

1 **Plant invasion is associated with higher plant-soil nutrient**
2 **concentrations in nutrient poor-environments**

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26 **Abstract**

27 Plant invasion is an emerging driver of global change worldwide. We aimed to disentangle
28 its impacts on plant-soil nutrient concentrations. We conducted a meta-analysis of 215
29 peer-reviewed articles and 1233 observations. Invasive plant species had globally higher
30 N and P concentrations in photosynthetic tissues but not in foliar litter, in comparison to
31 their native competitors. Invasive plants were also associated with higher soil C and N
32 stocks and N, P and K availabilities. The differences in N and P concentrations in
33 photosynthetic tissues and in soil total C and N, soil N, P and K availabilities between
34 invasive and native species decreased when the environment was richer in nutrient
35 resources. The results thus suggested higher nutrient resorption efficiencies in invasive
36 than in native species in nutrient-poor environments. There were differences in soil total N
37 concentrations but not in total P concentrations, indicating that the differences associated
38 to invasive plants were related with biological processes, not with geochemical processes.
39 The results suggest that invasiveness is not only a driver of changes in ecosystem species
40 composition but that it is also associated with significant changes in plant-soil elemental
41 composition and stoichiometry.

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43 Keywords: C:N, soil fertility, N:P, nitrogen, phosphorus, potassium

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51 Introduction

52 The structure, diversity and production capacity of terrestrial ecosystems is strongly linked
53 to the concentrations and stoichiometric ratios in the different ecosystemic compartments
54 and the soil availability of nitrogen, phosphorus and potassium (Sterner & Elser, 2002;
55 Reich & Oleksyn, 2004; Elser *et al.*, 2007; Vitousek *et al.*, 2010; Sardans *et al.*, 2011;
56 Peñuelas *et al.*, 2013; Sardans & Peñuelas, 2013). Most drivers of global change, such as
57 increasing atmospheric CO₂ concentrations, N eutrophication, drought, warming or land-
58 use changes change those elemental compositions and stoichiometries of ecosystemic
59 compartments and those relationships with ecological processes and species composition
60 (Seabloom *et al.*, 2006; Elser *et al.*, 2010; Sardans & Peñuelas, 2012; Sardans *et al.*,
61 2012; Peñuelas *et al.*, 2013; Yuan & Chen, 2015). The growing success of invasive plants
62 in many regions; 20% or more of plant species are exotics in many continental areas and
63 50% or more in islands (Seabloom *et al.*, 2006), e.g. plant invaders are affecting 405,000
64 Km² in United States (Seabloom *et al.*, 2015) is an emerging driver of Global Changes;
65 however, it has not received the same level of attention at this regard of the impacts on
66 plant-soil nutrient concentrations (Hulme *et al.*, 2009, 2015).

67 Previous studies have observed that several mechanisms involved in the uptake
68 and nutrient use efficiency by plants underlie the success of invasive plants (Daehler,
69 2003; González *et al.*, 2010). The mechanisms seem to differ between nutrient-poor and
70 nutrient-rich soils. In nutrient-poor soils most studies suggest that the success of invasive
71 plants depends on conservative strategies, such as a higher nutrient-use efficiency
72 (Ostertag & Verville, 2002; Funk & Vitousek, 2007; González *et al.*, 2010; Matzek, 2011),
73 especially on short time scales (Funk & Vitousek, 2007), long nutrient residence times
74 (Laungani & Knops, 2009), high resistance to low levels of nutrients (Kueffer, 2009;
75 Schumacher *et al.*, 2000) and high plasticity of stoichiometric ratios (González *et al.*,

