What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis

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Abstract

Exotic plant invasions can notably alter the nitrogen (N) cycle of ecosystems. However, there is large variation in the magnitude and direction of their impact that remains unexplained. We present a structured meta-analysis of 100 papers, covering 113 invasive plant species with 345 cases of invasion across the globe and reporting impacts on N cycle-related metrics. We aim to explain heterogeneity of impacts by considering methodological aspects, properties of the invaded site and phylogenetic and functional characteristics of the invaders and the natives. Overall, plant invasions increased N pools and accelerated fluxes, even when excluding N-fixing invaders. The impact on N pools depended mainly on functional differences and was greater when the invasive plants and the natives differed in N-fixation ability, plant height and plant/leaf habit. Further, the impact on N fluxes was related mainly to climate, being greater under warm and moist conditions. Our findings show that more functionally distant invaders occurring in mild climates are causing the strongest alterations to the N cycle.

Introduction

Nutrient availability controls primary production, carbon sequestration, water eutrophication and soil fertility, among other ecosystem services. Different global change drivers have caused strong alterations to these cycles. For instance, direct human actions from industry, agriculture and farming have increased nitrogen (N) pools at global scales (Vitousek *et al.* 1997). Invasions of exotic plants represent another important disruption of nutrient cycles. Invasive plants, sensu Richardson *et al.* (2000), are exotic, human transported species which attain self-sustaining populations over considerable areas. The pathways by which plant invasions alter nutrient cycles include, among others, changes in the quality and quantity of litter entering the soil, changes in rates of atmospheric N fixation and plant N uptake, changes in soil macro- and microbial communities, and alteration of soil properties and/or microclimatic conditions for decomposer activity (Vitousek & Walker 1989; Mack *et al.* 2001; D'Antonio & Corbin 2003; Yelenik *et al.* 2004; D'Antonio & Hobbie 2005; Mayer *et al.* 2005; Follstad Shah *et al.* 2010). The impact of invasive plants on N budgets at global scale is complex to assess because 1) most studies are limited to local scales (e.g., Vitousek & Walker 1989; Mack *et al.* 2001; Ehrenfeld 2010) and 2) the direction and magnitude of the impact may depend on particular species traits, on properties of the recipient site and/or on the interaction of both (Ehrenfeld 2010; Pyšek *et al.* 2012; Hulme *et al.* 2013). Accordingly, case studies with different histories of introductions report contradictory effects. For instance, exotic invasive plants have been observed to increase (Vitousek & Walker 1989; Haubensak *et al.* 2004; Jiang *et al.* 2009; Follstad Shah *et al.* 2010), decrease (Christian & Wilson 1999; Scott *et al.* 2001; González-Muñoz *et al.* 2013), or have no effect (Castro-Díez *et al.* 2009) on N pools in vegetation, litter and/or soils. The rates of N transfer between different ecosystem compartments, such as soil, litter or plant tissues, have also been found to increase (e.g. Ehrenfeld *et al.* 2001; Ashton *et al.* 2005; Hawkes *et al.* 2005; Castro-Díez *et al.* 2009; Leicht-Young *et al.* 2009), decrease (Johnson & Wedin 1997; Evans *et al.* 2001; Scott *et al.* 2001; Godoy *et al.* 2010) or remain unchanged (Stock *et al.* 1995; Mahaney *et al.* 2006; Castro-Díez *et al.* 2009) after invasion.

Motivated by the huge divergence of results, ecologists have been searching for generalizations. The first major review by Ehrenfeld (2003), following a vote-counting approach, reported that invasive plants tended to increase N pools in ecosystems and/or to speed up N transfer rates. Subsequent reviews by Liao *et al.* (2008) and Vilà *et al.* (2011), following a meta-analytical approach, and by Pyšek *et al.* (2012), using data mining tools, largely agreed with Ehrenfeld's results. Nevertheless, they also revealed large heterogeneity of impacts across studies, part of which was explained by the N fixing capacity and woodiness of the invasive plant (Liao *et al.* 2008; Vilà *et al.* 2011). A recent critique of quantitative field studies on the impacts of plant invasions highlighted this heterogeneity and argued that identifying the sources of variation is of fundamental importance (Hulme *et al.* 2013). The literature suggests an array of factors that may mediate the impact of exotic invasive plants on the N cycle, including the properties of the invaded site, such as climate, insularity, aspect, age of invasion, soil type or resource availability (Stock *et al.* 1995; Scott *et al.* 2001; D'Antonio & Corbin 2003; Daehler 2003; Levine *et al.* 2003; Jiang *et al.* 2009; Ehrenfeld 2010; Pyšek *et al.* 2012; Hulme *et al.* 2013). An important source of variation can also come from whether or not particular key traits of the invading species are present in the recipient community (Chapin *et al.* 1996; D'Antonio & Corbin 2003). For instance, the impact of a N-fixing invader is expected to be greater if the invaded community lacks N-fixing species (Levine *et al.* 2003), or the impact of an invasive tree will be greater in a treeless community (Mack 2003). Finally, effects can be influenced by phylogenetic relationships among species, an evolutionary factor that can also bias meta-analyses of impacts (Chamberlain *et al.* 2012). Unfortunately, how these factors modulate the impact of invasive plants on the N cycle has not been tested at a global scale.

The major aim of this study is to identify factors that explain variation in impacts of exotic plant invasions on the N cycle by conducting a structured meta-analysis of published information. Our meta-analytical approach focuses on metrics that cover most of the N cycle in terrestrial ecosystems and can be related to N pools within ecosystem compartments (soil, litter, plants) and with fluxes across them (Fig. 1). Specifically, we tested whether mean effect sizes depend on methodological aspects (i.e. the study approach - experimental or observational- and the criteria to select the native control), on some properties of the invaded site (whether the impact was mediated by disturbance, residence time of the invader, climate, insularity or biome), and/or on biotic properties of both the invader and the recipient community (i.e. the functional and phylogenetic distance between invasive and native species, and/or the position of the invader on the phylogenetic tree). We also explored whether the species pool covered by quantitative field studies is representative of invasive plant species worldwide. Because N-fixation is the most obvious pathway of impact (D'Antonio & Corbin 2003), we specifically explore whether an over-representation of N-fixing invasive plants may influence the results.

On the basis of the above information we developed several predictions. Given that the physiological processes involved in the N cycle are limited by drought and low temperatures (Schindlbacher *et al.* 2010; Szukics *et al.* 2010; Guntinas *et al.* 2012), we expected stronger impacts when the recipient ecosystems occur in warm and wet climates (hypothesis 1). We also expected that plant invaders that are functionally more distant from the natives would have larger impacts (hypothesis 2). Given that island communities are typically poor in species and usually differ in taxa frequencies from those of continents (Whittaker 1998), there were more chances for an invader to be functionally distant from natives, and therefore to cause stronger impacts (hypothesis 3). Given that functional differences between species may strongly depend on their evolutionary relatedness (Daehler 1998; Pyšek 1998; van Kleunen *et al.* 2007; van Kleunen *et al.* 2010), we expected phylogenetic distance between the invasive and native species to be proportional to the impact on the N cycle (hypothesis 4). Finally, invaders belonging to particular clades in the phylogenetic tree, such as the N-fixing families Fabaceae, Elaeagnaceae, Betulaceae, Myricaceae, were expected to cause larger impacts than others (hypothesis 5).

Methods

Data collection

We searched the literature for metrics related to the N pools and fluxes of the N cycle (Fig. 1). In some cases, we found direct measures of the target pool or flux (i.e. “target variables”, e.g. N mineralization rate), but in others we found one or more metrics standing for the target pool or flux (i.e. “other accepted metrics”; for instance, litter lignin and litter C/N are proxies for litter decomposition rate). We performed a meta-analysis selecting those variables with enough case studies (≥ 14). Selected variables and the rationale for their inclusion in the analysis are summarized in Table 1.

On 12 March 2010 we searched for articles reporting impacts of invasive terrestrial plant species invasions on any component of the N cycle, using ISI Web of Knowledge, with no restriction on publication year. Three search formulae were used: 1) (Exotic* OR alien* OR invasive*) AND (native*) AND (plant*) AND (leaf OR leaves OR litter) AND (LMA OR SLA OR SLM OR nitrogen or phosphorous OR lignin OR decomposition or C:N or C/N or (life SAME span) or turnover). 2) (Exotic* OR alien* OR invasive*) AND (native*) AND (plant*) AND (nitrogen) AND (soil*) AND (mineralization OR nitrification OR ammonification OR pH OR respiration OR (microb* SAME biomass*) OR fixation OR (organic SAME matter)). 3) (Exotic* OR alien* OR invasive*) AND (native*) AND (plant*) AND (RGR OR NPP OR (growth SAME rate) OR (primary SAME product*)) NOT (estuar* or marsh* or seawee* or macrophyte* or demograph* or mosquito* or earthworm* or amphipod*).

All formulae searched for papers comparing native and exotic invasive species or invaded/non-invaded communities. However, the first formula searched for data on leaf /litter properties or decomposition rates, the second searched for soil properties and rates of N transformations, and the third for plant productivity or relative growth rate. We also surveyed the references in relevant articles we retrieved. This search resulted in a set of 420 papers which was subsequently filtered out to reject those that did not meet the following conditions:

- Studies were carried out in terrestrial ecosystems. We excluded aquatic ecosystems because their N cycle is strongly affected by water flow, which moves

N within the ecosystem and creates a set of pools (i.e. water, sediments and water-sediment interface) different from those of terrestrial ecosystems.

- Studies either examined natural invasions in the field (observational studies) or performed experiments in common gardens or glasshouses (experimental studies).
- Studies explicitly mentioned the identity of the invasive species causing impacts, and compared any of the variables in Table 1 between the invasive species and coexisting natives, or between invaded and non-invaded sites.
- It was clear that the term "invasive" refers to exotic species, with self-sustained populations and with the potential to spread far beyond the introduction site.
- Variables were measured simultaneously in the invasive species/invaded site and in the native species/non-invaded site in the same (micro)environmental conditions, so that the influence of other factors on the effect size was minimized.
- The study reported average values of the variables, number of replicates and reliability (standard deviation or standard error) for all measurements.

