4

5 **Title:** Impacts of nitrogen addition on plant species richness and abundance: A global meta-analysis

6

7 **Running head**: Nitrogen addition reduces plant species richness and abundance.

8

9 **Manuscript category:** Meta-analysis

10 **Abstract**

11 *Aim* Experimental nitrogen (N) addition (fertilization) studies are commonly used to quantify the

12 impacts of increased N inputs on plant biodiversity. However, as plant community responses can vary

13 considerably among individual studies, there is a clear need to synthesize and generalize findings

14 with meta-analytical approaches. Our goal was to quantify changes in species richness and abundance

15 in plant communities in response to N addition across different environmental contexts, while

16 controlling for different experimental designs.

17 *Location* Global

18 *Time period* Data range: 1985 – 2016; Publication years: 1990-2018

19 *Major taxa studied* Plants

20 *Methods* We performed a meta-analysis of 115 experiments reported in 85 studies assessing the

21 effects of N addition on terrestrial natural and semi-natural plant communities. We quantified changes

22 in plant biodiversity in relation to N addition using four metrics: species richness (SR), individual

23 species abundance (IA), mean species abundance (MSA) and geometric mean abundance (GMA).

24 *Results* For all metrics, greater amounts of annual N addition resulted in larger declines in plant

25 diversity. Additionally, MSA decreased more steeply with N that was applied in reduced (NH_4^+)

26 rather than oxidised (NO_3^-) form. Species richness loss with increasing N amounts was found to be

27 larger in warmer sites. Further, greater losses in species richness were found in sites with longer

28 experimental duration, smaller plot sizes and lower soil cation exchange capacity (CEC). Finally,

29 abundance reductions of individual species were larger for N-sensitive plant life-form types (legumes

30 and non-vascular plants).

31 *Main conclusions* N enrichment decreases both species richness and abundance of plant communities

32 in N-addition experiments, but the magnitude of the response differs among biodiversity metrics and

33 with the environmental and experimental context. This underlines the importance of integrating

34 multiple dimensions of biodiversity as well as relevant modifying factors into assessments of

35 biodiversity responses to global environmental change.

36

37

Introduction

Nitrogen (N) deposition is among the main drivers of the loss of plant biodiversity in terrestrial ecosystems (Bobbink et al., 2010; Sala et al., 2000; Vellend et al., 2017). In the last century, enhanced emissions of nitrogenous compounds caused by agricultural and industrial activities have increased atmospheric nitrogen (N) deposition in natural and semi-natural ecosystems across the world (Erisman et al., 2013; Galloway et al., 2008), with concomitant consequences for the biodiversity of these ecosystems (Bobbink et al., 2010; Dise et al., 2011). Biodiversity is key for maintaining the functioning of ecosystems and the provision of ecosystem services (Cardinale et al., 2012; Hooper et al., 2005). Plant diversity, for example, enhances the ability of ecosystems to maintain multiple functions and processes, such as carbon sequestration, productivity, and the build-up of nutrient pools (Maestre et al., 2012). Apart from positive effects on ecosystem productivity, diversity also provides increased erosion control, resistance to invasive species and pest regulation (Quijas et al., 2012).

The responses of plant communities to N deposition vary depending on the environmental context (Simkin et al., 2016; Vellend et al., 2017; Perring et al., 2018[a]). Modifying factors include the amount and duration of N deposition, which determine the cumulative N input over time (Bernhardt-Römermann et al., 2015; Duprè et al., 2010); soil pH and acid neutralizing capacity (Clark et al., 2007; Simkin et al., 2016); the chemical forms of N input (Stevens et al., 2011) and environmental conditions such as climate (Clark et al., 2007; Humbert, Dwyer, Andrey, & Arlettaz, 2016; Limpens et al., 2011) and vegetation types (Pardo et al., 2011; Simkin et al., 2016). Additionally, land use history might play a relevant role, as this may drive the composition and function of plant communities into different trajectories of change (Perring et al., 2018[b]).