76 2010). In fact, all these traits are consistent with those expected in stress tolerant species
77 (Grime 1977), in this case by a stress due to nutrient limitation. The establishment of new
78 symbiosis (Hiltbrunner *et al.*, 2014) or the more effective use of existing symbiosis (Pringle
79 *et al.*, 2009) are other strategies frequently linked to plant invasiveness success, all them
80 increasing the availability of limiting soil resources. In contrast, in nutrient-rich soils, there
81 is an advantage of species with high rates of photosynthesis and growth (Schumacher *et*
82 *al.*, 2000; González *et al.*, 2010), high reproductive outputs (González *et al.*, 2010), large
83 body size (Van Kleunen *et al.*, 2010), low C:nutrient ratios in tissues (Schumacher *et al.*,
84 2000; Peñuelas *et al.*, 2009; González *et al.*, 2010), low costs of foliar construction (Nagel
85 & Griffin, 2001; González *et al.*, 2010), large investments of N in photosynthetic production
86 (Ehrenfeld, 2003; Shen *et al.*, 2011), high capacities of nutrient uptake (Zabinski *et al.*,
87 2002; Leffler *et al.*, 2011; Peng *et al.*, 2011) and high levels of plasticity in the acquisition
88 of resources as a function of pulses in nutrient availability (Leffler *et al.*, 2011). Nutrient
89 uptake and all foliar traits enabling rapid rates of growth (Zabinski *et al.*, 2002; Leihman *et*
90 *al.*, 2007) will thus help invading species to succeed when resources are not limited
91 (Leihman *et al.*, 2007; Peng *et al.*, 2011). Some authors have claimed that, independently
92 of growth conditions, invaders are more likely to have higher foliar areas, lower tissue
93 construction costs and greater phenotypical plasticity that increase the availability of soil
94 resources (Daehler, 2003).

95 Invasive-plant success has also been linked to differences in soil elemental
96 composition. In a recent review, Pysek *et al.* (2012) reported that 192 of 436 case studies
97 on the effects of invasive plants on soil nutrient concentrations found higher
98 concentrations, 72 found lower concentrations and 158 found no significant differences.
99 Sardans & Peñuelas (2012), by analyzing 65 case studies, showed that most processes of
100 invasion had higher availability of soil nutrients. In addition to these previous qualitative
101 studies, Vila *et al.* (2011) conducted a meta-analysis on the relationships of plant invasive

102 success with soil condition showing that invasive success is related with higher soil C, N
103 and P stocks.

104 There is, however, no general consensus on whether or not successful plant
105 invaders have different elemental compositions than the native species, or, if present,
106 whether differences are dependent or not on habitat nutrient richness. A quantitative study
107 comparing plant, litter and soil nutrient concentrations, i.e. the whole plant-soil system,
108 between invasive and their native competitors at the global scale is missing. Moreover,
109 there are no studies analyzing the differences for other important elements, such as K. In
110 addition to the possible influence of soil nutrient-richness, the possible influence of climate
111 conditions on these relationships warrants investigation since climatic shifts affect invasive
112 plant functional processes and in general invasion patterns (Lu *et al.*, 2013; Zenni &
113 Hoban, 2015), and thus could affect the differences in plant, litter and soil nutrient
114 concentrations between invasive and native plants at the global scale. In regions where
115 climate evolves towards characteristics more favorable to plant production (higher MAP
116 and/or MAT) and where invasive success is expected to be related to higher rates of
117 nutrient-uptake and in general to C and/or R ecological strategies (Grime, 1977), we
118 should expect more investment of nutrients in plant growth and faster nutrient cycling rates
119 in plant-soil system. Contrarily, in regions evolving towards more extreme and stressed
120 climatic conditions, we should expect invasive success to be related to more conservative
121 traits, less growth, traits typical of stress-tolerator biological strategy (T strategy, Grime
122 1977) that are less linked with higher-uptake capacity, but to a higher resorption and
123 retention of nutrients in the system and consequently with higher nutrient concentrations in
124 plant-soil system.