These criteria reduced the initial number of papers to 100 (see Appendix S1), 26 and 30 of them were also covered by the meta-analyses of Liao *et al.* (2008) and Vilà *et al.* (2011), respectively.

Among the selected papers, we adopted the following criteria to select case studies or units of analysis (i.e. the unit for calculating the effect sizes):

1. If the same study reported data for more than one independent pair of species/ sites, each pair was considered as an independent case study (Borenstein *et al.* 2009), matching the criteria of other meta-analyses (Liao *et al.* 2008; Benayas *et al.* 2009; Bertheau *et al.* 2010; Vilà *et al.* 2011).
2. If the study reported more than one value for the same pair (for different sites,

treatments or times), we pooled effect sizes and variances among all values reported for the same pair by doing a separate meta-analysis, following the formula to combine effect sizes across case studies in a grand mean effect size (d^+, see below). The estimated pooled mean effect size and the mean variance were used in the final data set (Borenstein *et al.* 2009).

3. In multispecies studies which explicitly assigned invasive species to native pairs, we used these pairs as independent observations, and noted which of the following criteria met the native control: 1) high abundance, 2) growth form similar to the invasive, 3) same genus or family as the invasive.
4. When there was one native control for two or more invasive species, each invasive-control combination was considered as a separated study case.
5. When several native controls were available for the invasive species, different criteria were used to select the native control: 1) random selection, 2) the most abundant, 3) the most similar to the invasive (according to the functional traits listed below), or 4) pooling the effects of all potential invasive-native pairs, (as in van Kleunen *et al.* 2010). In those cases where information on abundance was missing, or all the available natives were equally abundant and/or shared functional properties, we applied a random selection for criteria 1, 2 and 3, with the restriction that a different species had to be selected by each. By performing all analyses separately on the data sets resulting from each selection criterion, we tested the influence of the native selection criteria on the outcome of the meta-analysis. In the case of criterion 4), hypotheses 2 and 4 were tested with fewer cases, because species pooling prevented the computation of some functional and phylogenetic distances (see below).

For each case study we recorded information regarding characteristics of the study, abiotic properties of the invaded site, and biotic properties of the invasive plant and native control (see Table 2). Most of these characteristics were obtained from the papers. Whenever average climatic properties (mean annual temperature and precipitation) were not reported, we obtained them from the WorldClim database (Hijmans *et al.* 2009), on the basis of the coordinates or site names reported in the paper. WorldClim provides average climatic values for the period 1950-2000. Although the use of averages of climatic series did not allow us to test the effects of within-site climatic variability, these effects were assumed to be negligible compared to those driven by the broad climatic gradient covered by our dataset. Whenever possible, species (both invasive and native) were coded according to the following traits: woodiness (1: woody 0: non-woody), self-support (1: self support, 0: vine or climber), height (0: <1 m, 0.5: 1-5 m, 1: >5 m), N-fixation ability (1: fixing, 0: non-fixing) and plant/leaf habit (1: evergreen or perennial plant, 0: deciduous or annual plant). Subsequently, we subtracted the value of the native from the value of the invasive in each trait, which gave us a magnitude and a direction of each trait change upon invasion. To get an overall magnitude of the “functional distance” between the invasive and the native species (irrespective of the direction) we summed up the absolute values of all trait differences. When the target variable was measured in the ecosystem rather than in a species (e.g. soil properties), the functional distance was only computed if the authors made it clear that the property may be assigned to a single species (e.g. if the soil was collected in a site with a 100% covered by a single species). The information on species traits was obtained from the papers, Floras, and online databases (Appendix S2).

Phylogenetic relatedness was assessed by building a pruned phylogenetic tree with all invasive and native species as terminal tips using the maximally resolved seed plant tree (R20120829) available in Phylomatic (http://phylodiversity.net/phylomatic/). We calibrated the resulting tree by dating the nodes in Phylocom 4.1 with the Branch Length ADJustment function (BLADJ), on the basis of the lognormal clade age estimation of Bell *et al.* (2010). Ferns were excluded. With this phylogenetic tree, we estimated the phylogenetic distance for each invasive-native pair and we additionally tested for phylogenetic signal of the impacts of the invasive species across the dataset, (i.e. whether differences in effect size of invaders depends on their position on tree) using the K-statistic (Blomberg *et al.* 2003) in the R package Picante (Kembel *et al.* 2010). For both the phylogenetic distance and the phylogenetic signal, we conducted these analyses with the four pairing criteria described above.

Finally, to assess whether N-fixing invasive species were over-represented, we compared the proportion of N-fixing invasive plants and the proportion of case studies focused on N-fixing plants in our database with the N-fixing invasive species reported in several databases/checklists throughout the world (see Appendix S3).

Statistical analysis

The unit of analysis was a pair of invasive (*i*) and native species (*n*) or a pair of invaded (*i*) and non-invaded sites (*n*). For each case Hedges' *d* was used to estimate the effect size because 1) it weighs cases by their number of replication and the inverse of their variance, and 2) it accounts for the effects of small sample sizes (Rosenberg *et al.* 2000). Hedges' *d* for a given case study was calculated as:

$$d = \frac{\left(\overline{X}^{i} - \overline{X}^{n}\right)}{S} J \quad ,$$

where *S* is the pooled standard deviation and *J* is a weighting factor based on the number of replicates (*N*) in each case. J was calculated as:

$$J = 1 - \frac{3}{4\left(N^{n} + N^{i} - 2\right) - 1} \; .$$

The variance of Hedges' *d* was computed as:

$$Vd = \frac{N^{n} + N^{i}}{N^{n} N^{i}} + \frac{d^{2}}{2\left(N^{n} + N^{i}\right)}$$

Hedges' *d* ranges from -∞ to +∞. Largest effect sizes come from those cases with a large difference between the invasive and the native species (or invaded and non-invaded site) and low variability. A positive value of *d* indicates that the target variable in the invasive plant/invaded site has a larger value than the native control.

We performed the analysis in the following hierarchical way:

1) Synthetic analysis of all pools and fluxes: We used the target variables and other accepted metrics in categories “pools” and “fluxes” (see Table 1). Given that some studies reported more than one variable related with the same pool or flux, we applied the following rules to avoid pseudo-replication: 1) the “target variable” was preferred over “other accepted metrics”; 2) we pooled effect sizes and variances for several target variables or other accepted metrics in the same type of pool or flux and in the

same case study, by doing separate meta-analyses (see below computation of d^+). The variable “Soil total N” was excluded because it cannot be assigned to a single pool category (see Table 1). The final dataset contains 113 exotic invasive species and 345 case studies with only one effect size for each case study in each type of pool or flux.

2) Separate analysis of pools and fluxes: The data set was split into pools and fluxes, and two separate meta-analyses were performed on each subset.

3) Separate analysis of each target variable: We performed additional meta-analyses for each raw variable (Table 1), including soil total N, which added two new case studies to the initial dataset.

In each analysis, effect sizes across all comparisons were combined using the random effects model to provide the grand mean effect size (d^+), where the weight of each case is the reciprocal of its sampling variance. A random effects model was preferred because it accounts for the fact that, in addition to sampling error, there is a random component of variation in effect sizes among studies. The effect was considered significant if the bias-corrected 95% bootstrap-confidence interval (CI) of d^+, calculated with 999 iterations, did not bracket zero (Rosenberg *et al.* 2000).

For each grand mean effect size calculation, we computed the total heterogeneity of effect sizes across studies by means of the Q_T statistic as:

$$Q_T = \sum_{i=1}^{n} w_i \left(d_i - d^+\right)^2 ,$$

where n is the number of cases, d_i is the effect size of case i and w_i is the reciprocal of the sampling variance. A significant Q_T, tested against a chi-square distribution with n-1 degrees of freedom, indicates that the variance of effect sizes among studies is greater than expected by sampling error and implies that there may be some underlying structure to the data. In those cases, we performed structured meta-analyses, using all factors listed in Table 2 (characteristics of the study, abiotic and biotic properties), to explain heterogeneity of effect sizes. To test whether mean effect sizes of variables differed between the levels of each categorical factor (e.g. between islands and continents, between N-fixers and non N fixers, etc), we assessed the significance of the between-group heterogeneity (Q_B) with a chi-squared test (Rosenberg *et al.* 2000). Finally, we tested whether variation in effect sizes covaried with the continuous factors (precipitation, mean temperature of the invaded site, functional and phylogenetic distances between invasive and native species, etc.) by using weighted least squares regression. The amount of heterogeneity explained by the regression model (Q_M) was tested against a chi-square distribution with 1 degree of freedom to assess its significance. If the model was significant, we further assessed the slope of the model and its significance.

Meta-analysis results may be affected by publication bias, i.e. the selective publication of articles finding significant effects over those which found non significant effects (Begg 1994). We explored this possibility by correlating the standardized effect size with the sample size across studies. We found a negative (Spearman r = -0.032 to -0.064, depending on the pairing criteria) but non-significant (P>0.24 in all cases) correlation, which indicates that larger effect sizes in one direction are not more likely to be published than smaller effect sizes (Rosenberg *et al.* 2000). Besides, a plot of effect sizes versus sample sizes across studies revealed a funnel-shaped distribution (Appendix S4) which is expected in the absence of publication bias (Palmer 1999). A plot of the standardized effect sizes against normal quantiles followed a straight line, indicating that effect sizes are normally distributed

(Rosenberg *et al.* 2000) (Appendix S4). Finally, the fail-safe number (i.e. the number of null results (either non-significant, unpublished or missing studies) that would have to be added to make the overall test of an effect statistically non-significant) was calculated as a measure of the strength of the result (Rosenberg *et al.* 2000). We found values over 29925, which were larger than 5N+10 =1735, where N is the total number of cases in our analysis. This means that the observed result can be considered as a reliable estimate of the true effect (Rosenberg 2005).

