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META-ANALYSIS

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.

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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

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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; 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 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 jModelTest version 2.1.3 (best fit 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's 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 parameter, 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; Appendices S3 & 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 semi-arid) 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, was 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 the Akaike information criterion (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 the 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). The 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 of less than 2 is usually considered as non-significant. The rationale behind this choice is the following: when comparing nested models based on a log-likelihood ratio test, the more complex model should have an 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%, 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, $t = 0.953$, $P\text{-value} = 0.344$).

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 = 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.

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.).

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

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 (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 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).

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

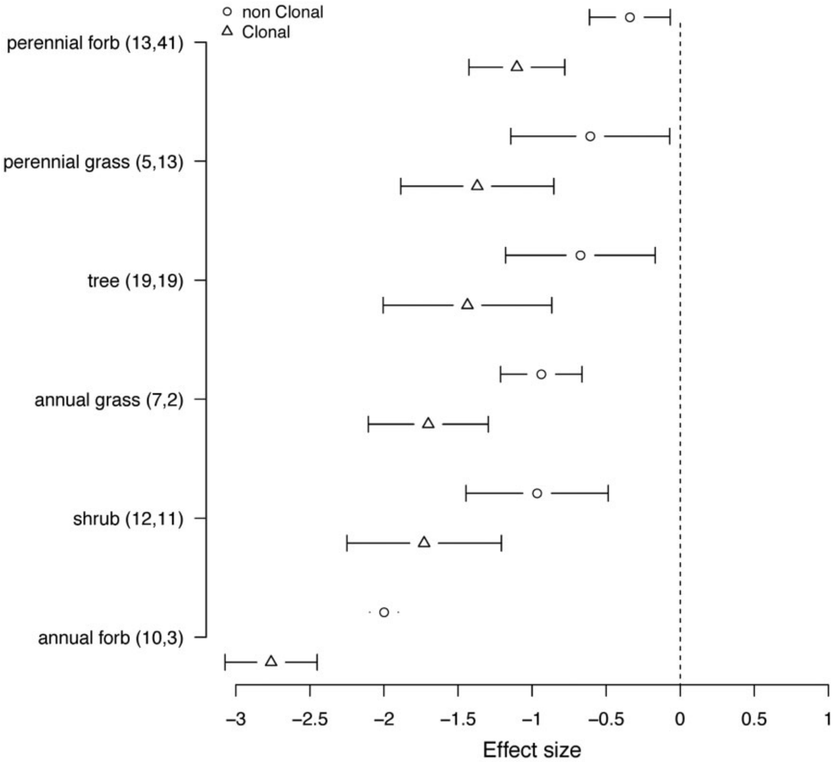

Figure 1 Effect size (± 1.96 SE) of the impact of non-native plant species on plant richness as a function of the life-form of the non-native species and clonality/vegetative reproduction. Effect size is computed as the log-ratio of the number of species in the invaded plot over the control plot. An effect size is significantly different from zero when its 95% confidence interval does 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.

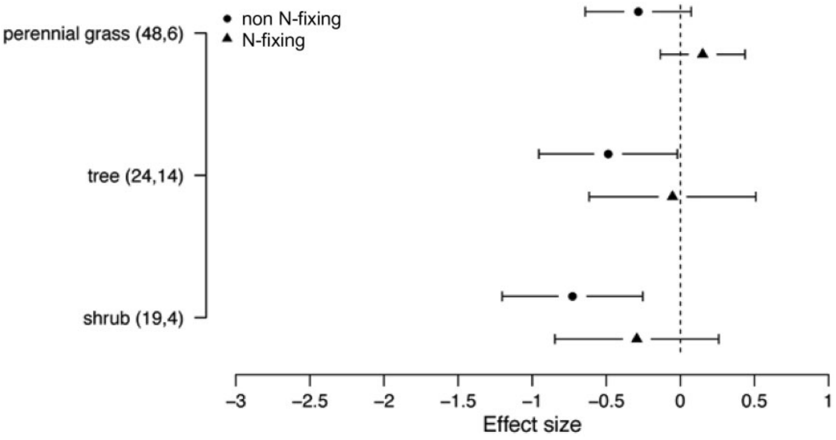

Figure 2 Effect size (± 1.96 SE) of the impact of non-native plant species on plant richness as a function of the non-native species life-form and N-fixing ability. Effect size is computed as the log-ratio of the number of species in the invaded plot over the control plot. An effect size is significantly different from zero when its 95% confidence interval does 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 parentheses, respectively.

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 disharmonious 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

Andreu, J., Vilà, M. & Hulme, P.E. (2009) An assessment of stakeholder perceptions and management of alien plants in Spain. *Environmental Management*, **43**, 1244–1255.

