

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

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4 Montserrat Vilà^{1*}, Rudolf P Rohr², José L Espinar¹, Philip E Hulme³, Jan Pergl⁴,
5 Johannes J Le Roux⁵, Urs Schaffner⁶ and Petr Pyšek^{4,7}

6
7 ¹ Estación Biológica de Doñana (EBD-CSIC), Avda. Américo Vespucio s/n, Isla de la
8 Cartuja, E-41092 Sevilla, Spain

9 ² Unit of Ecology and Evolution, University of Fribourg, CH-1700 Fribourg,
10 Switzerland

11 ³ The Bio-Protection Research Centre, Lincoln University, Christchurch, New
12 Zealand

13 ⁴ Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43,
14 Průhonice, Czech Republic

15 ⁵ Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch
16 University, Matieland, South Africa

17 ⁶ CABI Switzerland, CH-2800 Delémont, Switzerland

18 ⁷ Department of Ecology, Faculty of Science, Charles University in Prague, Viničná
19 7, CZ-128 44, Prague, Czech Republic

20
21 ***Corresponding author:** Montserrat Vilà, e-mail: montse.vila@ebd.csic.es

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27

28 **Abstract**

29

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

33 **Location** Global.

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

40 **Results** Plots with non-native plants had less resident plant (–20.5%) and animal
41 species richness (–26.4%) than paired uninvaded control plots. N-fixing ability,
42 followed by phylogeny and clonality were the best predictors of the magnitude of
43 impacts of non-native plants on native plant species richness. Non N-fixing and
44 clonal non-native plants reduced species richness more than N-fixing and non-clonal
45 invaders. However, life-form and characteristics of the invaded sites did not appear
46 important. In the case of resident animal species richness, only the phylogenetic
47 position of the non-native, and whether invaded sites were islands or not influenced
48 impacts, with a more pronounced decrease found on islands than mainland.

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

55

56 **Keywords:** alien species, biological invasion, ecological impact, insularity, meta-
57 analysis, N-fixing, phylogeny, phylogenetic regression, weeds.

58

59 **Introduction**

60

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

70 Both the direction (i.e. increase or decrease of a variable) and the magnitude
71 of impacts of non-native species are highly context-dependent (Hulme *et al.*, 2013a).
72 Disentangling the factors that determine the magnitude of impacts of non-native
73 species requires exploring the dependency of impacts on species traits and
74 ecosystem characteristics (Levine *et al.*, 2003; Gaertner *et al.*, 2009; Pyšek *et al.*,
75 2012). Yet, despite the significant advance in identifying species traits associated
76 with the potential of non-native species to invade (i.e. invasiveness; Pyšek &
77 Richardson, 2007; van Kleunen *et al.*, 2010) and differences in the vulnerability of
78 ecosystems to invasion (i.e. invasibility; Chytrý *et al.*, 2008), the factors modulating
79 impacts have rarely been explored in concert (Pyšek *et al.*, 2012; Leung *et al.*,
80 2012). This is problematic because there is no clear link between a species being
81 categorised as invasive and the magnitude of its impacts (Ricciardi & Cohen, 2007;
82 Andreu *et al.*, 2009; Hulme, 2012). Thus the countless studies attempting to identify
83 those traits that make a species invasive may not translate into a better
84 understanding of the determinants of impact.

85 When making generalizations about impact-driven traits, we need to consider
86 the phylogenetic non-independence of species (Sol *et al.*, 2008). Closely related
87 species share morphological, physiological and ecological traits due to their common
88 evolutionary history (Freckleton *et al.*, 2002). In consequence, the phylogenetic

89 position of non-native species might influence their impacts (Yessoufou *et al.*, 2014)
90 because phylogeny captures phenotypic traits and functional attributes of the
91 species (phylogenetic signal in functional traits, Blomberg & Garland 2002). It has
92 been suggested that phylogenetic relatedness among species should be included in
93 comparative analyses such as meta-analysis (Chamberlain *et al.*, 2012).
94 Unfortunately, most meta-analyses addressing the impacts of non-native plants have
95 failed to account for phylogeny (Liao *et al.*, 2008; Gaertner *et al.*, 2009; Powell *et al.*,
96 2011; Vilà *et al.*, 2011; but see Castro-Díez *et al.*, 2014).