Results

Characteristics of the database

Our data set covered 345 study cases, which included 113 exotic invasive species (16 N-fixing and 97 not N-fixing). Among these species, the most represented were *Robinia pseudoacacia* with 13 cases, *Acacia saligna* with 11, *Microstegium vimineum* and *Bromus tectorum* with 10, and *Elaeagnus angustifolia, Ailanthus altissima* and *Berberis thunbergii* with 9 cases each. Among the 46 families of invasive species Poaceae with 75 cases was the most common, followed by Fabaceae (54 cases), Asteraceae (30) and Elaeagnaceae (12). The proportion of N-fixing invasive plants across different databases worldwide varied from 2% in New Zealand to 32% in USA, being 15% on average (Appendix S3). This was similar to the proportion of N-fixing species covered by our dataset (14%). However, N-fixing species accounted for 21% of the study cases, suggesting that they were over-selected in studies testing the effects of invasive plants on the N cycle. The geographic distribution of case studies was uneven, 73% of them occurring in North America and Europe. By contrast, Africa was only represented by 5% (all occurring in South Africa), Australia + New Zealand by 5%, Asia by 3% and South America by 1%. It is noteworthy that the

Hawaiin Islands contributed 11% of the cases (Appendix S5). The average number of target variables reported for each case study was 2.4, with a maximum of 9. The most frequently reported variable was specific leaf area (SLA) with 58 case studies, followed by litter decomposition rate, soil total N, litter N and soil mineral N. Less often reported were litter lignin and litter mass, with 10 and 14 cases, respectively (Appendix S6). In 41% of the case studies comparing traits between species pairs, the native control was reported to be abundant. In 53% it belonged to the same growth form as the invader and in 28% it belonged to the same genus or family as the invader. Finally, in 70 case studies (20%), more than one native species was available for each invader, and we selected native controls using the four previously defined criteria. Results were consistent across selection criteria (see Appendices S7-S8), thus we focus on the random selection criterion because it represents a balance between all criteria (see Appendices S7-S8 for the full set of results for the four criteria).

Impacts on plant invasion to the N-cycle

We found a positive effect of plant invasions on all the N cycle-related metrics considering the full dataset (pools + fluxes) (d^+=0.63, bootstrap 95% confidence interval 0.41-0.82), although the effect disappeared when the native control was an invader-removed site (heterogeneity between case studies with each type of control (Q_B)=7.30, $P<0.05$, Appendix S7). We also found that the effect size was similar for pools and fluxes (Appendix S7), but as expected, there was large heterogeneity among case studies (Q_T=805, $P<0.001$). Each N pool increased with a similar magnitude following invasion (Q_B=3.54, P=0.49, Fig. 2). However, the effect on N fluxes varied (Q_B=10.05, $P<0.05$), so that the largest acceleration was found on the N transfer from organic matter to mineral form in soils, while the N transfer from plants to soils was not affected by invasions (Fig. 2). Correlations of effect sizes among target variables reported within the same studies revealed that several plant invasion impacts covaried (Appendix S9). For instance, increases of litter N upon invasion coincided with increases in litter mass, litter decomposition rate and soil mineral N; increases in soil organic matter also coincided with increases in soil mineral N.

Determinants of the impacts on N-cycles

Among all factors considered for explaining variation in effect size (Table 2), climate and invader-native functional distance were the most important, insularity and phylogeny had an intermediate effect, and study type, residence time, or if the impact was mediated by disturbance were poor predictors (Appendices S7-8).

In line with hypothesis 1, N fluxes were more accelerated following invasions in moist and warm locations, and this was robust to the removal of case studies with extreme effect sizes (see Fig. 3). Accordingly, effect sizes on N fluxes were larger in the Tropical Forest biome, as compared with Temperate (grasslands or forests) or Mediterranean biomes (Q_B=12.6, P<0.05, Fig. 4A, Appendix S7). Functional distance between the invasive plant and the native control did not explain heterogeneity of impacts, but some of its components did so (partial support to hypothesis 2). Specifically, the impact on N pools was larger when the invader was either N-fixing, tall, annual/deciduous or any combination of the three traits, and the native control was non-N-fixing, short and/or perennial/evergreen (Fig. 5, Appendices S7-S8). Plant/leaf habit distance similarly explained the variation of invasions impact on N fluxes (Appendix S8). Effect sizes on N pools + fluxes were also larger when the invaders were N-fixers (Q_B=9.75, P<0.01, Appendix S7). Although removing these species from the analysis reduced the effect size, it remained positive and significant (d^+=0.50, bootstrap 95% confidence interval 0.30 to 0.72).

The effect sizes of invaders on N fluxes were larger on islands than in continents (Fig. 4B, Appendix S7), partially supporting hypothesis 3. In addition, when impacts on pools and fluxes were considered together, the effect size in islands increased with the distance to the continent (Q_M=6.74, P<0.001, Appendix S8). However, this was driven by the over-representation of cases occurring in the Hawaiian islands.

In contrast to our expectation (hypothesis 4), phylogenetic distance between invasive and native plants did not influence the impacts (Q_M=0.30, P=0.58, Appendix S8). We also found no phylogenetic signal on the impact size of invaders either on the overall dataset, in N pools or in N fluxes (Appendix S10). However, when assessing particular target variables related with ecosystem N pools, we found significant effects on aboveground biomass; grass invaders (Poaceae) had a moderate negative effect, whereas N-fixing trees (Fabaceae and Elaeagnaceae) increased the standing biomass up to four times more than the rest of the invaders (Appendix S10-11).

Discussion

Effects of invasions on pools and fluxes

We found that exotic plant invasions accelerated N fluxes and increased N pools, in agreement with previous studies (Ehrenfeld 2003; Liao *et al.* 2008; Vilà *et al.* 2011). This result was robust to variation in some methodological aspects (such as criteria to select the native control or whether the approach was experimental or observational) and in properties of the invasion context (i.e. residence time, whether the impact was mediated by disturbances). This trend also was robust to the removal of N-fixing invaders from the analysis.

Our results indicate that plant invasions tend to increase N inputs to the ecosystem. The fact that the effect size on N pools notably declined after the removal of N-fixing invaders (Appendix S7) indicates that the main mechanism explaining this pattern is an increase of N fixation, as previously suggested (Chapin *et al.* 1996; D’Antonio & Corbin 2003; D’Antonio & Hobbie 2005). However, non-N fixing invaders still tended to increase pools (Appendix S7), suggesting that additional mechanisms may operate. For instance, non-symbiotic N fixation by microbes of the rhizosphere has been found to increase in some invaded systems (Williams & Baruch 2000), although the reverse has also been found (Ley & D'Antonio 1998; Mack *et al.* 2001). Non-N fixing invasive plants may increase N pools in the ecosystem by using it differently from natives (e.g. taking up N at different soil depths, at different times or accessing different forms of N than native species), which may increase total nutrient use in the ecosystem and reduce N losses of mineral forms by leaching (Fargione *et al.* 2003; D’Antonio & Hobbie 2005; Ehrenfeld 2010). Alternatively, the high N pools of invaded sites may also be the cause, rather than the consequence, of invasions, because some disturbances that increase N availability (e.g. fertilization or N deposition) may promote plant invasions (Davis *et al.* 2000; D’Antonio & Corbin 2003; D’Antonio & Hobbie 2005). However, this information was rarely reported.

We did not detect changes in the distribution of N across categories of pools, but did find wide variation of effect size within each ecosystem compartment. In fact, we might expect very different redistribution patterns depending on the nature of the invasive plant and the invaded community. For instance, if invasive herbaceous plants replace native trees, the main increase in ecosystem N would occur in litter or in soil, but not in above-ground plant biomass, whereas the reverse would be expected if invasive trees invade native grasslands. Unfortunately, the low number of case studies with different combinations of invasive-native growth forms did not allow us to test this hypothesis. Our results are in contrast to those by Liao *et al*. (2008), who reported a higher N increase in plant roots, followed by plant shoots, microbes and soil. However, in the case of N pool in roots, the seven case studies they reported are not sufficiently representative to merit general conclusions.

The overall trend for faster N fluxes following invasion agrees with previous reviews (Ehrenfeld 2003; Liao *et al.* 2008; Vilà *et al.* 2011) and is consistent with the hypothesis that invasive plants usually possess traits associated with faster N turnover, such as low leaf construction costs, high leaf N content and short leaf life span (Pattison *et al.* 1998; Durand & Goldstein 2001; D'Antonio & Corbin 2003; Pyšek & Richardson 2007). The finding that plant N uptake from soil was the most accelerated flux upon plant invasions (Fig. 2) is consistent with reports showing that invasive plants often grow faster (D'Antonio & Corbin 2003; Grotkopp & Rejmánek 2007; Leishman *et al.* 2007; Pyšek & Richardson 2007; van Kleunen *et al.* 2010), and therefore possess a higher potential for soil N uptake. The non significant impact of plant invasions on litter decomposition rate contrasts with the low C:N ratio found in invasive litter (Appendix S6), and may be partly explained by a high content of lignin, as this was found in leaves/shoots of many invasive plants (Ehrenfeld 2003; Knight *et al.* 2007; Godoy *et al.* 2010). Lignin bonds with protein N and produces complex molecules difficult to attack by microorganisms (Gallardo & Merino 1992, 1993), leading to an increase of N trapped in the litter and in the soil organic matter, which is not readily available for uptake by most terrestrial plants. Contrastingly, plant invasion enhanced N mineralization (Fig. 2, Appendix S6), maybe due to a larger or more balanced supply of resources to microorganisms by exotic litter (Rothstein *et al.* 2004; Chapuis-Lardy *et al.* 2006; Castro-Díez *et al.* 2009; Strickland *et al.* 2010), to an improvement of the microenvironmental conditions in the soil for microbial activity (Chapin *et al.* 1996; Mack & D'Antonio 2003; Norton *et al.* 2004; Marchante *et al.* 2008), and/or to a change in the composition of the soil biota (Hawkes *et al.* 2005; Peltzer *et al.* 2009; Rodriguez-Echeverria 2010).