125 We have conducted a global meta-analysis of both the past and the most recent
126 literature data on the nutrient concentrations in photosynthetic tissues, foliar litter and soil
127 with the aims to determine whether or not invasive-plant success (i) is associated with

128 different elemental compositions of photosynthetic tissues and foliar litter between
129 successful invasive plants and their native competitors, (ii) is associated with changes in
130 soil elemental composition and nutrient availability and stoichiometry, and (iii) how these
131 associations, if exist, depend on soil nutrient concentrations and availabilities, and climatic
132 condition.

133

134 **Materials and methods**

135 *Data collection*

136 We searched the ISI Web of Science using combinations of the following keywords: alien,
137 availability, available, carbon, concentration, C:K, C:N, C:P, foliar, invasion, invasive, leaf, needle,
138 nitrogen, N:K, N:P, phosphorus, plant, potassium, P:K, ratio, soil, solution, stoichiometric,
139 stoichiometry, success. We only selected studies providing the same equivalent information for
140 invasive successful species and their native competitors. Moreover, we only analyzed plant, litter
141 and soil variables with a minimum of 45 different reports that included the information for invasive
142 and the respective native species. These variables finally included N and P concentration and C:N
143 concentration ratio in photosynthetic tissues, foliar-litter N concentration and C:N concentration
144 ratio, and soil total C, N and P concentrations, total soil C:N concentration ratio, soil P-Olsen and
145 soil extractable K^+ , NO_3^- and NH_4^+ concentrations. In the few studies with different temporal data we
146 used the average mean values. Finally, only field non manipulative studies have been considered.
147 Applying these criteria we obtained 215 reports with 1233 observations across the world (Figure
148 S1).

149

150 *Climatic data*

151 We extracted climatic data for each study site from the WorldClim database (Hijmans *et al.*, 2005).
152 This database provides global maps of interpolated variables of climatological variables
153 extrapolated from extensive climatic time series (from 1950 to 2000), with a spatial resolution of 30
154 arc seconds (~1 km at the equator). We used MAT and MAP as climatic predictor variables.

155

156 *Data analyses*

157 We examined the effects of invasive-plant success on the differences of photosynthetic tissues
158 elemental compositions and stoichiometries and soil nutrient status between successful invasive
159 plants and their native competitors by calculating the ln response ratios from each study as
160 described by Hedges *et al.* (1999). The natural ln response -ratio (lnRR) was calculated as $\ln(X_i/X_n)$
161 $= \ln X_i - \ln X_n$, where X_i and X_n are the values of each observation in the invaded soil or invasive
162 plant and in the corresponding native situation, respectively. The sampling variance for each lnRR
163 was calculated as $\ln[(1/n_i) \times (S_i/X_i)^2 + (1/n_n) \times (S_n/X_n)^2]$ using the R package metafor 1.9–2, where
164 n_i , n_n , S_i , S_n , X_i and X_n are the invasive and native sample sizes, standard deviations, and mean
165 response values, respectively. The natural ln response ratios were determined by specifying studies
166 as random factors using the *rma* model in metafor. The effects on soil elemental variables and the
167 difference between the elemental compositions of invasive and native plants were considered
168 significant if the 95% confidence interval (CI) of lnRR did not overlap zero. All these statistical
169 analyses were performed in R 3.1.2 (R Core Team, 2015). Despite for most studied variables there
170 was a low proportion of studies containing N₂-fixing species, we performed these analyses twice,
171 once with the entire data another one with and after the removal of the studies that contained N₂-
172 fixing plant species for detecting the possible importance of N₂-fixing capacity in the ln response
173 ratio effect of the plant and soil variables studied. We analyzed variables with more than 45
174 observations available at the global scale. The number of reports and observations used by
175 statistical analyses of each studied soil, plant and litter variable are shown in Figures 1 and 2, and
176 described in Tables S1-S3.