There are two main empirical approaches to study the impact of N on plant diversity (Hettelingh, Stevens, Posch, Bobbink, & de Vries, 2015). These approaches are experimental N addition studies, and observational studies investigating plant species diversity over a gradient of N deposition, either in time series analysis (e.g. Stevens, Duprè et al., 2010; Stevens, Thompson, Grime, Long, and Gowing, 2010) or over a spatial gradient (e.g. Jones et al., 2004; Duprè et al., 2010). Observational

65　gradient studies can benefit from existing datasets (e.g. Simkin et al., 2016), but need to correct for

66　confounding site factors and cannot prove causality (Dise et al., 2011). Experimental studies, on the

67　other hand, allow for effects to be directly attributed to N addition. However, experimental studies

68　typically assess relatively short-term responses only and often use higher levels of N addition

69　compared to atmospheric deposition in the field. Furthermore, the results might be influenced by

70　experimental design and local environmental conditions, which limits the possibilities for regional

71　and global extrapolation (Hettelingh et al., 2015). The latter might be solved by setting up globally

72　distributed experiments such as the Nutrient Network (Firn et al., 2011; Borer et al., 2014), but also

73　by synthesizing multiple N-addition experiments with a meta-analysis, allowing to derive a more

74　general quantitative response of plant species diversity to N enrichment.

75　Previous meta-analyses that addressed impacts of N on plant assemblages focused on species richness

76　or biomass in specific ecosystems (i.e. Limpens et al., 2011; Humbert et al., 2016) or in specific

77　geographic regions (i.e. Clark et al., 2007; Fu and Shen, 2016) or continents (i.e. De Schrijver et al.,

78　2011; Soons et al., 2017). To our knowledge, a systematic meta-analysis covering multiple

79　dimensions of biodiversity in multiple ecosystems across the globe is yet lacking. In addition to

80　covering a large geographical extent, it is particularly important to consider metrics beyond species

81　richness, such as measures of species abundance, as different aspects of biodiversity may respond

82　differently to environmental change (Dornelas et al., 2014; Schipper et al., 2016; Winfree, Fox,

83　Williams, Reilly, & Cariveau, 2015). In this study we synthesized a large number of N-addition

84　studies worldwide, in order to reveal overall effects of N addition on various metrics of local plant

85　biodiversity and explore the role of potential experimental (amount of yearly N applied, experimental

86　duration, type of fertilizer, plot size) and environmental (temperature, precipitation, soil pH, soil

87　cation exchange capacity, atmospheric N deposition) moderators (Figure 1a). We considered four

88　metrics of biodiversity change to incorporate richness and abundance as two essential dimensions of

89　biodiversity (Schipper et al., 2016) (Figure 1b): species richness (SR), individual species abundance

90　(IA) (Benítez-López et al., 2017), mean species abundance (MSA) (Alkemade et al., 2009) and

geometric mean abundance (GMA) (Buckland, Magurran, Green, & Fewster, 2005; Buckland, Studeny, Magurran, Illian, & Newson, 2011). The metrics adopted cover different domains of the richness-abundance space and in our meta-analysis represent the changes observed between treatment and control plots (Figure 1b).

We expected local biodiversity to decrease with increasing yearly N addition amounts and experimental duration, reflecting the negative effect of cumulative N enrichment (De Schrijver et al., 2011; Humbert et al., 2016). We further hypothesized that larger negative impacts to N addition will occur in sites with low soil pH and low atmospheric N deposition, as plants growing in such conditions tend to be more adapted to low N availability (Bobbink et al., 2010; Simkin et al., 2016). We also expected that fertilizer types containing reduced N forms (NH_4^+) result in higher impacts on plant diversity than oxidised forms (NO_3^-), as reduced N tends to strongly acidify the soil and disadvantage the nutrient uptake of N-poor adapted species (van den Berg, Peters, Ashmore & Roelofs, 2008; Song et al., 2012). We further hypothesized that species losses would be larger in larger experimental plots, as these have higher chances of including rare species, which may also be more likely to go extinct in the treatment plots (Perring et al., 2018[b]). Higher impacts were also expected in sites with low soil cation exchange capacity (CEC), as lower CEC indicates higher susceptibility to acidification in response to N addition (De Vries, Posch & Kämäri, 1989; Clark et al., 2007). We further hypothesized losses to be larger in experiments conducted under higher mean annual temperature and precipitation, because these conditions are expected to result in higher N mineralisation rates hence enhanced N availability following fertilization (Dise et al., 2011; Yang, Ryals, Cusack & Silver, 2017).