What explains differences of impacts across studies?

By considering methodological aspects of the studies, properties of the recipient ecosystem and biotic properties of both invasive and native plants, we were able to identify new sources of cross-studies variation of plant invasion impacts on the N cycle, that were not considered in the previous reviews by Liao et al. (2008) and Vilà et al. (2011). The larger acceleration of N fluxes when plant invasions occur under warmer and moister conditions (Fig. 3, hypothesis 1), may be explained by the fact that physiological processes and enzymatic reactions (as those involved in nutrient cycles) are generally faster at higher temperatures (Wallenstein *et al.* 2011), particularly if there is no other limitations, such as water shortage. This may be useful for predicting impacts of invasive plants across locations. However, predictions over time at local scales cannot be made, mostly because we could not include (i.e. poorly described in the original sources) the effect of other variables likely affecting more strongly the size of the impact at local scales, such history of introduction, human use, and soil properties.

The fact that N-fixing plants caused stronger impacts on N pools when they become invasive, especially in communities lacking N-fixers (Fig. 5), had been suggested by previous reviews (Chapin *et al.* 1996; D'Antonio & Corbin 2003; Liao *et al.* 2008; Vilà *et al.* 2011). Besides, a large plant size may magnify the N-fixing impact to the ecosystem. Moreover, invaders with short-lived tissues (either entire plants or leaves) invest less in defense but more in production and have shorter turnover rates (Herms & Mattson 1992; Reich 1993; Castro-Díez *et al.* 2000); therefore they tend to accelerate N fluxes when they replace natives with long-lived tissues. This is why the most dramatic examples of invasive plants impacts on N pools involve situations with a combination of at least two of these features (Vitousek & Walker 1989; Rice *et al.* 2004; Yelenik *et al.* 2004). The failure of our functional distance to explain heterogeneity in the N cycle impacts (hypothesis 2) was due to the fact that this metric did not account for the overall direction of the functional change (it summed up the absolute values of particular distances). Indeed, the three components of the functional distance, which explained heterogeneity (N-fixation, plant height and plant/leaf habit distances), showed that sign matters, as the slope of the relation varied among them (Fig. 5).

Consistent with hypothesis 3, the acceleration of N fluxes caused by invasive plants was larger on islands than on continents (Fig. 4B). Also consistent with the hypothesis, the functional distance between invaders and natives was larger in islands (0.93±0.14 vs. 0.52±0.06, Student's t=2.71, P=0.01). However, this cannot explain the larger impacts of invaders on islands, because functional distance did not affect the impact size on N fluxes (Appendix S8). An over-representation of cases of N-fixing invaders in islands did not explain this result either, as this proportion was larger in continents (11 and 23%, respectively in the full data set, and 6 and 21% in the N fluxes dataset). Alternatively, this result may be explained by the milder climatic conditions typically found in islands, as compared with inland sites located at equivalent latitudes, and/or an over-representation of cases in Hawaii (a moist tropical climate). In fact, island sites in this study were on average wetter and warmer than continental sites (mean precipitation ± SE = 2227 ± 135 mm and 751± 24 mm, respectively, Student's t= 10.75 $P<0.001$; mean annual temperature = 18.9 ± 0.6 and 12.6 ± 0.3ºC for islands and continents, respectively, Student's t= 9.19 $P<0.001$). Therefore more studies in non-tropical islands are necessary to unravel whether the insularity effect was confounded with the climatic effect.

Phylogenetic distance between invaders and natives was not a good predictor of plant invasions impact either on N fluxes or on N pools, not supporting hypothesis 4. The poor correlation between phylogenetic distance and the distance for the three functional traits more relevant to this pattern -N-fixing ability, plant height and plant/leaf habit- could explain this result. Indeed, in our broad tree including disparate families, N-fixing ability was restricted to Fabales and a single species within Rosales (*E. angustifolia*). Moreover, plant height and plant/leaf habit are labile traits within families, so that several families have tall and short species (e.g. Rosaceae, Solanaceae), and perennial and annual species (e.g. Poaceae). Similarly, impacts on the N cycle did not depend on the position of invasive species on the phylogenetic tree (little support for hypothesis 5). Only the impact on aboveground plant biomass (one component of N pools) showed phylogenetic signal, because of the opposite effects that N-fixing clades and the Poaceae had on this target variable. This reinforces the idea that, although some families may possess certain traits that can potentially increase or decrease N pools, their final impact seems to be related more to the interaction between invaders traits and the biotic and abiotic properties of the invaded site.

Limitations of the dataset inherent to published literature.

We present the most extensive review conducted to date on the impact of invasive plants on the N-cycle. However, our database was sensitive to the bias that the literature on plant invasion impacts has in the selection criteria of species and target variables (Hulme *et al.* 2013). For instance, our analysis included a small fraction (N = 113) of invasive species worldwide, which is estimated in the thousands (Hulme *et al.* 2013). In addition, some taxa were over-represented (the seven most studied taxa accounted for 21% of the case studies). Some N-fixing invaders are over-selected, probably because they represent the most obvious and dramatic examples. Despite these limitations, our work shows that even not considering the effect of N-fixers, invasive plants still generally increase N pools and accelerate N fluxes. We also found a gap of knowledge for several continents, as most studies were conducted in North America and Europe. Therefore, more research effort is needed in the remaining (sub)continents. Finally, we found that the effect size of invaders for several target variables were correlated, suggesting that impacts on the N cycle can be assessed by exploring a few easy-to-measure key effects of the invaders. For instance, an increase in litter N upon invasion may involve impacts in other several ecosystem N pools (e.g. litter and in soil) and in N fluxes (e.g. litter decomposition rate).

Another limitation of this meta-analysis relies on the fact that the effect size of invaders was often calculated using a single native species as representative of the entire native community. A more realistic approach would be using the average community trait value, weighed by species abundances, as the native control. However, detailed information on community structure is rarely being reported. This is an important point that we ecologists need to start considering. Until this information is available, we faced this shortcoming by exploring different rationale to select the native control. Our similar findings across criteria give strength to our approach and suggest that all potential native pairs for the same invader did not largely differ in their implications to the N cycle.

Conclusions

Using a meta-analytical approach we have shown that the wide variation of plant invasion impacts on the N cycle can be explained by certain characteristics of the studies, plant functional properties and environmental conditions. A relevant outcome was that moist and warm environments are more vulnerable to alterations to the N cycle following invasions by exotic plants, presumably because such conditions exacerbate the acceleration of N fluxes. In addition,, we found that when the invasive plants are more distant from the native control in terms of N-fixing ability, plant height and plant/leaf habit may cause larger impacts on the N cycle. Our results suggest that different approaches used for weed risk assessment would continue to be unfruitful to predict the impacts of invasive species if they only considered their characteristics (Hulme 2012). We have shown that these impacts are more related to the functional differences between the invaders and the native residents and the climatic characteristics of the invaded site. Taken together, our results show that invasive species are causing the greatest impacts on the N cycle when they are functionally distant from natives in functionally poor ecosystems with warm and wet climates.

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Table 1. Variables selected to evaluate the impacts of exotic plant invasion on the N cycle. In some cases, other metrics were accepted when the target variable was not available or when both have been found to correlate in the literature (a negative sign means that they correlate negatively with the target variable). The part of the N cycle that each metric is related to is shown in the third column. The last column classifies target variable between pools or fluxes.

Target variable	**Other accepted metrics**	**Related with***	**Category**
Above-ground plant mass Leaf or shoot N concentration		N pools in above-ground vegetation (1)	N pools
Litter mass Litter N concentration		N pools in plant litter mass (2)	
Soil organic matter		Soil N pools in organic matter (3)	
Soil mineral N		Soil N pools in mineral form (4)	
Soil total N		(3) and (4)	
Litter decomposition rate	Litter lignin (-) Litter C:N (-)	Litter decomposition rate (6 and to a minor extent 7)	N fluxes
N Mineralization/nitrification/ammonification rate		N transfer rate from soil organic matter to mineral soil (7)	
Plant RGR†	SLA‡	Vegetation N uptake rate from soil (8), litter production rate (5)	

* The number in parentheses refers to boxes and arrows in Figure 1.

†RGR-plant relative growth rate

‡SLA-specific leaf mass

Table 2: Factors used to explain the heterogeneity of plant invasion effect size across studies by means of structured meta-analysis. The third column indicates the data set to which it was applied (full dataset with all pools and fluxes; dataset with pools: dataset with fluxes).

Structure factor	**Categories /Values of the factor**	**Data set to which it was applied**
Category	Pool flux	Pools+fluxes
Type of pool	In litter In aboveground vegetation In soil in mineral form In soil organic matter	Pools
Type of flux	Soil→Plant Plant→Soil SOM(1)→ Soil N min(2)	Fluxes
Study type	Experimental Observational Mixed	Pools+fluxes
Removal experiment	Yes (the control is a site where the invasive plant was removed) No (the control is a non invaded site)	Pools+fluxes
Impact mediated by disturbance	Yes No	Pools+fluxes
Residence time	1:<50 years 2: 50-100 years 3:100-200 years 4:200-500 years 5:>500 years	Pools+fluxes
Insularity	The invaded site is an island The invaded site is a continent	All
Distance to the continent(3)	(Continuous)	All
Biome(4)	Tropical forest Mediterranean Temperate forest Temperate grassland	All
Mean annual precipitation	(Continuous)	All
Mean annual temperature	(Continuous)	All
Invasive plant is N-fixing	Yes No	All
Functional distance	(Continuous)	All
Woodiness distance	(invasive value - native value)	All
Self support distance	(invasive value - native value)	All
Plant height distance	(invasive value - native value)	All
Plant/leaf habit distance	(invasive value - native value)	All
N-fixation distance	(invasive value - native value)	All
Phylogenetic distance	(Continuous)	All

(1) SOM- Soil organic matter

(2) Soil N min- Soil N in mineral form

(3) only when the invaded site is an island

(4) initially we included “Savanna”, “Subtropical desert” and “Boreal forest”, but we considered that the number of cases was not large enough to get representative patterns (N<11) so we do not show them in results.

