Explaining the variation in impacts of non-native plants on local-scale species richness: the role of phylogenetic relatedness

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ABSTRACT

Aim To assess how the magnitude of impacts of non-native plants on species richness of resident plants and animals varies in relation to the traits and phylogenetic position of the non-native as well as characteristics of the invaded site.

Location Global.

Methods Meta-analysis and phylogenetic regressions based on 216 studies were used to examine the effects of 96 non-native plant species on species richness of resident plants and animals while considering differences in non-native species traits (life-form, clonality or vegetative reproduction, and nitrogen-fixing ability) and characteristics of the invaded site (ecosystem type, insularity and climatic region).

Results Plots with non-native plants had lower resident plant (–20.5%) and animal species richness (–26.4%) than paired uninvaded control plots. Nitrogen-fixing ability, followed by phylogeny and clonality were the best predictors of the magnitude of impacts of non-native plants on native plant species richness. Non-nitrogen-fixing and clonal non-native plants reduced species richness more than nitrogen-fixing and non-clonal invaders. However, life-form and characteristics of the invaded sites did not appear to be important. In the case of resident animal species richness, only the phylogenetic position of the non-native and whether invaded sites were islands or not influenced impacts, with a more pronounced decrease found on islands than mainlands.

Main conclusions The presence of a phylogenetic signal on the magnitude of the impacts of non-native plants on resident plant and animal richness indicates that closely related non-native plants tend to have similar impacts. This suggests that the magnitude of the impact might depend on shared plant traits not explored in our study. Our results therefore support the need to include the phylogenetic similarity of non-native plants to known invaders in risk assessment analysis.

Keywords Alien species, biological invasion, ecological impact, insularity, meta-analysis, N-fixing, phylogeny, phylogenetic regression, weeds.

INTRODUCTION

The empirical evidence for negative ecological impacts of plant invasions is mounting (Hulme et al., 2013a). One of the most prevalent impacts is a reduction in the species richness of the invaded community (Levine et al., 2003; Powell et al., 2011; Vilà et al., 2011). Local changes in species richness are important because biodiversity determines ecosystem production, efficient use of resources and ecosystem stability (Cardinale et al., 2006). The positive link between biodiversity and ecosystem
functioning is challenged by many ecosystems being invaded by non-native plant species which compete with native species, reduce the species richness of recipient communities and therefore often diminish the value of ecosystem services.

Both the direction (i.e. increase or decrease of a variable) and the magnitude of impacts of non-native species are highly context dependent (Hulme et al., 2013a). Disentangling the factors that determine the magnitude of impacts of non-native species requires exploring the dependency of impacts on species traits and ecosystem characteristics (Levine et al., 2003; Gaertner et al., 2009; Pyšek et al., 2012). Yet, despite the significant advance in identifying species traits associated with the potential of non-native species to invade (i.e. invasiveness; Pyšek & Richardson, 2007; van Kleunen et al., 2010) and differences in the vulnerability of ecosystems to invasion (i.e. invasibility; Chytrý et al., 2008), the factors modulating impacts have rarely been explored in concert (Leung et al., 2012; Pyšek et al., 2012). This is problematic, because there is no clear link between a species being categorized as invasive and the magnitude of its impacts (Ricciardi & Cohen, 2007; Andrea et al., 2009; Hulme, 2012). Thus the countless studies attempting to identify those traits that make a species invasive may not translate into a better understanding of the determinants of impact.

When making generalizations about impact-driven traits we need to consider the phylogenetic non-independence of species (Sol et al., 2008). Closely related species share morphological, physiological and ecological traits due to their common evolutionary history (Freckleton et al., 2002). In consequence, the phylogenetic position of non-native species might influence their impacts (Yessoufou et al., 2014) because phylogeny captures phenotypic traits and functional attributes of the species (phylogenetic signal in functional traits; Blomberg & Garland, 2002). It has been suggested that phylogenetic relatedness among species should be included in comparative analyses such as meta-analysis (Chamberlain et al., 2012). Unfortunately, most meta-analyses addressing the impacts of non-native plants have failed to account for phylogeny (Liao et al., 2008; Gaertner et al., 2009; Powell et al., 2011; Vilà et al., 2011; but see Castro-Diez et al., 2014).