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

108

109 **Methods**

110

111 *Literature search and data extraction*

112

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

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

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

137

138 *Statistical analysis*

139

140 Since shared evolutionary history may lead to the statistical non-independence of
141 data (Felsenstein, 1985), we combined meta-analysis and phylogenetic regressions.
142 Meta-analysis takes into account the between-effect size variance and the within-
143 effect size variance (Gurevitch & Hedges, 1999), whereas the phylogenetic
144 regression controls for the non-independence between the data points (Grafen,
145 1989).

146 For phylogenetic reconstruction we collated genetic data for the ribulose-
147 biphosphate carboxylase (rbcL) gene region for all non-native plant taxa with
148 available data in the online GenBank/EBI repository (ncbi.nlm.nih.gov). Species with
149 no DNA data on Genbank/EBI were replaced by closely related species (within the
150 same genus) for which DNA data were available (15 species). Our final dataset
151 consisted of 1402 characters (base pairs) for 96 species. DNA sequence data were
152 aligned in BioEdit version 7.0.5.3 (Hall 1999) and manually edited. Phylogenetic
153 relationships were estimated using Bayesian search criteria with parameter

154 estimates obtained from the program jModelTest v2.1.3 (bestfit model: GTR + I + G;
155 Darriba *et al.*, 2012) in MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003). MrBayes
156 was run for 1 000 000 generations and trees sampled every 1000 generations. Nodal
157 support for the retrieved tree topology was determined as posterior probabilities in
158 MrBayes. The phylogeny resolved all taxa with high overall support (Appendix S1).

159 To incorporate phylogeny in the meta-analysis, we followed the methodology
160 of Dawson *et al.* (2012). In the meta-analysis, the effect size was calculated as the
161 reduction or increase in resident plant or animal richness, computed as the log of the
162 ratio of species richness between invaded and uninvaded plots. We took into account
163 the phylogenetic autocorrelation of data by using phylogenetic regression (Grafen,
164 1989) with Grafen correlation structure (Freckleton *et al.*, 2002). The parameter
165 adjusts the strength of the correlation induced when assuming a Brownian motion
166 like model of trait evolution. The higher, the greater the strength of the phylogenetic
167 signal in the residuals. equal to zero implies that there is no phylogenetic
168 correlation, and equal to one is equivalent to a Brownian motion model. In the meta-
169 analysis, each individual effect size has to be represented as a tip on the
170 phylogenetic tree. Some species were related to more than one individual effect size,
171 resulting in polytomies in the phylogenetic tree. Branch lengths at these polytomies
172 were set to a length of 0.0001 (number of substitutions per site), and we tested that
173 the results were robust to changes of this length from 0.0001 to 0.000001.

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

178 As predictors, we used six categorical variables and the phylogeny of the non-
179 native species. Three variables were species descriptors: the non-native plant life-
180 form (i.e. tree, shrub, perennial forb, annual forb, perennial grass and annual grass),
181 clonality or vegetative reproduction (yes or no) and ability to fix N (yes or no). We
182 chose these three plant traits because they are among those that have received
183 most attention in plant invasions (Pyšek & Richardson, 2007). The three other
184 variables were related to the type of the invaded ecosystem (i.e. forest, shrubland,
185 grassland, oldfield, ruderal, desert, riparian, coastal, wetland), biogeographic region

186 (i.e. temperate, Mediterranean, tropical, subtropical, arid and semiarid) and insularity
187 (i.e. whether the study was conducted on an island or not).

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

209

210 **Results**

211

212 *General patterns*

213

214 Among the 96 plant species included in the analysis, the most represented were
215 *Acacia* spp. and *Carpobrotus* spp. with 14 and 10 cases of recorded impacts,
216 respectively. N-fixing species accounted for 12.6% of the total, and species with
217 clonal growth or vegetative reproduction 63.1%. The biogeographic distribution of the

218 studies was uneven with the majority conducted in either temperate (40.6%) or
219 Mediterranean (35.2%) regions. Twenty percent of studies were conducted on
220 islands. There were 177 and 39 cases relating to the impact on native plant and
221 animal species richness, respectively. Most studies on impacts on animal species
222 richness refer to impacts on invertebrates (81.6%) mainly arthropods.