Methods

Selection of primary studies

In April 2018, we used the Scopus and Web of Science databases to collect primary studies. The search strings were composed of 'OR' and 'AND' statements combining terms related to N-addition

117   experiments and different dimensions of plant species diversity, for example ("nitrogen fertilization"

118   OR "nitrogen addition") AND ("abundance" OR "composition" OR "number" OR "richness") (see

119   the complete search strings in Supporting Information Appendix S1). We selected relevant studies

120   based on title and abstract, and then scanned their full texts and supporting materials to extract data

121   on N-addition experiments. Where factorial treatment combinations were present, we retained data

122   from control and N addition plots alone to avoid confounding effects. Thus, we excluded data from

123   plots where N addition was performed together with watering, temperature increase, litter removal,

124   grazing, fire manipulation or where N was added in combination with other nutrients. We limited our

125   selection to experiments conducted on natural or semi-natural vegetation excluding studies conducted

126   on crops, mono-cultures or where species were artificially introduced in plots. Finally, we removed

127   studies that reported the same data as other studies already included in our database. To avoid over-

128   representation, we collected data on species richness and abundance change at the final year of each

129   experiment.

130   Our literature search yielded a total of 2314 studies, of which we selected 85 relevant studies

131   (published between March 1990 and January 2018) that reported data from 115 N-addition

132   experiments performed between 1985 and 2016 in different geographical locations (Figure 2; Table

133   S2.1, Appendix S2). Of the 85 studies, 48 reported data on species richness, 15 on individual species

134   abundance, and 22 on both species richness and abundance (a list of the data sources is found in

135   Appendix A). We extracted the number of species and species-specific abundance data separately

136   from treatment and control plots and calculated the four biodiversity metrics as described in Table 1.

137   Abundance data were extracted for each species reported in both the treatment and control plots, for

138   a total of 403 taxa. The majority of these were identified to species level, but 32 were indicated with

139   the genus name only. Thus, the total number of species in our dataset might be slightly overestimated.

140   We recorded a total of 220 pairwise comparisons for SR. At the species level, we included 871

141   individual species abundance comparisons (IA), some across multiple N fertilization levels within

142   the same experiment, which resulted in 89 observations for MSA and GMA. Nitrogen addition levels

143   ranged from 3.75 to 572 kg N ha^{-1} yr^{-1} in the species richness dataset (mean = 124.8 kg ha^{-1} yr^{-1};

144   median = 92 kg ha^{-1} yr^{-1}), and from 7 to 480 kg N ha^{-1} yr^{-1} in the species abundance dataset (mean =

145   96.5 kg ha^{-1} yr^{-1}; median = 70 kg ha^{-1} yr^{-1}).

146

147   ***Calculation of the effect sizes***

148   We calculated four biodiversity metrics for the meta-analysis, including the species richness ratio

149   (SR), individual species abundance ratio (IA), mean species abundance (MSA), and geometric mean

150   abundance (GMA) (Table 1). Both SR and IA were obtained by log-transforming the ratio between

151   the species richness and individual species abundance in each N-treatment plot and control plot,

152   respectively (Hedges, Gurevitch, & Curtis, 1999). Some species had zero abundance in treatment

153   plots, precluding log-transformation for IA calculation. Therefore, we transformed IA effect sizes

154   using a modification of the transformation proposed by Smithson and Verkuilen (2006) to shrink the

155   ratios and avoid zero values (Benítez-López et al., 2017) (eq.1):

156     $$y_i = \frac{(y*N+0.5)}{N}$$ (eq. 1)

157   where y is the ratio (A_T/A_C) of individual species abundance in the treatment (A_T) and control (A_C) and

158   N is the number of observations in the individual species abundance dataset ($N = 871$). This resulted

159   in a distribution of ratios (y_i) slightly displaced towards larger values (before transformation: [0, 82.5],

160   after transformation: [0.0006, 82.5006]). The new ratios were then log-transformed to obtain IA.