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Figure legends

Figure 1. Schematic representation of the nitrogen (N) cycle. Blue diamonds indicate N pools in different compartments. Block arrows indicate rates of N transfer between different compartments. Numbers are explained in Table 1.

Figure 2. Mean effect size (Hedges' *d*) of plant invasions impacts on the overall nitrogen (N) pools (first row) and on different N pools across the ecosystem (A) and on the overall N fluxes (first row) and on different fluxes among compartments (B). Lines indicate 95%-bootstrap confidence intervals. A mean effect size is significantly different from zero when its 95% confidence interval does not bracket the zero line. Positive mean effect size indicates that the invasive species possess larger value for the trait than the native species. Sample sizes for each trait are indicated in parentheses.

Figure 3. Variation of the plant invasion effect size (Hedges' *d*) on ecosystem nitrogen (N) fluxes according to the mean annual precipitation (A) and mean annual temperature (B) of the invaded site. Q_M is the heterogeneity explained by the model and its significance. Arrows mark cases with extreme effect size, which might have a large influence on the result. Therefore analyses were repeated without each of these cases and without all of them. Results for the mean annual precipitation model ranged from Q_M=26.26 to 35.51, P<0.001 in all cases. Results for the mean annual temperature model ranged from Q_M=6.756 to 10.52, P<0.01 in all cases.

Figure 4. Variation of the plant invasion effect size (Hedges' *d*) on ecosystem nitrogen (N) fluxes according to the biome (A) and the insularity (B) of the invaded site. Lines indicate 95%-bootstrap confidence intervals. Statistics for these analyses are shown in Appendix S7.

Figure 5. Variation of the plant invasion effect size (Hedges' *d*) on ecosystem nitrogen (N) pools according to three components of the functional distance between invasive and native plants, namely, plant height, N-fixation and plant/leaf habit. Q_M is the heterogeneity explained by the model and its significance.

Appendix S1.

References of the papers from which the study cases were derived

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Appendix S2

Sources of information where plant functional traits where searched for

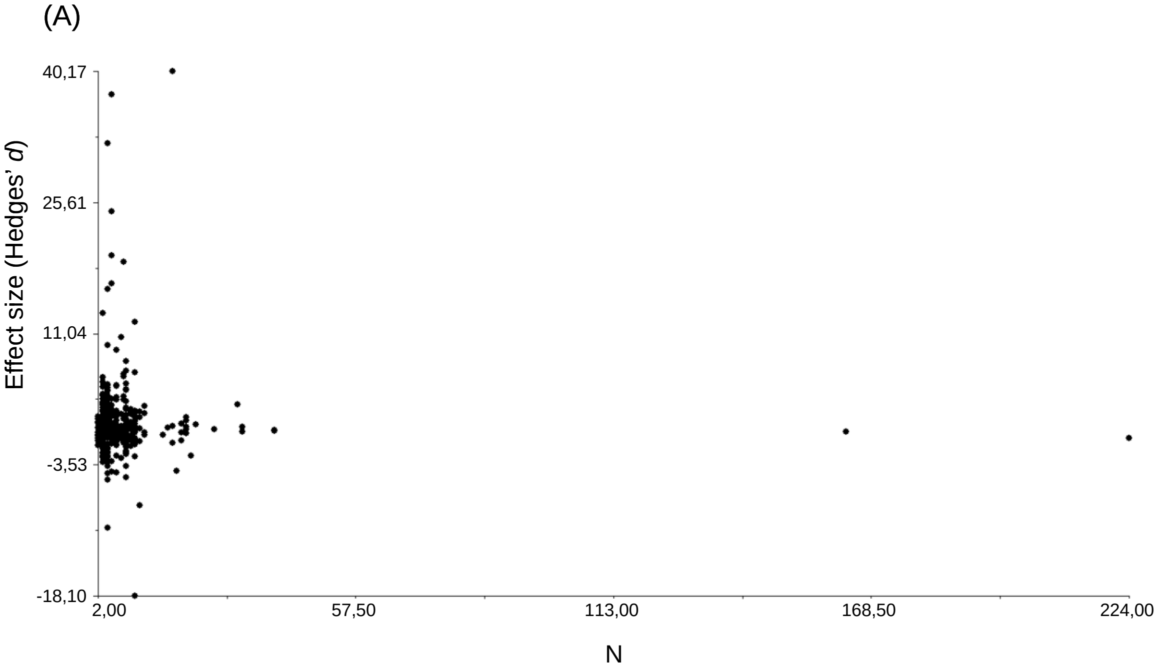
Region	Source	Website
Pacific Region	Hawaiian Alien Plant Studies	http://www.botany.hawaii.edu/faculty/cw_smith/aliens.htm
	Plant Threats to Pacific Ecosystems	http://www.hear.org/Pier/scientificnames/scinameb.htm
	Flora of Australia	http://www.environment.gov.au/biodiversity/abrs/online-resources/flora/main/
USA/ North America	Weeds Gone Wild: Alien Plant Invaders of Natural Areas	http://www.nps.gov/plants/ALIEN/index.htm
	USDA Plants Database	http://plants.usda.gov/java/
	California Invasive Plant Council	http://www.cal-ipc.org/
	Nature Serve Explorer	http://www.natureserve.org/explorer/servlet/NatureServe?init=Species
	Kansas Wildflowers & Grasses	http://www.kswildflower.org/index.php
	Center for Invasive Species and Ecosystem Health	http://www.invasive.org/index.cfm
	National Park Service	http://www.nature.nps.gov/biology/invasivespecies/
	Invaders Database System (NW USA)	http://invader.dbs.umt.edu/
Europe	Delivering Alien Invasive Species Inventories for Europe Project (DAISIE)	http://www.europe-aliens.org/
	European and Mediterranean Plant Protection Organization	http://www.eppo.int/
	Flora Europaea	http://rbg-web2.rbge.org.uk/FE/fe.html
	Flora Iberica (in Spanish)	http://www.floraiberica.org/
	Flora Arvense de Navarra (Spain) (in Spanish)	http://www.unavarra.es/servicio/herbario/htm/inicio.htm
	Herbario Virtual del Mediterráneo Occidental (in Spanish)	http://herbarivirtual.uib.es/cas-med/index.html
Global	Global Invasive Species Database	http://www.issg.org/database/welcome/
	Invasipedia	http://wiki.bugwood.org/Invasipedia

Appendix S3

Table S3.- Consulted databases/checklists of exotic invasive plants to assess the proportion of N-fixing species among them. The last two rows indicate the proportion of N-fixing invasive plants covered by our study and the proportion of case studies involving N-fixing invaders.

Country/region	Database	Website	Total number of invasive plants	Number of N-fixing invasive plants	% of N-fixing invasive plants
California	Cal-Flora	www.calflora.org/	223	17	8%
Florida	Florida Exotic Pest Plant Council	www.fleppc.org/	77	8	10%
USA	Federal Noxius Weed List- plants.	www.usda.gov/java/noxious	91	29	32%
New Zealand	Department of Conservation	www.doc.govt.nz/conservation/threats-and-impacts/	328	7	2%
Australia	Australian Government Department of the Environment and Heritage	www.environment.gov.au/biodiversity/invasive/weeds/weeds/lists/alert.html	60	15	25%
South Africa	Minister of Environmental Affairs and Tourism	www.sana.co.za/alien-invasive-plants/	287	39	14%
Europe	DAISIE- 100 worst alien species	www.europe-aliens.org/	18	3	17%
	Mean				15%
Global	Our study (no. of N-fixing invasive species)		113	16	14%
Global	Our study (no. of cases containing N-fixing invasives)		334	70	21%

Appendix S4



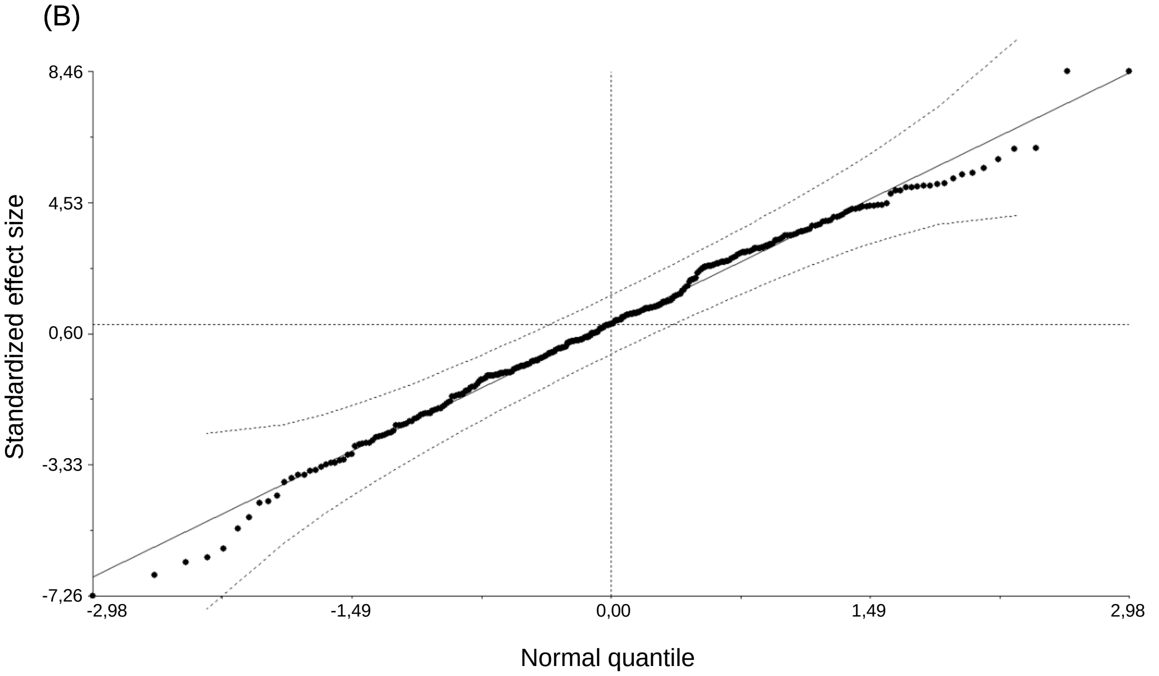


Figure. S4. Metawin output for A) funnel-plot of effect sizes (Hedges' *d*) versus sample size (N) and B) normal quantile plot.