177 We also examined whether the differences in the ln response ratio of plants and soils depend
178 on environmental circumstances such as climate or soil total nutrient concentration and soil
179 available nutrient concentration. For these analyses, we related the ln response ratio effect
180 mentioned above (lnRR) with climatic variables at each study site. We used MAP and MAT data
181 from the WorldClim database (Hijmans *et al.*, 2005). We also tested whether lnRR is dependent on
182 native plant and soil total nutrient concentrations and soil nutrient availability. We conducted a

183 regression of the ln response ratio of the soil N concentration (ln invaded soil N value - ln native soil
184 N value) relative to the concentration in the natural (native site) soil (ln native soil N value). In the
185 case of foliar plant tissues, nutrient concentration has generally been well correlated with soil
186 nutrient availability across natural gradients or fertilization experiments (Porder *et al.*, 2005; Alvarez-
187 Clare & Mack, 2015). We thus used the native foliar concentrations as a proxy of site soil availability
188 to relate the possible differences in the ln response ratio effect in foliar and foliar-litter variables (ln
189 invasive plant N value - ln native plant N value), with the corresponding variable availability in soil
190 (ln native foliar N value). We used regression type II for these analyses, because both dependent
191 and independent variables were interchangeable and random, so the error of the independent
192 variable could not be neglected. We ran a standardized major axis method (SMA) using the SMATR
193 package (Warton *et al.*, 2006) (<http://www.bio.mq.edu.au/ecology/SMATR>).

194 Finally, in the cases of total soil N concentration, soil P-Olsen and foliar N and P
195 concentrations, for which we have the larger number of observations, we divided the observations
196 of each one of these variables according with their values in native soils or plants in three groups
197 with similar number of observations. Thus, the groups corresponded to low, intermediate and high
198 values in native conditions as a proxy of site nutrient richness. Thereafter we conducted an one-
199 way ANOVA with Bonferroni post-hoc test to detect possible differences in the ln response ratio
200 among the three groups.

201 **Results**

202 *Differences in photosynthetic tissues and foliar litter*

203 A meta-analysis of the entire data set indicated that invasive plant species had higher N ($z = 8.93$, $P < 0.0001$) and P ($z = 3.44$, $P < 0.001$) concentrations (41% and 32%,
204 respectively) and lower (26%) C:N ratios ($z = -5.02$, $P < 0.0001$) in their photosynthetic
205 tissues than the native competitors (Fig. 1a). An analysis of the same data set but without
206 excluding N₂-fixing species also indicated higher N ($z = 6.57$, $P < 0.0001$) and P ($z = 2.67$,
207 $P < 0.01$) concentrations (29% and 32%, respectively) and lower (22%) C:N ratios ($z = -$
208 4.84 , $P < 0.0001$) in the photosynthetic tissues of the invasive species (Fig. 1b). The N
209 concentration and the C:N ratio in foliar litter were, however, not significantly different
210 either for the entire data set (Fig. 1c) or when the data for the N₂-fixing plant species were
211 excluded (Fig. 1d). Not significant differences were either found for litter P concentrations
212 (only 13 observations, data not shown).

214

215 *Differences in soil conditions*

216 The soil concentrations of extractable K ($z = 2.53$, $P < 0.05$), soluble nitrate ($z = 7.40$, $P <$
217 0.0001), P-Olsen ($z = 2.83$, $P < 0.01$) and total N ($z = 4.34$, $P < 0.0001$) and C
218 concentrations ($z = 3.62$, $P < 0.001$) were higher (13%, 117%, 21%, 19% and 12%,
219 respectively) in soils of invasive plants than in soils of their corresponding native
220 competitor species. The concentration of soluble ammonium was also marginally ($z = 1.81$,
221 $P = 0.07$) higher (11%) in the soils of the invasive than the native species. The ln response
222 ratio effects on the soil C:N ratio and total P concentration were not statistically significant.
223 An analysis of the same data set but without the data for the N₂-fixing species produced
224 similar results (Fig. 2b). The soluble nitrate ($z = 6.37$, $P < 0.0001$), P-Olsen ($z = 2.83$, $P <$
225 0.001), total N ($z = 2.32$, $P < 0.05$) and C ($z = 3.13$, $P < 0.001$) concentrations, were higher
226 (118%, 27%, 10% and 7%, respectively) in the soils of the invasive plants than in the soils

227 of the native competitors. The concentration of extractable K was marginally ($z = 1.80$, $P =$
228 0.072) higher (11%) in the soils of the invasive species.