161   Since ratios A_T/A_C cannot be calculated when abundance in the control is equal to 0, we decided to

162   exclude species that were present only in the treatments from the calculation of the IA and GMA

163   metrics, following the definitions and approaches applied in previous studies (Table 1).

164   We calculated MSA as the mean of the ratios of individual species abundance in each treatment versus

165   the corresponding control (Alkemade et al., 2009; Benítez-López, Alkemade, & Verweij, 2010).

166   Following the definition of MSA, the individual ratios were truncated at 1 for species with a higher

167   abundance in the treatment group compared to the control group (Table 1). As MSA captures losses

168   in abundance of species that are found in reference conditions (control plots) only, it cannot go beyond

the original abundance and richness (Figure 1b). Finally, GMA was calculated as the back-transformed mean of the log-transformed individual abundance ratios, without truncation (Buckland et al., 2011). The GMA metric (Buckland et al., 2005; Buckland et al., 2011) also combines abundance and species richness into one index but allows for gains in the abundance dimension (Figure 1b).

Moderators

Factors influencing plant community responses to N were selected *a priori* based on literature study (Figure 1a; Table S3.1, Appendix S3) and data availability. Nine moderators were considered in the analysis: 1) the annual amount of N added in the experiment (kg N ha^{-1}yr^{-1}); 2) the annual amount of background N deposition (kg N ha^{-1}yr^{-1}) (i.e. the amount of N deposited from the atmosphere, which is independent from the experimental N addition); 3) mean annual temperature (°C); 4) mean annual precipitation (mm yr^{-1}); 5) duration of the experiment (number of years of N addition); 6) the type of N fertilizer, categorized as fertilizers containing nitrate (NO_3) (i.e. ammonium nitrate or alkali nitrates) or fertilizers containing ammonium (NH_4) as the only source of N (i.e. urea, urine, ammonium sulphate and ammonium chloride) (see details in Table S4.1, Appendix S4); 7) plot size (m^2) (i.e. the area of vegetation surveyed to estimate richness or abundance in each experiment); 8) initial soil pH at the experimental sites (estimated before N addition); 9) soil cation exchange capacity (CEC) (cmol kg^{-1}). Additionally, we examined overall biodiversity responses among the ecosystem type where the study/experiment took place, with ecosystems categorized into five broad categories (temperate grasslands and heathlands, semi-arid ecosystems, bogs/peatlands, arctic/alpine ecosystems, and forests) (see details about grouping criteria in Table S4.2, Appendix S4). Further, we categorized each taxon into plant life-form types (herbaceous forbs, graminoids, legumes, ferns, woody plants and non-vascular plants; see Table S4.3, Appendix S4) and used this to assess possible differences in individual abundance response among different species groups.

We collected from each study the location (geographic coordinates), experimental setup (yearly amount of N addition, experimental duration, type of N fertilizer, plot size) and ecosystem type.

195   Because many studies did not report atmospheric N deposition levels, we collected these data from

196   the global TM5 model for the year 2000 (Dentener et al., 2006). For the same reason, we extracted

197   estimates of cation exchange capacity (CEC) and soil pH from the 250 m resolution global SoilGrids

198   data (Hengl et al., 2014; Hengl et al., 2017), by averaging values provided for soil depths of 0-5, 5-

199   15 and 15-30 cm. Data on temperature and precipitation were derived from the global Climate

200   Research Unit database, which comprises series of monthly meteorological data on a 0.5° * 0.5° grid

201   (New, Hulme, & Jones, 1999). For each observation we extracted data for the corresponding year and

202   calculated the mean temperature and precipitation over the 12 monthly values.