Appendix S5

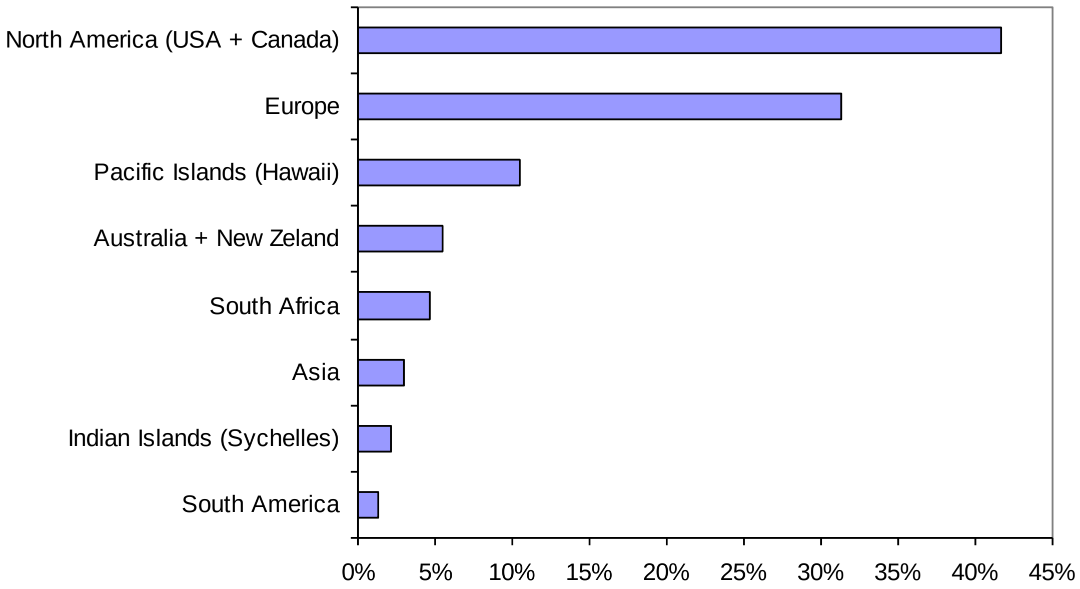


Figure S5. Proportion of case studies located in different regions. Some regions, such as the Caribbean, Central America and Africa -except South Africa- were not represented in our dataset.

Appendix S6

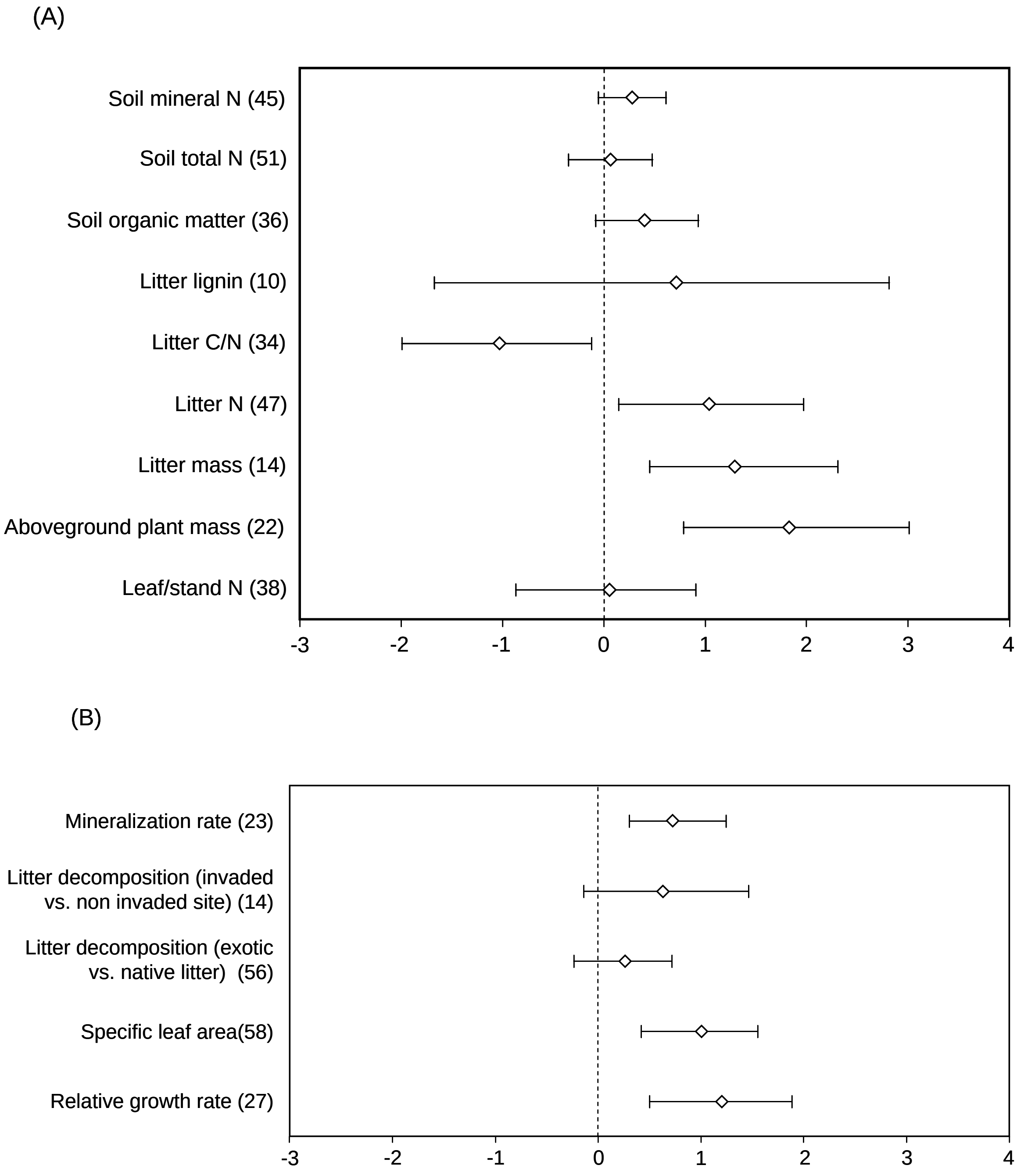


Figure S6. Mean effect sizes (Hedges' *d*) and 95% bootstrap confidence intervals of plant invasions on the raw variables related with A) N pools and B) N fluxes of the invaded ecosystem. The number of cases in each variable is indicated in parenthesis. These values were calculated by randomly selecting the native control in multispecies studies.

Appendix S7

Table S7.- Mean effect sizes, 95% bootstrap confidence intervals and sample sizes of plant invasion impacts on the N cycle in different categories defined by qualitative factors. The last columns indicate the heterogeneity between groups (Q_B) and its significance (P) on the basis of randomization tests. Results are shown for the four criteria applied to select the native control in multispecies studies (1- random selection, 2-the most abundant native, 3- the native more similar to the invader, 4- effect size calculated for all potential native controls were pooled). Factors already shown for pools+fluxes are only reported for pools or fluxes if they are significant.

