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 resident plant and animal species richness 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 resident plant and animal species richness while considering differences in non-native species traits (i.e. life-form, clonality or vegetative reproduction, and nitrogen-fixing ability), and characteristics of the invaded site (i.e. ecosystem type, insularity and climatic region).

Results Plots with non-native plants had less resident plant (–20.5%) and animal species richness (–26.4%) than paired uninvaded control plots. N-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 N-fixing and clonal non-native plants reduced species richness more than N-fixing and non-clonal invaders. However, life-form and characteristics of the invaded sites did not appear 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 mainland.

Main conclusions The presence of a phylogenetic signal on the magnitude of non-native plant impacts on resident plant and animal richness indicates that closely related non-native plants tend to cause similar impacts. This suggests that the magnitude of the impact might depend on shared plant traits not explored in our study. Our results support therefore the need to include 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; Vilà *et al*., 2011; Powel *et al*., 2011). Local changes in species richness are important because biodiversity determines ecosystem production, efficient resource use 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 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 (Pyšek *et al*., 2012; Leung *et al*., 2012). This is problematic because there is no clear link between a species being categorised as invasive and the magnitude of its impacts (Ricciardi & Cohen, 2007; Andreu *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-Díez *et al*., 2014).

Disentangling the relative importance of ecosystem type, species traits and phylogenetic relatedness is essential to build over-arching hypotheses on impacts and develop 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 impact studies 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 (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 to 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, 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 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). 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 size variance and the 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 (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 jModelTest v2.1.3 (bestfit model: GTR + I + G; Darriba *et al*., 2012) in MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003). MrBayes was run for 1 000 000 generations and trees sampled every 1000 generations. Nodal support for the retrieved tree topology was determined as posterior probabilities in MrBayes. The phylogeny resolved all taxa with high overall support (Appendix S1).

To incorporate phylogeny in the meta-analysis, we followed the methodology of Dawson *et al.* (2012). In the meta-analysis, the effect size was calculated as the reduction or increase in resident plant or animal richness, computed as the log of the ratio of species richness between invaded and uninvaded plots. We took into account the phylogenetic autocorrelation of data by using phylogenetic regression (Grafen, 1989) with Grafen correlation structure (Freckleton *et al*., 2002). The parameter adjusts the strength of the correlation induced when assuming a Brownian motion like model of trait evolution. The higher, the greater the strength of the phylogenetic signal in the residuals. equal to zero implies that there is no phylogenetic correlation, and equal to one is equivalent to a Brownian motion model. In the meta-analysis, each individual effect size has to be represented as a tip on the phylogenetic tree. Some species were related to more than one individual effect size, resulting in polytomies in the phylogenetic tree. Branch lengths at these polytomies were set to a length of 0.0001 (number of substitutions per site), and we tested that the results were robust to changes of this length from 0.0001 to 0.000001.

We weighted the data using the inverse of the within-effect size variance plus the estimate of the between-effect size variance (Borenstein *et al*., 2009). The analyses were performed in R (R Core Team 2013), using the libraries *ape* (Paradis *et al*., 2004) and *nlme* (Pinheiro *et al*., 2013; Appendix S3 and S4).

As predictors, we used six categorical variables and the phylogeny of the non-native species. Three variables were species descriptors: the non-native plant life-form (i.e. tree, shrub, perennial forb, annual forb, perennial grass and annual grass), clonality or vegetative reproduction (yes or no) and ability to fix N (yes or no). We chose these three plant traits because they are among those that have received most attention in plant invasions (Pyšek & Richardson, 2007). The three other variables were related to the type of the invaded ecosystem (i.e. forest, shrubland, grassland, oldfield, ruderal, desert, riparian, coastal, wetland), biogeographic region (i.e. temperate, Mediterranean, tropical, subtropical, arid and semiarid) and insularity (i.e. whether the study was conducted on an island or not).

The effect sizes for the different levels of the categorical variables were computed as the maximum likelihood estimators of the phylogenetic regression. Their 95% confidence intervals were computed as ±1.96 times the standard errors of the maximum likelihood estimations. The difference between two levels, e.g., the difference between clonal and non-clonal plants, were computed with the library *multcomp* in R (Hothorn *et al.,* 2008), using the result of the phylogenetic regression. The analysis was undertaken separately for the impacts on plant and on animal richness. For the impact on plants, we started the analysis with the model including all categorical variables. Then, we selected the significant predictors, based on AIC, and finally we tested for potential interactions between them. For the impact on animals, due to the small number of data points, we used a forward-stepwise variable selection procedure based on AIC. The AIC was computed from the maximum likelihood estimate and the number of fitted parameters by its usual formula AIC = - 2*log(maximum likelihood) + 2*number of parameters. AIC is given in the standard output of the phylogenetic regression. A difference in AIC of more than 2 from the null model is considered as a strong indication that the variable is important, while a difference less than 2 is usually considered as non-significant. The rationale behind this choice is the following: when comparing nested model based on a log-likelihood ratio test, the more complex model should have a AIC that is at least smaller than the AIC of the null model minus 2, so that the test is significant at a level of 0.05 (Burnham & Anderson, 2002).