203

204   ***Data analysis***

205   We performed the meta-analysis using multilevel mixed-effect models to control for non-

206   independence in the data due to multiple effect sizes per study and species (Nakagawa & Santos,

207   2012). We first fitted single meta-regression models using yearly N addition as the only moderator,

208   in order to compare changes among the metrics for a given amount of N applied. Then, we fitted

209   multiple meta-regression models by including other moderators as well as interaction terms between

210   the amount of N addition and these other moderators. Except for mean annual temperature and soil

211   pH, we log-transformed all continuous moderators, as the data showed strong positive skewness, and

212   we scaled and centred all continuous variables. The only moderate correlation among moderators was

213   between mean annual precipitation and soil pH (richness dataset ρ=-0.75; abundance dataset ρ=-0.68).

214   Based on this, we decided not to exclude any moderators upfront. We performed stepwise backward

215   selection based on the Bayesian Information Criterion (BIC), whereby we excluded a moderator only

216   in case it was also dropped from the interaction term. We estimated the amount of heterogeneity

217   reduced in the best models selected and by each moderator using the omnibus Wald-type test of

218   moderators (Benítez-López et al., 2017).

219   We accounted for the correlation in the true effects by using experiments as the random effect in the

220   models. For the IA metric, we used a crossed random effect structure including both experiment and

221 species as random components. We nested the individual estimates within the experiment grouping-

222 level in the random structure of the models to account for the possibility that the underlying true

223 effects within experiments are not homogeneous (Konstantopoulos, 2011). We weighted the

224 importance of the effect sizes of SR and IA by the inverse of the sampling variance (Hedges et al.,

225 1999) (Table 1). Because of non-independence of the effect sizes, we computed the variance-

226 covariance matrix based on Lajeunesse (2011). For SR and IA, the models were fitted with the *rma.mv*

227 function of the R package 'metafor' (Viechtbauer, 2010). Observations were weighted by the inverse

228 of the sampling variance (Table 1), which we calculated from standard deviation directly from papers

229 or through personal contact with the authors. We imputed missing standard deviations using the

230 coefficient of variation from all complete cases with the R package 'metagear' (Lajeunesse, 2016).

231 Since MSA and GMA have a different structure compared to log-transformed response ratios and

232 standard deviations are not reported for these derived metrics, we used the number of replicates in

233 each experiment to weight the observations (Soons et al., 2017). We fitted multi-level linear mixed-

234 effect models for MSA and GMA with the *lme* function of the R package 'nlme' (Pinheiro, Bates,

235 DebRoy, Sarkar, & R Core Team, 2017).

236 Finally, we used null models to estimate the weighted mean pooled effect size, namely the overall

237 amount of plant diversity change across all experiments, independently from the amount of N

238 addition. Based on these models, we also investigated publication bias with visual estimation of the

239 funnel plots (Nakagawa & Santos, 2012). We tested the significance of funnel plots asymmetry with

240 the Egger's test by fitting the residuals of the null model with observation precision (1/SE or the

241 inverse of number of replicates) as a moderator (Møller & Jennions, 2001; Nakagawa & Santos,

242 2012). Results of null models and publication bias are reported in Appendix S5. All analyses were

243 performed in the R environment (version 3.4.2) (R Core Team, 2017).

244

245 **Results**

246 We found all metrics of plant diversity to respond negatively to increasing yearly N addition (Figure

247 3). The single meta-regression models estimated different amounts of plant diversity loss per unit of

248 N addition, depending on the metric considered. For example, with a yearly amount of 100 kg N ha^{-1}

249 ^{1} yr^{-1} the models indicated a relative loss in species richness by 17% and in individual abundance by

250 64%, whereas the MSA and GMA were estimated to be reduced by 34% and 36%, respectively,

251 compared to the control plots. Only the GMA metric showed a non-linear relationship with yearly N

252 amounts, indicating that a small amount of N addition may lead to an increase in abundance or

253 evenness (Figure 3d).