Disentangling the relative importance of ecosystem type, species traits and phylogenetic relatedness is essential for building over-arching hypotheses on impacts and developing models to predict future invasions and their consequences. In a previous study (Vilà et al., 2011) we quantified the magnitude of the impacts of invading non-native plants on a wide range of ecological characteristics of resident species, communities and ecosystems. Here we use a substantially updated database of impact studies and focus on the effect of non-native plant species on species richness of plant and animal communities in invaded sites. To account for context dependence we test whether the direction and magnitude of impacts varies between trophic levels, characteristics of the non-native plant and the invaded site, while accounting for phylogenetic relatedness among the invading plant species.

METHODS

Literature search and data extraction

We updated the database on studies of the impact of terrestrial non-native plants on resident plant and animal species richness used by Vilà et al. (2011). We searched relevant papers on the ISI Web of Knowledge (http://www.isiwebofknowledge.com) database on 31 August 2012 with no restriction on publication year. We used the following search term combinations: (plant invader OR exotic plant OR alien plant OR plant invasion*) AND (impact* OR effect*) AND (diversity* OR richness* OR competition*). We screened the reference lists from all retrieved papers for other relevant publications, and we also included unpublished data from our own teams.

The main selection criterion for a study to be included in the database was that it quantitatively compared species richness in plots dominated by a single non-native plant species with a paired uninvaded control plot. Species richness is defined as the number of plant or animal species recorded in experimental plots. Other selection criteria with regard to the type of study and experimental design are described in Vilà et al. (2011).

From each study, we extracted mean, statistical variation (usually SE or SD) and sample size of species richness values for invaded and non-invaded plots. These data were extracted directly from tables or figures using the datathief II software (B. Thumers; http://www.datathief.org) or, in some situations, by measuring the mean and statistical variation manually using a ruler. Where it was not possible to extract the data from the published papers, we obtained them directly from the corresponding authors. Overall we examined 216 case studies on the impact of 96 non-native plant species on resident plant and animal richness (Appendix S2 in Supporting Information). This database includes 170 more cases on 12 additional non-native plant species than in Vilà et al. (2011).

Statistical analysis

Since shared evolutionary history may lead to the statistical non-independence of data (Felsenstein, 1985), we combined meta-analysis and phylogenetic regressions. Meta-analysis takes into account the between-effect and within-effect size variance (Gurevitch & Hedges, 1999) whereas the phylogenetic regression controls for the non-independence between the data points (Grafen, 1989).

For phylogenetic reconstruction we collated genetic data for the ribulose-bisphosphate carboxylase (rbcL) gene region for all non-native plant taxa with available data in the online GenBank/EBI repository (http://www.ncbi.nlm.nih.gov/). Species with no DNA data on GenBank/EBI were replaced by closely related species (within the same genus) for which DNA data were available (15 species). Our final dataset consisted of 1402 characters (base pairs) for 96 species. DNA sequence data were aligned in BioEdit version 7.0.5.3 (Hall, 1999) and manually edited. Phylogenetic relationships were estimated using Bayesian search criteria with parameter estimates obtained from the program
Impacts of non-native plants on biodiversity

RESULTS

General patterns

Among the 96 plant species included in the analysis, the most represented were Acacia spp. and Carpobrotus spp. with 14 and 10 cases of recorded impacts, respectively. N-fixing species accounted for 12.6%, and species with clonal growth or vegetative reproduction 63.1% of the total number of species, respectively. The biogeographic distribution of the studies was uneven, with the majority conducted in either temperate (40.6%) or mediterranean (35.2%) regions. Twenty per cent of studies were conducted on islands. There were 177 and 39 cases relating to the impact on native plant and animal species richness, respectively. Most studies on impacts on animal species richness refer to impacts on invertebrates (81.6%), mainly arthropods.

Non-native plants significantly decreased resident plant and animal species richness in 78.3% and 78% of the studies, respectively. On average, non-native plants decreased species richness of resident plants by 20.5% and that of resident animals by 26.4%. There was no significant difference between the magnitude of impacts on plant and animal richness (t-test, $t = 0.953$, P-value = 0.344).