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

228

229 *Impact on plant species richness of invaded communities*

230

231 Clonal growth/vegetative reproduction and N-fixing ability had a significant effect on
232 the magnitude of impact on plant species richness of the resident community, but
233 there were no significant differences among life-forms, ecosystem types,
234 biogeographic regions or insularity (Table 1). Grafen= 0.517 indicated that there was
235 a correlation structure induced by shared evolutionary history (i.e. a phylogenetic
236 signal), in the impact of non-native plants on resident plant species richness. The
237 best predictor of the magnitude of impact was N-fixing ability, followed by phylogeny
238 and clonal growth.

239 The effect of clonal growth was tested for all life-forms except vines. Clonal
240 invaders decreased resident plant richness more than non-clonal invaders (Figure
241 1). The effect of N-fixation could only be tested for trees, perennial forbs and shrubs.
242 For each of these life-forms, non N-fixing species decreased plant species richness
243 while N-fixing species did not have a significant effect (Figure 2).

244

245 *Impact on animal species richness of invaded communities*

246

247 Only the phylogenetic position of invading plants (Grafen's = 0.205) and insularity
248 influenced the effect size of impact on animal richness in invaded communities
249 (Table 1). These two significant predictors were of about the same relative

250 importance. On average, the decrease on animal richness in invaded communities
251 was stronger on islands than in mainland.

252

253 **Discussion**

254

255 Overall, non-native plants decrease plant and animal species richness in the invaded
256 community to the same extent. Some studies reported impacts on both resident plant
257 and animal species richness. There were cases reporting reductions of vertebrate
258 species richness due to habitat alteration or changes in feeding resources caused by
259 non-native plants. For example, invasion of European meadows by goldenrods,
260 *Solidago* spp., reduces bird species richness, as a result of there being fewer native
261 plant and insect species and thus host less food resources for birds (Skorka *et al.*,
262 2010). Similarly, in south-eastern Australia, riparian areas invaded by willows, *Salix*
263 *rubens*, host fewer bird species because a reduction in native shrub and tree cover
264 leads to fewer arthropods upon which to forage (Holland-Clift *et al.*, 2011). These
265 examples show that in terrestrial ecosystems, plant invasions can inflict cascading
266 effects across trophic levels.

267 Clonality and N-fixation are traits that influence the magnitude of the impact
268 on plant species richness but not so for animals. Identifying which shared life-history
269 traits determine the magnitude of impact remains a challenge. A previous global
270 analysis found that the probability of a significant decrease in resident species
271 richness increased if the non-native species was an annual grass (Pyšek *et al.*,
272 2012). In contrast, in our analysis we did not find an influence of life-form. Our result
273 that factors determining the likelihood of detecting an impact, as measured in Pyšek
274 *et al.* (2012), might not be the same as those driving how large this impact might be
275 (i.e. magnitude of the impact). On average, non-native N-fixers did not reduce plant
276 richness while non N-fixing invaders did. Since the seminal studies on the impacts of
277 the introduced tree *Morella faya* in Hawaiï (Vitousek & Walker, 1989), major
278 emphasis has been placed on assessing the influence of N-fixing species on nutrient
279 cycling. In general, N-fixing plants accelerate soil N fluxes and increase N pools
280 (Liao *et al.*, 2008). However, N-fixing species do not always decrease plant richness
281 (e.g. Valtonen *et al.*, 2006; Giantomasi *et al.*, 2008) possibly because in communities
282 invaded by N-fixing species there is less competition for N than in N poor soils. The

283 effect of N-fixing on the recipient community might be more related to the similarity in
284 N use between the non-native and native species (Chapin *et al.*, 1996; Castro-Díez
285 *et al.*, 2014) than to the capacity of a non-native species to fix N.

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

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

307 The type of invaded ecosystem and region were not of high significance in
308 determining the net magnitude of impacts, except for a stronger decrease in animal
309 species richness on islands compared to mainland regions. Our results suggest that
310 any ecosystem type in any region could be vulnerable to the impact of non-native
311 plants. This explains why impacts of non-native plants are often similar within and
312 outside protected areas (Hulme *et al.*, 2013b).