		Selection criteria 1						**Selection criteria 2**						**Selection criteria 3**						**Selection criteria 4**					
Structure variable	**Category**	N	d^+	**95%CI**		Q_B	P	N	d^+	**95%CI**		Q_B	P	N	d^+	**95%CI**		Q_B	P	N	d^+	**95%CI**		Q_B	P
Pool+flux																									
Category	Flux	163	0,70	0,41	0,98	0,66	0,489	163	0,77	0,51	1,04	1,29	0,342	163	0,70	0,40	0,98	0,80	0,435	163	0,71	0,43	1,00	1,18	0,368
	Pool	182	0,57	0,26	0,84			182	0,58	0,32	0,85			182	0,55	0,29	0,83			182	0,52	0,24	0,82		
Study type	1-Observational	176	0,65	0,40	0,89	0,66	0,782	168	0,73	0,46	0,97	0,61	0,814	168	0,61	0,33	0,87	1,74	0,535	168	0,67	0,40	0,97	2,80	0,364
	3-Experimental	108	0,53	0,18	0,92			108	0,58	0,20	0,98			108	0,50	0,10	0,92			108	0,42	0,03	0,80		
	2-Mixed	44	0,74	0,17	1,33			44	0,60	0,09	1,13			44	0,87	0,33	1,40			44	0,87	0,33	1,45		
Exotic removal experiment	No	323	0,69	0,46	0,92	7,30	**0,032**	323	0,71	0,50	0,93	3,01	0,152	323	0,69	0,49	0,90	9,54	**0,017**	323	0,68	0,46	0,88	9,51	**0,020**
	Yes	22	-0,25	-1,00	0,47			22	0,11	-0,44	0,70			22	-0,37	-1,04	0,23			22	-0,39	-1,08	0,17		
Impact mediated by disturbance	No	202	0,87	0,58	1,17	0,42	0,588	202	0,99	0,70	1,29	4,45	0,087	202	0,85	0,56	1,14	0,62	0,526	202	0,84	0,56	1,14	0,34	0,662
	Yes	39	0,69	0,21	1,25			39	0,39	-0,15	0,89			39	0,63	0,13	1,14			39	0,67	0,15	1,22		
Insularity	Island	59	0,93	0,29	1,65	2,26	0,211	59	0,98	0,36	1,55	2,45	0,209	59	0,94	0,25	1,62	2,62	0,186	59	0,84	0,24	1,49	1,35	0,345
	Continent	286	0,58	0,38	0,79			286	0,61	0,42	0,82			286	0,56	0,35	0,76			286	0,57	0,35	0,77		
Biome	Tropical	54	1,29	0,59	2,02	12,66	**0,041**	54	1,32	0,72	1,98	12,35	**0,037**	54	1,30	0,53	2,04	11,95	**0,035**	54	1,18	0,51	1,89	9,87	0,063
	Temperate forest	101	0,52	0,17	0,90			101	0,59	0,23	1,00			101	0,55	0,20	0,93			101	0,63	0,28	0,98		
	Mediterranean	119	0,37	0,08	0,65			119	0,41	0,12	0,70			119	0,40	0,13	0,72			119	0,37	0,05	0,68		
	Temperate grassland	56	0,69	0,30	1,12			56	0,66	0,21	1,10			56	0,51	0,05	0,96			56	0,46	0,03	0,88		
Invasive species is N-fixer	No	258	0,50	0,30	0,72	9,75	**0,005**	258	0,55	0,34	0,77	10,79	**0,011**	258	0,50	0,30	0,72	10,94	**0,013**	258	0,47	0,25	0,70	12,47	**0,008**
	Yes	69	1,17	0,66	1,67			70	1,27	0,76	1,79			70	1,22	0,73	1,77			70	1,25	0,73	1,78		
N-fixation distance*	0	201	0,55	0,27	0,82	6,40	**0,034**	203	0,67	0,40	0,95	5,18	0,057	208	0,56	0,29	0,85	6,06	**0,034**	181	0,53	0,23	0,84	5,27	0,058
	1	34	1,37	0,73	1,98			35	1,41	0,79	2,20			34	1,37	0,74	2,13			33	1,30	0,69	1,95		
Pools																									
Pool type	In litter	54	0,88	0,20	1,56	3,54	0,486	54	0,91	0,28	1,51	3,85	0,436	54	0,89	0,21	1,57	3,38	0,507	54	0,85	0,18	1,56	2,77	0,583
	In aboveground vegetation	47	0,69	0,03	1,32			47	0,67	0,04	1,32			47	0,57	-0,06	1,25			47	0,50	-0,16	1,24		
	In soil N min	45	0,29	-0,05	0,64			45	0,29	-0,06	0,64			45	0,30	-0,07	0,66			45	0,31	-0,03	0,65		
	In SOM	36	0,42	-0,13	0,95			36	0,42	-0,12	0,97			36	0,42	-0,12	0,95			36	0,43	-0,07	0,99		
Invasive species is N-fixer	No	130	0,26	-0,03	0,56	21,61	**0,001**	130	0,27	-0,02	0,55	21,77	**0,001**	130	0,24	-0,06	0,53	22,33	**0,001**	130	0,20	-0,10	0,50	23,24	**0,001**
	Yes	41	1,65	0,92	2,43			41	1,66	0,94	2,48			41	1,64	0,91	2,43			41	1,65	0,96	2,36		
N-fixation distance*	0	82	0,30	-0,13	0,77	12,59	**0,003**	82	0,34	-0,12	0,77	12,57	**0,004**	84	0,27	-0,20	0,70	13,30	**0,006**	73	0,29	-0,22	0,80	10,14	**0,01**
	1	21	1,97	1,13	3,07			21	2,00	1,06	3,20			21	1,95	1,08	3,14			20	1,88	0,97	3,10		
Fluxes																									
Flux type	Soil->plant	69	1,12	0,62	1,62	10,05	**0,029**	69	1,30	0,76	1,81	13,62	**0,009**	69	1,16	0,71	1,65	10,69	**0,024**	69	1,12	0,66	1,60	9,63	**0,04**
	SOM->Soil N min	23	0,77	0,30	1,27			23	0,69	0,24	1,15			23	0,61	0,15	1,10			23	0,74	0,28	1,26		
	Plant->SOM	71	0,28	-0,16	0,66			71	0,30	-0,13	0,75			71	0,29	-0,14	0,69			71	0,29	-0,10	0,69		
Insularity	Island	31	1,65	0,80	2,70	12,08	**0,003**	31	1,81	1,03	2,65	14,58	**0,002**	31	1,60	0,74	2,62	10,82	**0,007**	31	1,47	0,65	2,37	8,10	**0,024**
	Continent	132	0,52	0,24	0,80			132	0,56	0,24	0,86			132	0,52	0,22	0,80			132	0,54	0,23	0,85		
Biome	Tropical	34	1,69	0,85	2,62	21,36	**0,007**	34	1,83	1,14	2,65	24,90	**0,001**	34	1,64	0,76	2,52	18,65	**0,002**	34	1,52	0,81	2,34	18,67	**0,005**
	Temperate forest	44	0,60	0,09	1,12			44	0,66	0,11	1,19			44	0,63	0,16	1,19			44	0,83	0,28	1,45		
	Mediterranean	64	0,16	-0,25	0,56			64	0,17	-0,23	0,57			64	0,18	-0,25	0,61			64	0,12	-0,26	0,51		
	Temperate grassland	16	0,89	0,32	1,46			16	1,00	0,21	1,72			16	0,74	0,18	1,36			16	0,71	0,10	1,27		

*1- the invasive species is N-fixer and the native species is not; 0- both species are N fixers or non N-fixers

Appendix S8

Table S8.- Results of the structured meta-analyses testing whether variation of plant invasions effect sizes on the N cycle across case studies covaried with continuous independent factors. We report the heterogeneity explained by the regression model (Q_M) and its significance (P) on the basis of a chi-square distribution with 1 degree of freedom. The regression slope, its standard error (SE) and its significance (P) are shown when Q_M was significant ($P \leq 0.05$). Results are shown for the four criteria applied to select the native control in multispecies studies (1- random selection, 2-the most abundant native, 3- the native more similar to the invader, 4- effect size calculated for all potential native controls were pooled). Factors already shown for pools+fluxes are only reported for pools or fluxes if they are significant.