254 The multiple meta-regression models showed that responses of plant biodiversity to N addition are

255 influenced by various environmental and experimental covariates (Table 2; see Appendix S6 for

256 detailed model outputs). Climatic moderators were found to influence the responses of the abundance

257 metrics, indicating stronger declines in areas with greater mean annual precipitation (for IA and

258 GMA) or higher mean annual temperature (for MSA). In addition, the lowest BIC model for SR

259 retained a significant interaction between yearly N addition amounts and mean annual temperature

260 (Table 2). Species richness decreased not only with yearly N addition amounts, but also with

261 experimental duration, indicating cumulative effects over time. We also found that plot size was a

262 relevant moderator for SR, with larger relative losses occurring in smaller plots. Additionally, we

263 found that overall losses in SR were less pronounced in soils with higher cation exchange capacity

264 (CEC). For instance, after a 5-year experiment with an addition level of 100 kg N ha^{-1} yr^{-1}, the model

265 estimates 10% of species richness loss for soils with a moderately high buffering capacity to

266 acidification (CEC = 35 cmol kg^{-1}). However, estimated species richness loss drops to 30% if the

267 same experiment (i.e. same duration and yearly N addition) is conducted on a poorly buffered soil

268 (CEC = 8 cmol kg^{-1}). The best model for MSA retained a significant interaction between yearly N

269 addition amount and fertilizer type, with stronger declines for N applied in a reduced form (NH_4^+ in

270 urea or ammonium sulphate) as compared to fertilizer containing oxidised N forms (NO_3^- in

271 ammonium nitrate or alkali nitrates).

272   We did not find a significant interaction between N application and ecosystem type for any metric,

273   indicating that the overall direction of biodiversity change with increasing yearly N addition was the

274   same in all the ecosystem types considered (Figure 4). For plant life-form types, we did not find a

275   significant interaction with N application either, i.e., all plant groups decreased with increasing N

276   addition amounts. A single regression model with life-form types as moderator indicated the largest

277   mean losses for the most N-sensitive groups (-85% for legumes; -75% for non-vascular plants; Figure

278   5). The responses of woody species and ferns showed larger variation and was not significantly

279   different from zero.

280

281   **Discussion**

282   *N dose-response relationships*

283   The biodiversity loss observed was strongly driven by the amount of yearly N addition. The higher

284   the N addition to the soil, the larger the negative impact on local plant diversity, reflecting that the

285   coexistence of different species is promoted by nutrient limitation (Harpole et al., 2011; Soons et al.,

286   2017). Growing accumulation of N in the soil increases soil acidification, which progressively

287   determine abundance loss up to the complete extirpation of species adapted to N-poor conditions

288   (Bobbink et al., 2010). In addition, eutrophication caused by N enrichment causes plant diversity

289   losses through enhanced light competition (Hautier, Niklaus, & Hector, 2009). The negative

290   relationships between plant biodiversity and the amount of N addition agree with the results of

291   previous meta-analyses conducted on a large geographical extent across multiple ecosystems types

292   (De Schrijver et al., 2016; Soons et al., 2017) and in mountain grasslands specifically (Humbert et

293   al., 2016), although these studies did not consider species abundance. Abundance metrics and species

294   richness were found to decrease at different rates as N addition increased. The largest declines were

295   observed for IA, possibly because at the assemblage level extremely negative responses of some

296   species (like the full extirpation occurring in the treatment plot) might be buffered by positive

297   responses of other species in the same plot.

298 *Experimental duration and cumulative N enrichment*

299 For species richness, we found that experimental duration had a negative additive effect comparable

300 in magnitude to the effect of the yearly N addition amount (Table 2), in accordance with the results

301 of Humbert et al. (2016). This suggests that plant communities respond similarly to cumulative N

302 application and cumulative atmospheric N deposition (Stevens et al., 2004; Duprè et al., 2010) and

303 indicates that large diversity losses may occur even at low yearly N amounts when fertilization is

304 protracted over a long-time period (Clark & Tilman, 2008). In the short term, species richness loss

305 due to N application is likely to be buffered by species gain. However, species turnover tends to

306 decline after several years of N addition (i.e. long experimental duration), when plant communities

307 have become adapted to N inputs and populations of a few well-established N-tolerant species

308 dominate the plots (Dise et al., 2011; Bobbink & Hettelingh, 2011). The absence of an effect of

309 experimental duration on the responses of the species abundance metrics may reflect that these

310 metrics do not capture effects of species replacement, because they include only species that were

311 already present in the controls. Further, our models did not reveal a significant modifying influence

312 of the background N deposition on the biodiversity responses (Table 2). This might reflect that

313 background annual N deposition rates were too small (0.7-46.3 kg N ha^{-1}yr^{-1}) compared to N amounts

314 applied in the experiments. In addition, it may reflect that the data source used to retrieve the N

315 deposition levels (50 * 50 km resolution) was not detailed enough to adequately capture the site-

316 specific deposition rates.

