduces native diversity", while Badgery et al. (2005) stated that their focal species "occurs over more than a million hectares" and "reduces grassland plant species diversity". Rodríguez-Echeverría et al. (2013), meanwhile, reported their invasive species "can compete with native trees," therefore "posing a threat to the conservation of forests". Elsewhere, weeds are described as having "displaced native grassland" (Malmstrom et al. 2006). These are typical examples, yet species selection biases in supporting literature are not mentioned among the acknowledged limitations in the meta-analysis.

The conclusions of the meta-analysis could be interpreted correctly if qualified as being only relevant to problematic species and not all non-natives. The only reference to degree of invasiveness made by Kuebbing and Nuñez (2016) was to categorize non-native species as 'naturalized' or 'invasive'. Those classed as naturalized, having a more benign connotation, represented a minority of the observations included, and species-level classifications were not reported. Though defining 'naturalized' as not spread beyond the point of introduction, the classification of species in the study was "based on the information provided by each study" only, suggesting species were considered naturalized if they were locally ubiquitous and sampled incidentally in the original study. It is possible that these species were in fact more widespread and could be classified as 'invasive'. Furthermore, the majority of species presumably coded as invasive very likely fall within the 'transformers' category of invasiveness sensu Richardson et al. (2000), which is reserved for species with extraordinary impacts, because they are typically introduced as relevant for intensive study in their respective papers because of their pervasive impacts. Such species are clearly not representative of non-native species impacts generally.

We analyzed and classified all 117 papers cited in the meta-analysis and found that in 44% of cases, all of the focal species were native to the study area, and no non-native species were studied. Of the remaining 56% of studies, 65% stated that the focal non-native

species was already known or assumed to be causing significant impacts or to be particularly problematic. A further 16% did not pre-empt any impacts but selected the non-native species because it was either locally dominant in the study ecosystem or because it was widely invasive and impacts were unknown. In only 19% of studies was the focal non-native species selected more incidentally.

Kuebbing and Nuñez (2016) propose asymmetric competition among non-natives and natives as a general mechanism for the accumulation of non-native species within habitat patches. Specifically, they suggested that non-native species interact negatively with other non-natives species, but even more negatively with native species, creating ecological space for further invasions. While the validity of this interesting hypothesis deserves further testing, we suggest the meta-analysis can only support it for problematic species—those hand picked for detailed investigation.

## Vilà et al.

Our second example involves a meta-analysis that considered community-level impacts of non-native species on native biodiversity, rather than interspecific interactions per se. Vilà et al. (2011) set out to find general predictions of deleterious impacts, depending on the invaded system and nature of the invading species. This approach is promising, because it may reveal more general, system-wide, impacts and is less likely to get bogged down in the idiosyncrasies of the responses of particular species.

The scope of Vilà et al. (2011) to make general conclusions from their meta-analysis was limited by the fact that they only selected studies that investigated the impact of a single non-native species rather of non-native assemblages collectively. As we have seen, studies on the impact of individual non-natives species frequently arise from existing concern over the high impacts of particularly problematic species. The literature cited in Vilà et al. (2011) is no exception. To illustrate, supporting articles for the meta-analysis introduce individual weeds they target for study as "the most important invasive species" (Witkowski 1991), a "serious environmental weed" (Turner et al. 2008), "considered to be a noxious weed in 14 states in the Eastern United States, frequently invading moist forests and stream banks and displacing native vegetation" (Oswalt et al. 2007) and having the "potential to significantly alter mediterranean-type ecosystems" (Lambrinos 2000).

To quantify the degree of selection bias, we assessed the stated reason for species selection in each of the 200 studies included in the meta-analysis. Out of 198 of the papers we could access, we found that 70% stated that the focal non-native species had major known or suspected impacts or that is was already believed to be problematic. A further 13% were not explicitly described as problematic or having impacts but were identified as dominant in the study ecosystem or more broadly. In two of the studies (1%), the focal invasive species was identified in the text as a native species. The final 16% made no reference to impact or dominance but selected the species for more incidental reasons or were neutral as to the impacts, for example testing the potential impacts of widespread but poorly investigated species.

Vilà et al. (2011) found a trend towards non-native species presence decreasing native diversity. However, ecosystem functions such as nutrient cycling were found to increase and the magnitude and direction of responses across impact categories was far from uniform. They concluded that, on average, non-native plant species reduced local plant species diversity and increased primary production, and stated that diversity impacts were

significant whereas functional impacts were minor. The article has had a major impact in the ecological literature, amassing over 800 citations. Whilst recognizing nuances in the tested responses, the study's conclusions were only qualified as to selection bias and its implications in the statement that "understanding of invasive plant impacts is restricted to relatively few dominant non-native species", while general statements throughout without qualification lead to a take-home message that non-native species generally have negative consequences for native diversity.

## Conclusion

Studies biased towards the worst offending invaders make up the majority of literature on the impacts of non-native species. Conclusions drawn from these studies should be tempered and the results discussed in a balanced light. Cases of tolerance or facilitation between natives and non-native species at ecological community level (Sax 2002; Martín-Forés et al. 2016) or of positive interactions between non-native species and native fauna (Ward-Fear et al. 2017) suggest that generalization of impact is not so straightforward and often case and impact specific. The meta-analyses we have discussed were, themselves, objective and lead to interesting conclusions. We do not suggest that such analyses should not be conducted at all. However, non-native species are far more diverse in function and impact than the relatively small number that are important enough to be singled out for individual investigation. Therefore, the conclusions of these studies are only relevant to highly invasive species, and cannot be extrapolated to diverse non-native species assemblages or to other individual non-native species. We encourage more cautious interpretation of the invasion literature in light of the obvious species and impact metric biases we have illustrated and warn that it may be erroneous to extrapolate conclusions of meta-analysis beyond those species selected for investigation.

Studies on specific non-natives, even those with a broader biodiversity context, no doubt focus on problem species because of their cost to environment and economy (Zavaleta et al. 2001) and their difficulty of control. However, species have individual attributes (Davis et al. 2011). Generalizing from studies largely targeting problematic species, without strong caveats around species selection bias, risks building a skewed evidence-base that does not recognize the positive role non-native species can play. For example, case studies revealing positive non-native–native interactions at higher ecological levels indicate that, in those cases at least, eradication may harm native biodiversity. This perhaps counter-intuitive fact deserves more attention in future research, in competition with reports of the deleterious effects of the worst species, to provide a more balanced evidence-base for conservation management.

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