313 Compared to mainland regions, islands are poor and disharmonic in species
314 and host numerous endemics (Whittaker, 1998); species have low vagility and form
315 few and small populations which are more susceptible to the effects of non-native

316 species (Berglund *et al.*, 2009). The lack of differences on the magnitude of impact
317 of non-native plants on plant species richness between mainland and islands is
318 surprising given that it is widely accepted that islands are highly susceptible to
319 invasions (D'Antonio & Dudley, 1995; Berglund *et al.*, 2009; Pyšek *et al.*, 2012). The
320 ecological impacts of plant invasions on island biodiversity might be more closely
321 associated with changes in species composition (e.g. endemic species being
322 replaced by non-native species) than with the number of species. Further work
323 comparing paired island and mainland ecosystems is needed to assess the
324 relationships between the susceptibility to invasion and subsequent impact.

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

334

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346

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509 Additional references to the sources of data used in this study can be found in
510 Appendix S2 at [URL].

511
512 **Biosketch**

513
514 **M. Vilà** (<http://www.montsevila.org>) is Professor of Research at Estación Biológica
515 de Doñana (EBD-CSIC). Her major research interests are ecological impacts of
516 biological invasions and the role of biotic and environmental factors on the success
517 of plant invasions in Mediterranean ecosystems. Authors of the paper have long
518 collaborated through several EU projects such as EPIDEMIE, ALARM, DAISIE and
519 PRATIQUE.

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521 For this article, M.V. designed research and wrote the manuscript; M.V., J.L.E., J.P.,
522 U.S., P.E.H. and P.P. compiled data; M.V. and J.L.E. provided unpublished data;
523 J.L-R and R.R reconstructed the phylogeny and performed meta-analyses and
524 phylogenetic regressions; all authors contributed substantially to revisions of the
525 manuscript.

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532 Table 1. Relative importance of the variables and the phylogeny in explaining the
533 size of the impact of non-native plant species on plant and animal richness. We
534 present the differences in AIC between the full model and the model without the
535 variable of interest. A difference in AIC of more than 2 is considered as a strong
536 indication that the variable is important and can be considered to be significant, while
537 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 |