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% of the total, and species with clonal growth or vegetative reproduction 63.1%. The biogeographic distribution of the studies was uneven with the majority conducted in either temperate (40.6%) or Mediterranean (35.2%) regions. Twenty percent 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 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= 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 resident plant species richness. The best predictor of the magnitude of impact was N-fixing ability, followed by phylogeny and clonal growth.

The effect of clonal growth was tested for all life-forms except vines. Clonal invaders decreased resident plant richness more than non-clonal invaders (Figure 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 (Figure 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 on animal richness in invaded communities was stronger on islands than in mainland.

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 of 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 host less food resources for birds (Skorka *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. Our result 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. 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 Hawaiï (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 species at all steps of the invasion process (Procheş *et al*., 2008) including establishment (Cassey *et al*., 2004; Dawson *et al*., 2009), naturalization (Diez *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 non-native species' impacts, 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).

The type of invaded ecosystem and region were not of high significance in determining the net magnitude of impacts, except for a stronger decrease in animal species richness on islands compared to mainland regions. Our results suggest 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 to mainland regions, islands are poor and disharmonic 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 differences on 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 types. 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 phylogenetic similarity of non-native plants to known invaders in risk assessments 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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Additional references to the sources of data used in this study can be found in Appendix S2 at [URL].

Biosketch

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

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 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.

Predictor	Plant richness	Animal richness
Clonal growth	10.89	N.S.
Life-form	N.S.	N.S.
N-fixing	172.57	N.S.
Phylogeny	24.66	2.53
Ecosystem type	N.S.	N.S.
Biogeographic region	N.S.	N.S
Insularity	N.S.	4.99

Figure legends

Figure 1: Effect size (± 1.96*SE) of the impact of non-native plant species on plant richness as a function of the non-native species life-form and clonality/vegetative reproduction. Effect size is computed as the log-ratio of the number of species in the invaded plot over the control plot. An effect size is significantly different from zero when its 95% confidence interval do not bracket zero. A negative effect size indicates a decrease in plant species richness. Sample sizes for non-clonal and clonal species are indicated in parentheses, respectively.

Figure 2: Effect size (± 1.96*SE) of the impact of non-native plant species on plant richness as a function of the non-native species life-form and N-fixing ability. Effect size is computed as the log-ratio of the number of species in the invaded plot over the control plot. An effect size is significantly different from zero when its 95% confidence interval do not bracket zero. A negative effect size indicates a decrease in plant species richness. Sample sizes for N-fixing and non N-fixing species are indicated in parenthesis, respectively.