		Selection criteria=1						Selection criteria=2						Selection criteria=3						Selection criteria=4					
Factor	Model	*df*	Q_M	*P*	Slope	SE	*P*	*df*	Q_M	*P*	Slope	SE	*P*	*df*	Q_M	*P*	Slope	SE	*P*	*df*	Q_M	*P*	Slope	SE	*P*
Pools+fluxes																									
	Regression	1	0,02	0,897				1	0,48	0,490				1	0,00	0,991				1	0,17	0,682			
Residence time	Residual	197	506,12	0,000				197	452,45	0,000				197	495,70	0,000				197	484,14	0,000			
	Total	198	506,14	0,000				198	452,93	0,000				198	495,70	0,000				198	484,31	0,000			
Distance to	Regression	1	6,74	**0,009**	0,001	0,000	**0,002**	1	8,05	**0,005**	0,001	0,000	**0,003**	1	6,84	**0,009**	0,001	0,000	**0,007**	1	5,66	**0,017**	0,001	0,000	**0,015**
continent(1)	Residual	54	126,23	0,000				54	100,90	0,000				54	118,71	0,000				54	116,24	0,000			
	Total	55	132,97	0,000				55	108,95	0,000				55	125,55	0,000				55	121,90	0,000			
Mean annual	Regression	1	25,45	**0,000**	0,001	0,000	1,000	1	21,52	**0,000**	0,0005	0,000	0,999	1	27,77	**0,000**	0,0006	0,000	1,000	1	23,02	**0,000**	0,0006	0,000	1,000
precipitation	Residual	312	737,93	0,000				312	689,85	0,000				312	726,64	0,000				312	718,81	0,000			
	Total	313	763,38	0,000				313	711,37	0,000				313	754,41	0,000				313	741,83	0,000			
Mean annual	Regression	1	4,27	**0,039**	0,038	0,019	0,627	1	3,99	**0,046**	0,0363	0,018	0,580	1	6,30	**0,012**	0,0467	0,019	0,781	1	5,66	**0,017**	0,0444	0,019	0,72
temperature	Residual	312	749,18	0,000				312	698,20	0,000				312	737,88	0,000				312	726,71	0,000			
	Total	313	753,45	0,000				313	702,19	0,000				313	744,18	0,000				313	732,37	0,000			
Fucntional	Regression	1	1,65	0,199				1	1,17	0,279				1	1,68	0,195				1	2,21	0,137			
distance	Residual	252	608,54	0,000				252	546,92	0,000				254	603,36	0,000				225	536,23	0,000			
	Total	253	610,19	0,000				253	548,09	0,000				255	605,04	0,000				226	538,44	0,000			
Woodiness	Regression	1	0,27	0,603				1	0,13	0,715				1	0,00	0,945				1	1,74	0,187			
distance	Residual	243	547,77	0,000				243	486,23	0,000				245	542,92	0,000				217	476,27	0,000			
	Total	244	548,04	0,000				244	486,36	0,000				246	542,93	0,000				218	478,01	0,000			
Self support	Regression	1	1,77	0,183				1	3,13	0,077				1	1,76	0,184				1	0,11	0,737			
distance	Residual	242	545,95	0,000				242	483,59	0,000				244	540,78	0,000				216	475,03	0,000			
	Total	243	547,73	0,000				243	486,73	0,000				245	542,55	0,000				217	475,14	0,000			
Plant height	Regression	1	3,65	0,056				1	2,45	0,117				1	1,27	0,259				1	0,28	0,598			
distance	Residual	242	543,86	0,000				242	483,18	0,000				244	540,49	0,000				216	474,92	0,000			
	Total	243	547,50	0,000				243	485,63	0,000				245	541,76	0,000				217	475,20	0,000			
Plant/leaf habit	Regression	1	11,83	**0,001**	-0,749	0,218	**0,001**	1	9,24	**0,002**	-0,693	0,228	**0,001**	1	7,79	**0,005**	-0,625	0,224	**0,001**	1	6,60	**0,010**	-0,5929	0,231	**0,001**
distance	Residual	234	532,04	0,000				234	470,34	0,000				236	529,00	0,000				208	463,06	0,000			
	Total	235	543,87	0,000				235	479,59	0,000				237	536,79	0,000				209	469,66	0,000			
Phylogenetic	Regression	1	0,30	0,581				1	2,28	0,131				1	0,84	0,358				1	3,71	0,054			
distance	Residual	237	572,59	0,000				232	512,16	0,000				234	565,42	0,000				214	516,97	0,000			
	Total	238	572,89	0,000				233	514,44	0,000				235	566,26	0,000				215	520,68	0,000			
Pools																									
Plant height	Regression	1	8,04	**0,005**	1,279	0,451	**0,001**	1	12,55	**0,000**	1,515	0,428	**0,001**	1	6,82	**0,009**	1,226	0,470	**0,001**	1	4,04	**0,044**	1,0171	0,506	**0,001**
distance	Residual	107	225,72	0,000				106	207,08	0,000				107	236,38	0,000				95	206,00	0,000			
	Total	108	233,75	0,000				107	219,63	0,000				108	243,19	0,000				96	210,04	0,000			
Plant/leaf habit	Regression	1	6,99	**0,008**	-0,883	0,334	0,340	1	5,48	**0,019**	-0,821	0,351	**0,019**	1	5,24	**0,022**	-0,787	0,344	0,078	1	3,79	**0,051**	-0,7137	0,367	**0,013**
distance	Residual	105	220,51	0,000				104	205,07	0,000				105	230,27	0,000				93	199,79	0,000			
	Total	106	227,49	0,000				105	210,55	0,000				106	235,51	0,000				94	203,59	0,000			
Fluxes																									
Mean annual	Regression	1	34,08	**0,000**	0,001	0,000	**0,001**	1	31,28	**0,000**	0,001	0,000	**0,001**	1	34,52	**0,000**	0,001	0,000	**0,001**	1	29,38	**0,000**	0,001	0,000	**0,001**
precipitation	Residual	144	303,65	0,000				144	273,79	0,000				144	288,90	0,000				144	284,04	0,000			
	Total	145	337,74	0,000				145	305,07	0,000				145	323,42	0,000				145	313,42	0,000			
Mean annual	Regression	1	9,37	**0,002**	0,085	0,028	**0,002**	1	8,25	**0,004**	0,078	0,027	**0,003**	1	10,48	**0,001**	0,091	0,028	**0,002**	1	8,68	**0,003**	0,082	0,028	**0,002**
temperature	Residual	144	314,38	0,000				144	281,17	0,000				144	299,09	0,000				144	291,19	0,000			
	Total	145	323,75	0,000				145	289,42	0,000				145	309,57	0,000				145	299,87	0,000			
Plant/leaf habit	Regression	1	5,51	**0,019**	-0,689	0,293	**0,001**	1	4,35	**0,037**	-0,633	0,304	**0,001**	1	3,02	0,082	-0,519	0,299	**0,001**	1	3,01	0,083	-0,5245	0,302	**0,001**
distance	Residual	127	305,37	0,000				128	260,05	0,000				129	292,78	0,000				113	255,432	0,000			
	Total	128	310,88	0,000				129	264,40	0,000				130	295,80	0,000				114	258,441	0,000			

(1) Only for cases where the invaded site is an island

Appendix S9

Table S9. Pearson's correlation coefficients among plant invasions effect sizes on N cycle-related variables. Correlations were calculated for pairs of variables reported in the same studies. Significant correlations are shown in bold letters. Correlations with less than 5 cases are not shown. These values were calculated by randomly selecting the native control in multispecies studies.

		AGmass	Leaf/stand N	Litter C/N	Litter decomp (site effect)	Litter decomp (species effect)	Litter lignin	Litter mass	Litter N	SLA	N mineralization	Soil mineral N
Leaf/stand N	Pearson R	**- .556***										
	P	**.048**										
	N	**13**										
Litter decomp (species effect)	Pearson R		.568	**- .578****	- .011							
	P		.318	**.001**	.982							
	N		5	**29**	7							
Litter lignin	Pearson R			- .186		- .726						
	P			.725		.165						
	N			6		5						
Litter N	Pearson R			**- .837****	- .146	**.551****	- .268	**.822***				
	P			**.000**	.782	**.001**	.485	**.023**				
	N			**33**	6	**36**	9	**7**				
SLA	Pearson R		**.690***	- .109		.271	**- .926****		.165			
	P		**.013**	.603		.180	**.003**		.422			
	N		**12**	25		26	**7**		26			
N mineralization	Pearson R				**.966****	.624			.346			
	P				**.007**	.261			.502			
	N				**5**	5			6			
RGR	Pearson R									- .462		
	P									.083		
	N									15		
Soil mineral N	Pearson R	- .474	.195	.345	**.667***	.289		.395	**.663***		.047	
	P	.166	.614	.503	**.050**	.389		.381	**.037**		.844	
	N	10	9	6	**9**	11		7	**10**		20	
Soil organic matter	Pearson R				- .644				.524		.240	**.941****
	P				.241				.183		.453	**.000**
	N				5				8		12	**35**

Appendix S10

Table S10.- Results for phylogenetic signal on the effect size for different types of pools and fluxes (Blomberg's *K* and its significance *P*), for the full dataset (pools + fluxes, and for each type of pool and flux). Significant results (highlighted in bold letters) indicate that the impact of the invasive plant on the pool/flux type depends on the clade the species belong to. Results are shown for the four criteria applied to select the native control in multispecies studies (1- random selection, 2-the most abundant native, 3- the native more similar to the invader, 4- effect size calculated for all potential native controls were pooled).

		Selection criterion 1		*Selection criterion 2*		*Selection criterion 3*		*Selection criterion 4*	
		K	*P*	*K*	*P*	*K*	*P*	*K*	*P*
Full dataset	(Pools + Fluxes)	0.070	0.713	0.069	0.750	0.070	0.712	0.071	0.699
Type of N flux	SOM-> Soil N min	0.164	0.412	0.129	0.636	0.109	0.727	0.152	0.475
	Plant->Soil	0.185	0.136	0.150	0.275	0.149	0.302	0.145	0.348
	Soil->plant	0.278	0.083	0.141	0.472	0.280	0.086	0.292	0.074
N Pool type	In litter	0.154	0.496	0.189	0.362	0.151	0.512	0.146	0.522
	In soil in mineral form	0.164	0.412	0.049	0.896	0.049	0.904	0.049	0.910
	In soil organic matter	0.086	0.953	0.086	0.969	0.086	0.957	0.086	0.962
	In aboveground plant mass	0.228	**0.031**	0.182	0.091	0.231	**0.034**	0.220	**0.024**

Appendix S11

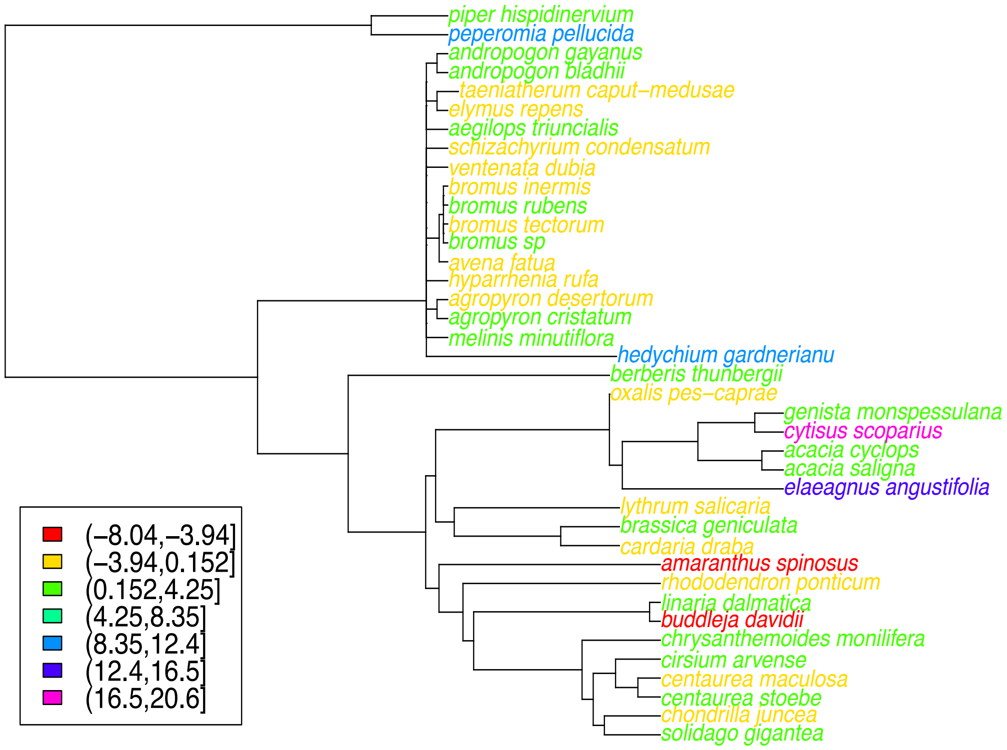


Figure S11.- Phylogenetic tree of the invasive species and its signal on invaders effect sizes on the pool of N in aboveground plant biomass. Tips correspond to species and their colours to their impact size (see legend). Negative values (red and yellow) represent the invasive species which reduce this N pool, and positive values (green, blue and purple) represent the invasive species that increased this pool.