229

230 *Ln response ratios along gradients of nutrient availability and climate*

231 The ln response ratio of total N and P concentrations in photosynthetic tissues of invasive
232 plants were negatively correlated to the corresponding values for the photosynthetic
233 tissues of the native plant competitors (Figs. 3a and 3b). The ln response ratio of foliar N
234 concentration was positively different from zero in sites with low and intermediate values,
235 whereas for foliar P concentrations the ln response ratio was only positively different from
236 zero in sites with low values (Figs. S2a and S2b). No significant relationships were
237 observed between foliar litter N and P ln response ratio and the corresponding values for
238 the foliar litter of the native plant competitors (Figs. 3c and 3d).

239 The ln response ratio for soil total N, P-Olsen, soluble nitrate and extractable K
240 concentrations in invaded soils were negatively correlated with the corresponding values in
241 the soils of the native plant competitors (Figs. 4a–d). For soil nitrate concentration, total N
242 concentration and soil P-Olsen, the ln response ratio was positively different than zero in
243 sites with low and intermediate values, whereas for soil available K^+ the ln response ratio
244 was positively different than zero only in sites with low values (Fig. S3).

245 Interestingly, few relationships between climatic gradients and ln response-ratio
246 effects were detected. MAT was positively but weakly correlated with the ln response
247 ratios for soil total N concentration ($R = 0.27$, $P < 0.001$) and with N concentration in
248 photosynthetic tissues ($R = 0.16$, $P < 0.05$). MAP was positively and also weakly
249 correlated with the ln response ratio for soil soluble nitrate concentration ($R = 0.25$, $P <$
250 0.01) (Fig. S4).

251 **Discussion**

252 Our study showed higher N and P concentrations in the photosynthetic tissues of invasive
253 species in nutrient-poor environments. These higher concentrations were found in
254 photosynthetic tissues but not in foliar litter, suggesting a higher N and P resorption
255 capacity in resource-poor than in resource-rich environments. These results are consistent
256 with previous studies observing that the competitive advantage over native plant species
257 competitors and the success of invasive plants in resource-poor environments has
258 frequently been correlated with a more conservative use of nutrients, higher residence
259 time due to higher nutrient-resorption capacities (Ostertag & Verville, 2002), and higher
260 photosynthetic nitrogen use efficiency (Ens *et al.*, 2015).

261 The soils under the invasive plants had higher soil P-Olsen, soluble nitrate and
262 potassium concentrations and therefore higher availability of the three most important soil
263 macronutrients for plant growth. The higher soil NO_3^- concentrations in soils under invasive
264 species than under their native competitors is consistent with previous studies observing a
265 positive relationship between soil NO_3^- concentration and the intensity of plant species
266 invasive success (Gilliam, 2006). The studies compiled in this meta-analysis did not allow
267 a clear determination of whether these higher concentrations were the cause or the effect
268 of the success of invasive plant species. The studies that have experimentally tested
269 whether soil differences were the cause or the consequence of plant invasion, however,
270 have reported that soil differences were mainly due to the effect of the success of the
271 invasive species (Li *et al.*, 2006; Dassonville *et al.*, 2008; Elgersma *et al.*, 2011; Lee *et al.*,
272 2012; Kuedding *et al.*, 2014; Stark & Norton, 2014). A few number of reports that have
273 studied the changes in soil conditions during 4 (Belnap *et al.*, 2005) and 7 (Hawkes *et al.*,
274 2005) years have observed that the invasive species changed soil conditions over time.
275 Several studies have also observed a direct impact of invasive-plant establishment on soil