Figure 1

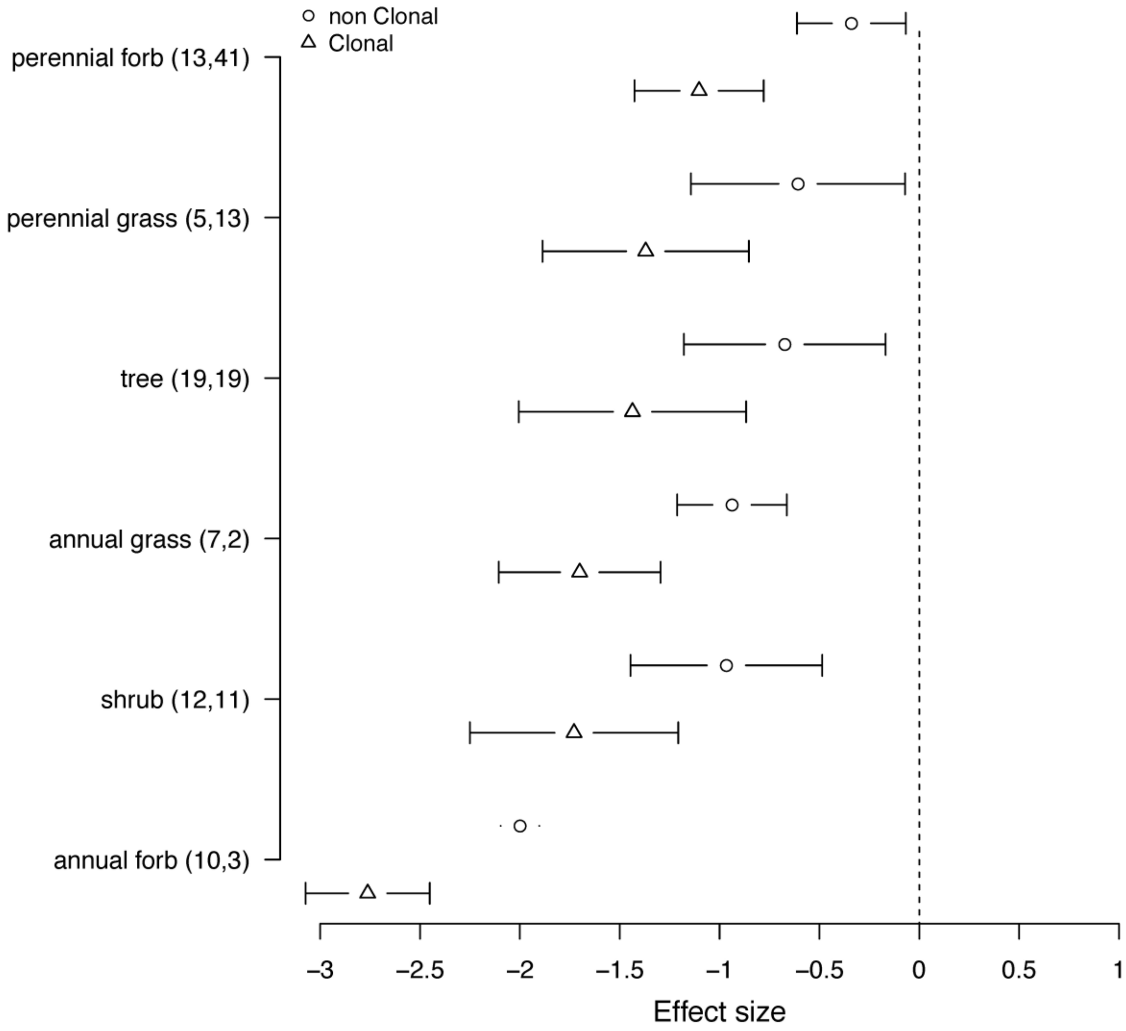
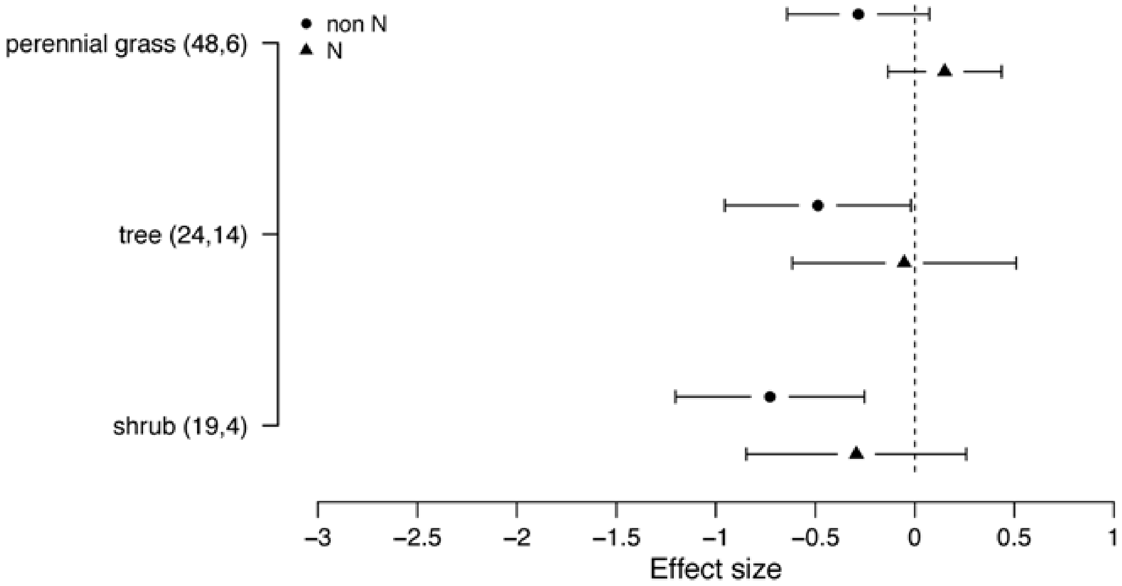

○ non Clonal
△ Clonal
perennial forb (13,41)
perennial grass (5,13)
tree (19,19)
annual grass (7,2)
shrub (12,11)
annual forb (10,3)
−3
−2.5
−2
−1.5
−1
−0.5
0
0.5
1
Effect size

Figure 2



● non N
▲ N
perennial grass (48,6)
tree (24,14)
shrub (19,4)
−3
−2.5
−2
−1.5
−1
−0.5
0
0.5
1
Effect size