Impact on plant species richness of invaded communities

Clonal growth/vegetative reproduction and N-fixing ability had a significant effect on the magnitude of the impact on plant species richness of the resident community, but there were no significant differences among life-forms, ecosystem types, biogeographic regions or insularity (Table 1). Grafen’s $s = 0.517$ indicated that there was a correlation structure induced by shared evolutionary history (i.e. a phylogenetic signal) in the impact of non-native plants on species richness of resident plants. The best predictor of the magnitude of impact was N-fixing ability, followed by phylogeny and clonal growth.
invasions can inflict cascading effects across trophic levels. These examples show that in terrestrial ecosystems, plant invasions can reduce bird species richness as a result of there being fewer arthropods upon which to forage (Holland-Clift et al., 2011). The type of invaded ecosystem and region were not of great significance in determining the net magnitude of impacts, except for a stronger decrease in animal species richness on islands compared with mainland regions. Our results suggest that in terrestrial ecosystems, plant invasions can inflict cascading effects across trophic levels.

**Table 1** Relative importance of the variables and the phylogeny in explaining the size of the impact of non-native plant species on plant and animal richness. We present the differences in the Akaike information criterion (AIC) between the full model and the model without the variable of interest. A difference in AIC of more than 2 is considered as a strong indication that the variable is important and can be considered to be significant, while a difference less than 2 is usually considered as non-significant (n.s.).

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Plant richness</th>
<th>Animal richness</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clonal growth</td>
<td>10.89</td>
<td>n.s.</td>
</tr>
<tr>
<td>Life-form</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>N-fixing</td>
<td>172.57</td>
<td>n.s.</td>
</tr>
<tr>
<td>Phylogeny</td>
<td>24.66</td>
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<td>4.99</td>
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The effect of clonal growth was tested for all life-forms except vines. Clonal invaders decreased resident plant richness more than non-clonal invaders (Fig. 1). The effect of N-fixation could only be tested for trees, perennial forbs and shrubs. For each of these life-forms, non-N-fixing species decreased plant species richness while N-fixing species did not have a significant effect (Fig. 2).

**Impact on animal species richness of invaded communities**

Only the phylogenetic position of invading plants (Grafen’s = 0.205) and insularity influenced the effect size of impact on animal richness in invaded communities (Table 1). These two significant predictors were of about the same relative importance. On average, the decrease in animal richness in invaded communities was stronger on islands than mainlands.

**DISCUSSION**

Overall, non-native plants decrease plant and animal species richness in the invaded community to the same extent. Some studies reported impacts on both resident plant and animal species richness. There were cases reporting reductions in vertebrate species richness due to habitat alteration or changes in feeding resources caused by non-native plants. For example, invasion of European meadows by goldenrods, *Solidago* spp., reduces bird species richness as a result of there being fewer native plant and insect species and thus fewer food resources for birds (Skórka et al., 2010). Similarly, in south-eastern Australia, riparian areas invaded by willows, *Salix rubens*, host fewer bird species because a reduction in native shrub and tree cover leads to fewer arthropods upon which to forage (Holland-Clift et al., 2011). These examples show that in terrestrial ecosystems, plant invasions can inflict cascading effects across trophic levels.

Clonality and N-fixation are traits that influence the magnitude of the impact on plant species richness but not so for animals. Identifying which shared life-history traits determine the magnitude of impact remains a challenge. A previous global analysis found that the probability of a significant decrease in resident species richness increased if the non-native species was an annual grass (Pyšek et al., 2012). In contrast, in our analysis we did not find an influence of life-form. We found that factors determining the likelihood of detecting an impact, as measured in Pyšek et al. (2012), might not be the same as those driving how large this impact might be (i.e. the magnitude of the impact). On average, non-native N-fixers did not reduce plant richness while non-N-fixing invaders did. Since the seminal studies on the impacts of the introduced tree *Morella faya* in Hawai‘i (Vitousek & Walker, 1989), major emphasis has been placed on assessing the influence of N-fixing species on nutrient cycling. In general, N-fixing plants accelerate soil N fluxes and increase N pools (Liao et al., 2008). However, N-fixing species do not always decrease plant richness (e.g. Valtonen et al., 2006; Giantomasi et al., 2008), possibly because in communities invaded by N-fixing species there is less competition for N than in N-poor soils. The effect of N-fixing on the recipient community might be more related to the similarity in N use between the non-native and native species (Chapin et al., 1996; Castro-Díez et al., 2014) than to the capacity of a non-native species to fix N.

The phylogenetic signal on the magnitude of non-native plant impacts indicates that differences in impact between two particular non-native plant species depend, in part, on their evolutionary relatedness (see Yessoufou et al., 2014, for non-native mammals). Because phylogenetic relatedness can be considered as a surrogate of phenotypic, or even ecological, similarity (Losos, 2008), the phylogenetic signal suggests that a suite of plant traits that are shared by closely related species partly determines the magnitude of the impact inflicted by plant species. Therefore, besides life-form, other functional traits might provide great insight in future analyses of invasion impacts (Díaz & Cabido, 1997) because there is a link between phylogenetic relatedness, functional diversity of traits and ecosystem functioning (Cadotte et al., 2009).