276 function such as increases in soil enzymatic activities associated with increases in some
277 soil elemental concentrations (Hawkes *et al.*, 2005; Alison *et al.*, 2006; Caldwell, 2006;
278 Aragon *et al.*, 2014; Kuebbing *et al.*, 2014), mineralization (Haubensak & Parker, 2004;
279 Fickbohm & Zhu, 2006; Li *et al.*, 2006) and respiration (Souza-Alonso *et al.*, 2015). Other
280 studies, although fewer than the above, did not observe these differences in soil enzymatic
281 activity and mineralization (Zabinsky *et al.*, 2002, Meisner *et al.*, 2011) or found different
282 results depending on species and site (Koutika *et al.*, 2007) or on the enzymatic activities
283 (Chacón *et al.*, 2009). Kulmatiski *et al.* (2006) in 660 experimental plots in abandoned
284 croplands (from 50 to 7 years ago) with different management histories observed that
285 invasive success explained the soil C, N and P concentrations more significantly than the
286 previous agricultural histories, suggesting that the invasive plants facilitated their own
287 growth by maintaining beneficial fungal communities and fast nutrient-cycling rates.

288 Our results showed a general globally higher soil total N concentration under
289 invasive-plants than under their native competitors but we did not observe a higher total P
290 concentration. Cycling and concentrations of soil N mainly depends on biological
291 processes, whereas mineral rocks are the sources of soil P, and its soil total concentration
292 is primarily driven by physicochemical processes (Gómez-Aparicio & Canhan, 2008;
293 Vitousek *et al.*, 2010; Peñuelas *et al.*, 2013). Both N and P are important soil components
294 that could be involved in facilitating plant invasion, but only soil total N concentration can
295 thus be associated mostly with the biological process of plant invasion. This fact is
296 consistent with the hypothesis that the differences between the soils under invasive and
297 native plants are most likely due to the effects of species invasion itself. Rather
298 surprisingly, the effects of plant-invasions on soil and plant N concentrations, C:N ratios
299 and most other significant stoichiometry parameters were not different when including N₂-
300 fixing plants than when excluding them from the global analysis. Changes in soil physical

301 conditions or in microbial communities, including soil N-fixing microbes, could be involved,
302 warranting further research.

303 The differences in soil total C and N, and in N, P and K availabilities and in N and P
304 concentrations in photosynthetic tissues between invasive and native species decreased
305 with increasing values of the corresponding variables in natural-native conditions to the
306 point that the differences disappeared in resource-rich environments. These lower
307 differences in resource-rich environments could be due to the higher nutrient up-take in
308 invasive species being counteracted by its higher growth capacity, and the corresponding
309 dilution effect. In nutrient-rich sites, moreover, native species are also highly competitive,
310 having traits that enable native plants to be very effective in taking up resources. On the
311 other hand, the frequently observed higher mineralization capacity and enzyme activity
312 under invasive than under native species in nutrient-rich soils (Allison *et al.*, 2006; Gómez-
313 Aparicio & Canham, 2008; Aragón *et al.*, 2014) would increase the rates of nutrient
314 released from organic matter, but this would be also counteracted by the higher plant
315 nutrient uptake so that soil nutrient concentrations would remain similar than under native
316 species.

317 Climate variables had few correlations with the studied ln response ratio of the
318 studied variables. MAT had weak but positive correlation with ln response ratio of total soil
319 N concentration and N concentration in plant tissues and MAP had also a positive
320 relationship with soil nitrate ln response ratio. These results suggest thus that climatic
321 conditions are less influential on the ln response ratio of the studied soil total and available
322 nutrient concentrations than the environmental nutrient richness.