Berglund, H., Jaremo, J. & Bengtsson, G. (2009) Endemism predicts intrinsic vulnerability to non-indigenous species on islands. *The American Naturalist*, **174**, 94–101.

Blomberg, S.P. & Garland, T. Jr (2002) Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *Journal of Evolutionary Biology*, **15**, 899–910.

Borenstein, M., Hedges, L.V., Higgins, J.P.T. & Rothstein, H.R. (2009) *Introduction to meta-analysis*. John Wiley & Sons, Chichester.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. Springer-Verlag, Berlin.

Cadotte, M.W., Cavener-Bares, J., Tilman, D. & Oakley, T.H. (2009) Using phylogenetic functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE*, **4**, e5695.

Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M. & Jouseau, C. (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, **443**, 989–992.

Cassey, P., Blackburn, T.M., Sol, D., Duncan, R.P. & Lockwood, J.L. (2004) Global patterns of introduction effort and establishment success in birds. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 405–408.

Castro-Díez, P., Godoy, O., Alonso, A., Gallardo, A. & Saldaña, A. (2014) What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis. *Ecology Letters*, **17**, 1–12.

Chamberlain, S.A., Hovick, S.M., Dibble, C.J., Rasmussen, N.L., Van Allen, B.G., Maitner, B.S., Ahern, J.R., Bell-Dereske, L.P., Roy, C.L., Meza-Lopez, M., Carrillo, J., Siemann, E., Lajeunesse, M.L. & Whitney, K.D. (2012) Does phylogeny matter? Assessing the impact of phylogenetic information in ecological meta-analysis. *Ecology Letters*, **15**, 627–636.

Chapin, F.S., Reynolds, H., D'Antonio, C.M. & Eckhart, V. (1996) The functional role of species in terrestrial ecosystems. *Global change in terrestrial ecosystems* (ed. by B. Walker and W. Steffen), pp. 403–428. Cambridge University Press, Cambridge.

Chytrý, M., Maskel, L.C., Pino, J., Pyšek, P., Vilà, M., Font, X. & Smart, S.M. (2008) Habitat invasions by alien plants: a quantitative comparison between Mediterranean, subcontinental and oceanic regions of Europe. *Journal of Applied Ecology*, **45**, 448–458.

D'Antonio, C.M. & Dudley, T.L. (1995) Biological invasions as agents of change on islands compared with mainlands. *Biological diversity and ecosystem function* (ed. by P.M. Vitousek, L. Loope and H. Andersen), pp. 103–121. Springer-Verlag, Berlin.

Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods*, **9**, 772.

Dawson, W., Burslem, D.F.R. & Hulme, P.E. (2009) Factors explaining alien plant invasion success in a tropical ecosystem differ at each stage of invasion. *Journal of Ecology*, **97**, 657–665.

Dawson, W., Rohr, R.P., Mark van Kleunen, M. & Fischer, M. (2012) Alien plant species with a wider global distribution are better able to capitalize on increased resource availability. *New Phytologist*, **194**, 859–867.

Díaz, S. & Cabido, M. (1997) Plant types and ecosystem function in relation to global change. *Journal of Vegetation Science*, **8**, 463–474.

Diez, J.M., Williams, P.A., Randall, R.P., Sullivan, J.J., Hulme, P.E. & Duncan, R.P. (2009) Learning from failures: testing broad taxonomic hypotheses about plant naturalization. *Ecology Letters*, **12**, 1174–1183.

Diez, J.M., Hulme, P.E. & Duncan, R.P. (2012) Using prior information to build probabilistic invasive species risk assessments. *Biological Invasions*, **14**, 681–691.

Felsenstein, J. (1985) Phylogenies and the comparative method. *The American Naturalist*, **125**, 1–15.

Freckleton, R.P., Harvey, P.H. & Pagel, M. (2002) Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist*, **166**, 712–726.

Gaertner, M., Breeyen, A.D., Hui, C. & Richardson, D.M. (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Progress in Physical Geography*, **33**, 319–338.

Gerhold, P., Pärtel, M., Tackenberg, O., Hennekens, S.M., Bartish, I., Schaminée, J.H.J., Fergus, A.J.F., Ozinga, W.A. & Prinzing, A. (2011) Phylogenetically poor plant communities receive more alien species, which more easily coexist with natives. *The American Naturalist*, **177**, 668–680.

Giantomasi, A., Tecco, P.A., Funes, G., Gurvich, D.E. & Cabido, M. (2008) Canopy effects of the invasive shrub *Pyracantha* *angustifolia* on seed bank composition, richness and density in a montane shrubland (Cordoba, Argentina). *Austral Ecology*, **33**, 68–77.

Grafen, A. (1989) The phylogenetic regression. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **326**, 116–157.