While the importance of phylogenetic relatedness has been considered in predicting differences among non-native species at all steps of the invasion process (Prochý et al., 2008), including establishment (Cassey et al., 2004; Dawson et al., 2009), naturalization (Díez et al., 2009) and invasion success (Strauss et al., 2006; Lososová et al., 2008; Yessoufou et al., 2014), its effect on ecological impacts on recipient communities has rarely been considered (but see Castro-Díez et al., 2014). To provide a general understanding of the importance of phylogenetic position for the impacts of non-native species, a greater focus should be placed on the phylogenetic similarity between the non-native and the resident species in the recipient community (Gerhold et al., 2011).

**Table 1** Relative importance of the variables and the phylogeny in explaining the size of the impact of non-native plant species on plant and animal richness. We present the differences in the Akaike information criterion (AIC) between the full model and the model without the variable of interest. A difference in AIC of more than 2 is considered as a strong indication that the variable is important and can be considered to be significant, while a difference less than 2 is usually considered as non-significant (n.s.).

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that any ecosystem type in any region could be vulnerable to the impact of non-native plants. This explains why impacts of non-native plants are often similar within and outside protected areas (Hulme et al., 2013b).

Compared with mainland regions, islands are poor and dis harmonious in species, and host numerous endemics (Whittaker, 1998); species have low vagility and form few and small populations which are more susceptible to the effects of non-native species (Berglund et al., 2009). The lack of difference in the magnitude of impact of non-native plants on plant species richness between mainland and islands is surprising given that it is widely accepted that islands are highly susceptible to invasions (D’Antonio & Dudley, 1995; Berglund et al., 2009; Pyšek et al., 2012). The ecological impacts of plant invasions on island biodiversity might be more closely associated with changes in species composition (e.g. endemic species being replaced by non-native species) than with the number of species. Further work comparing paired island and mainland ecosystems is needed to assess the relationships between the susceptibility to invasion and subsequent impact.

In sum, our quantitative review shows that the magnitude of the impact of plant invaders on plant richness is dependent on plant traits regardless of ecosystem type. In contrast, the impact on animal richness, mainly arthropods, is generally stronger on islands but independent of the particular plant traits examined in this study. The phylogenetic signal identified here pinpoints that closely related non-native species exert similar impacts on native communities. Therefore, our results support the need to
include in risk assessments the phylogenetic similarity of non-native plants to known invaders to identify non-native species of potentially high impact (Pheloung et al., 1999; Diez et al., 2012; Hulme, 2012; Yessoufou et al., 2014).

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References


Yessoufou, K., Gere, J., Daru, B.H. & van der Bank, M. (2014) Differences in evolutionary history translates into differences in invasion success of alien mammals in South Africa. *Ecology and Evolution*, 4, 2115–2123. Additional references to the sources of data used in this study can be found in Appendix S2.

**SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of this article at the publisher’s web-site.

**Appendix S1.** Bayesian phylogeny based on *rbcL* DNA sequence data illustrating the phylogenetic relationships among non-native plants included in this study.

**Appendix S2.** List of studies for meta-analysis on non-native plant species impact on plant and animal species richness.

**Appendix S3.** R code to test the effect sizes of the impact of non-native plant species on resident plant species richness.

**Appendix S4.** R code to test the effect sizes of the impact of non-native plant species on resident animal species richness.

**BIOSKETCH**

M. Vilà (http://www.montsevila.org) is professor of research at Estación Biológica de Doñana (EBD-CSIC), Spain. Her major research interests are the ecological impacts of biological invasions and the role of biotic and environmental factors on the success of plant invasions in mediterranean ecosystems.

The authors of this paper have long collaborated through several EU projects such as EPIDEMIE, ALARM, DAISIE and PRATIQUE. For this article, M.V. designed research and wrote the first draft of the manuscript; M.V., J.L.E., J.P., U.S., P.E.H. and P.P. compiled data; M.V. and J.L.E. provided unpublished data; J.L.-R. and R.R. reconstructed the phylogeny and performed meta-analyses and phylogenetic regressions; all authors contributed substantially to revisions of the manuscript.

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