323 Summarizing, this is the first study that has analyzed globally the association
324 between plant invasion and nutrient concentration and stoichiometry of photosynthetic
325 tissues, leaf litter and soils. Invasive plant species had globally higher N and P
326 concentrations in photosynthetic tissues but not in foliar litter, in comparison to their native

327 competitors. Invasive plants were also associated with higher soil C and N stocks and N, P
328 and K availabilities. The differences in N and P concentrations in photosynthetic tissues
329 and in soil total C and N, soil N, P and K availabilities between invasive and native species
330 decreased when the environment was richer in nutrient resources. These global trends
331 may be explained by (i) larger differences in resorption and nutrient-use efficiency between
332 invasive and native species in nutrient-poor environments, and (ii) a higher competitive
333 capacity associated with larger nutrient uptake and plant growth capacity with a dilution
334 effect in invasive than in native species when environments become richer in resources.
335 Moreover, some other mechanisms such as enhancement of soil enzymatic activity and
336 mineralization, and more effective symbiotic relationships can be also involved in these
337 global trends. Clearly determining whether invasive-plant success is the cause or the
338 consequence of soil elemental composition and nutrient availability is currently not
339 possible, but research up to now suggests that these plant and soil nutritional changes are
340 more the consequence than the cause of plant invasion. Plant invasiveness should thus
341 not be neglected as a driver of global change in plant-soil elemental and stoichiometric
342 composition and soil fertility.

343

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522 Figure captions

523

524 Figure 1. Ln response ratios of N and P concentrations and the C:N ratio in photosynthetic tissues
525 (including data for N₂-fixing plants) (A), and excluding the data for N₂-fixing plants (B). Ln responses
526 ratios of N concentrations and the C:N ratio in foliar litter to plant invasion for the entire data set
527 (including data for N₂-fixing plants) (C) and excluding the data for N₂-fixing plants (D) to plant
528 invasion. Values are means and 95% confidence intervals. Plus (+) and minus (–) signs represent
529 positive and negative log response ratios, respectively, when the corresponding ln response ratios
530 confidence intervals do not overlap with zero value. Zero in the X-axes represents neutral response
531 ratio that means equal values in native than in invasive species. The numbers between brackets
532 indicate the number of articles and studies (each article can have more than one single study),
533 respectively, used in the meta-analysis of each variable.

534

535 Figure 2. Ln response ratios of soil concentrations of extractable potassium (K⁺), ammonium (NH₄⁺),
536 nitrate (NO₃⁻), P-Olsen, and total P, N and C and the soil C:N ratio to plant invasion for the entire
537 data set (including data for N₂-fixing plants) (A) and excluding the data for N₂-fixing plants (B).
538 Values are means and 95% confidence intervals. Plus (+) and minus (–) signs represent positive
539 and negative log response ratios, respectively, when the corresponding ln response ratios
540 confidence intervals do not overlap with zero value. Zero in the X-axes represents neutral response
541 ratio that means equal values in native than in invasive species. The numbers between brackets
542 indicate the number of articles and studies, respectively, used in the meta-analysis of each variable.

543

544 Figure 3. Relationships between ln response ratio of foliar N and P concentrations and the
545 total N (A) and P (B) concentrations in the leaves of native plants, and relationships
546 between the ln response ratio of the foliar-litter N and P concentrations and the total N (C)
547 and P (D) concentrations in the leaf litter-tissues of native plants based on percent dry
548 weight (%DW). Dotted line highlights the zero value of ln response ratio (equal values of
549 the corresponding variable for native and in invasive species or for soils under them).

550

551 Figure 4. Relationships between the ln response ratio of soil NO₃⁻ and the site soil NO₃⁻
552 concentration (A), between the ln response ratio of soil total N and site soil total N
553 concentration (B), between ln response ratio of soil P-Olsen and site soil P-Olsen
554 concentration (C) and between ln response ratio of soil K⁺ concentration and site soil K⁺
555 concentration (D). Dotted line highlights the zero value of ln response ratio (equal values
556 of the corresponding variable for native and in invasive species or for soils under them).