Gurevitch, J. & Hedges, L.V. (1999) Statistical issues in ecological meta-analyses. *Ecology*, **80**, 1142–1149.

Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis. Available at: http://www.mbio.ncsu.edu/BioEdit/bioedit.html (accessed 10 June 2012).

Holland-Clift, S., O'Dowd, D.J. & Mac Nally, R. (2011) Impacts of an invasive willow (*Salix* × *rubens*) on riparian bird assemblages in south-eastern Australia. *Austral Ecology*, **36**, 511–520.

Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, **50**, 346–363.

Hulme, P.E. (2012) Weed risk assessment: a way forward or a waste of time? *Journal of Applied Ecology*, **49**, 10–19.

Hulme, P.E., Pyšek, P., Jarošík, V., Pergl, J., Schaffner, U. & Vilà, M. (2013a) Bias and error in understanding plant invasion impacts. *Trends in Ecology and Evolution*, **28**, 212–218.

Hulme, P.E., Pyšek, P., Pergl, J., Jarošík, V., Schaffner, U. & Vilà, M. (2013b) Greater focus needed on alien plant impacts in protected areas. *Conservation Letters*. doi: 10.1111/conl.12061.

van Kleunen, M., Weber, E. & Fischer, M. (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, **13**, 235–245.

Leung, B., Roura-Pascual, N., Bacher, S., Heikkilä, J., Brotons, L., Burgman, M.A., Dehnen-Schmutz, K., Essl, F., Hulme, P.E., Richardson, D.M., Sol, D. & Vilà, M. (2012) Teasing apart alien species risk assessments: a framework for best practices. *Ecology Letters*, **15**, 1475–1493.

Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impact of exotic plant invasions. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 775–781.

Liao, C.Z., Peng, R.H., Luo, Y.Q., Zhou, X.H., Wu, X.W., Fang, C.M., Chen, J. & Li, B. (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytologist*, **177**, 706–714.

Losos, J.B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, **11**, 995–1007.

Lososová, Z., Chytrý, M. & Kühn, I. (2008) Plant attributes determining the regional abundance of weeds on central European arable land. *Journal of Biogeography*, **35**, 177–187.

Paradis, E., Claude, J. & Strimmer, K. (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289–290.

Pheloung, P.C., Williams, P.A. & Halloy, S.R. (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *Journal of Environmental Management*, **57**, 239–251.

Pinheiro, J., Bates, D., DebRoy, S., Sarker, D. & the R Development Core Team (2013) *nlme: linear and nonlinear mixed effects models*. R package version 3.1-117. Available at: http://CRAN.R-project.org/package=nlme.

Powell, K.I., Chase, J.M. & Knight, T.M. (2011) A synthesis of plant invasion effects on biodiversity across spatial scales. *American Journal of Botany*, **98**, 539–548.

Procheş, S., Wilson, J.R.U., Richardson, D.M. & Rejmánek, M. (2008) Searching for phylogenetic pattern in biological invasions. *Global Ecology and Biogeography*, **17**, 5–10.

Pyšek, P. & Richardson, D.M. (2007) Traits associated with invasiveness in alien plants: where do we stand? *Biological invasions* (ed. by W. Nentwig), pp. 97–125. Springer-Verlag, Berlin.

Pyšek, P., Jarošík, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U. & Vilà, M. (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology*, **18**, 1725–1737.

R Core Team (2013) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.

Ricciardi, A. & Cohen, J. (2007) The invasiveness of an introduced species does not predict its impact. *Biological Invasions*, **9**, 309–315.

Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, **19**, 1572–1574.

Skórka, P., Magdalena, L. & Tryjanowski, P. (2010) Invasive alien goldenrods negatively affect grassland bird communities in eastern Europe. *Biological Conservation*, **143**, 856–861.

Sol, D., Vilà, M. & Kühn, I. (2008) The comparative analysis of historical alien introductions. *Biological Invasions*, **10**, 1119–1129.

Strauss, S.Y., Webb, C.O. & Salamin, N. (2006) Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences USA*, **103**, 5841–5845.

Valtonen, A., Jantunen, J. & Saarinen, K. (2006) Flora and lepidoptera fauna adversely affected by invasive *Lupinus polyphyllus* along road verges. *Biological Conservation*, **133**, 389–396.

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J., Pergl, J., Schaffner, U., Sun, Y. & Pyšek, P. (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, **14**, 702–708.

Vitousek, P.M. & Walker, L.R. (1989) Biological invasion by *Myrica faya* in Hawaii: plant demography, nutrient fixation, ecosystem effects. *Ecological Monographs*, **59**, 247–265.

Whittaker, R.J. (1998) *Island biogeography: ecology, evolution and conservation*. Oxford University Press, Oxford.

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

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