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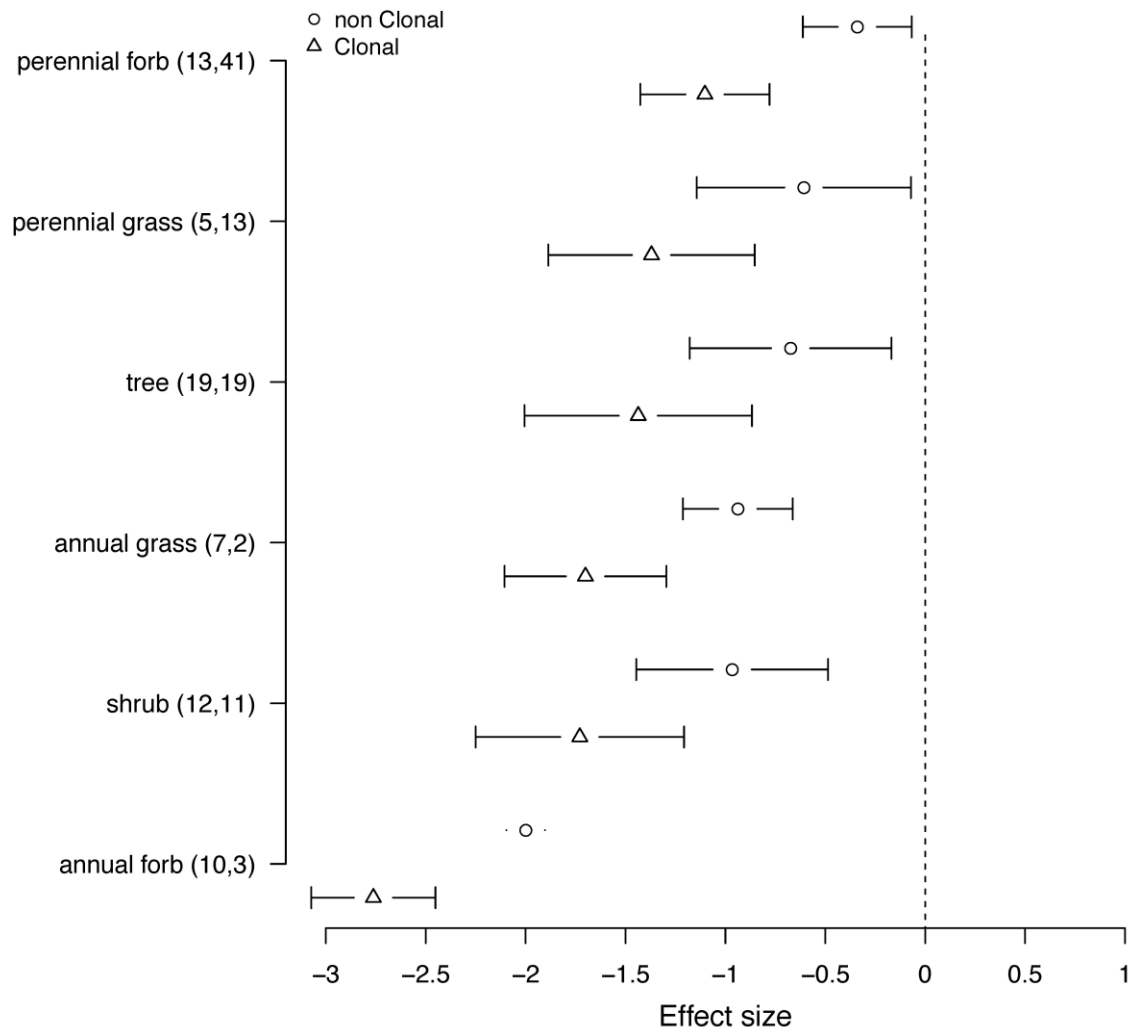
543 **Figure legends**

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

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

558 Figure 1

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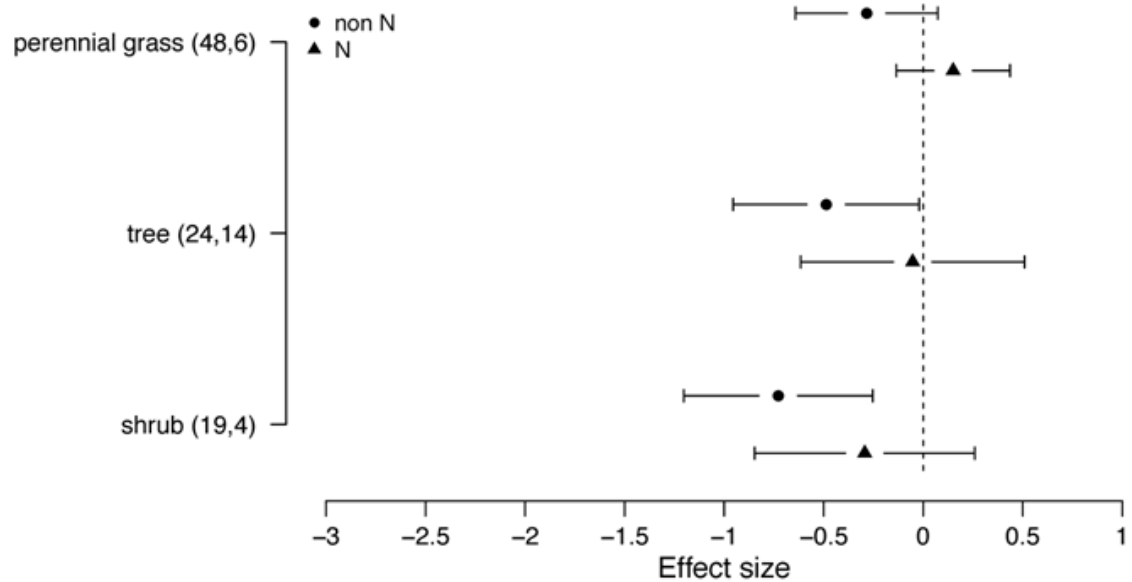
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564 Figure 2

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