317 *Scale dependence*

318 There is evidence that effects of experimental N addition on local species richness are scale-

319 dependent. For example, Lan et al. (2015) found that proportional loss following N addition was

320 significantly higher in larger plots (> 8 m^2). Contrary to these findings, we did not find a significant

321 interaction between the rate of species richness change and plot size and we found overall larger

322 richness loss in smaller plot sizes (1 x 1 m or less) compared to larger ones (3 x 3 m or more). Possibly,

323 in larger plots chances are bigger to survey a few remaining individuals of the same species,

324 decreasing the chance of full extirpation from the sampled area. Like our results, Perring et al. (2018[b])

325 found that richness response ratios across 1814 survey-resurvey plots in European temperate forest

326 understories were positively related to the plot size of the survey. This may reflect that chances to

327 encounter the same species in two different plots increase with plot size.

328 As we studied effects on local or site-level biodiversity only, we cannot make inferences on the

329 impacts of N on plant biodiversity at larger extents. Trends in local biodiversity have implications for

330 changes in biodiversity at larger scales, but the mechanisms involved in these links are not yet fully

331 understood (McGill, Dornelas, Gotelli & Magurran, 2015). Chase (2010) found that higher beta

332 diversity (specifically spatial turnover) in more productive mesocosms yielded higher overall

333 (gamma) diversity at greater nutrient levels. However, the extent to which such effects will also occur

334 in response to atmospheric N deposition remains elusive, as atmospheric deposition levels are lower

335 than typical experimental N addition doses and because responses may be confounded by influences

336 of other environmental pressures. This may also explain why previous analyses of temporal changes

337 in site-level plant diversity revealed no clear trends in species richness (Vellend et al. 2013; Vellend

338 et al., 2017), despite increasing atmospheric N deposition levels occurring in the last century.

339 ***Effect of N fertilizer type***

340 In our analysis, fertilizer type itself did not induce a significant response in any of the metrics

341 considered, indicating similar overall impacts of the two types of N fertilizer. However, we found

342 that MSA decreased more strongly when N was added as urea or ammonium nitrate (containing only

343 NH_4^+) rather than ammonium nitrate or alkali nitrate (fertilizers also containing NO_3^-). In general,

344 differences in the chemical form of fertilizer applied are very often neglected in the experimental

345 design of N addition studies (but see Dias, Malveiro, Martins-Loução, Sheppard, & Cruz, 2011; Song

346 et al., 2012). Yet, evidence suggests that plant species occurring in the same community differ in their

347 ability to take up NO_3 and NH_4 forms, implying that plant community composition and abundance

348 may strongly depend on the partitioning of differentially available soil N forms (Kahmen, Renker,

349 Unsicker, & Buchmann, 2006; McKane et al., 2002; Miller & Bowman, 2002). Various studies in

350   Northern Europe suggest that larger species losses are expected with increasing NH_4^+ deposition due

351   to increased acidification, especially in case of oligotrophic ecosystems that are sensitive to

352   $NH_4^+{:}NO_3^-$ increase, such as heathlands, bogs, and acidic grasslands (Kleijn, Bekker, Bobbink, Graaf,

353   & Roelofs, 2008; Paulissen, van der Ven, Dees, & Bobbink, 2004), while acidification tends to be

354   less severe when NO_3^- fertilizers are applied instead (van den Berg et al., 2008). Future nutrient

355   addition experiments should account for the type of fertilizer applied to better elucidate such

356   differences.

357   *Soil properties*

358   Soil acidification is one of the major processes to drive biodiversity loss following atmospheric N

359   enrichment (Stevens et al., 2011). Yet, we did not find any evidence of soil pH modifying the

360   relationship between local plant biodiversity and N addition, similar to the results of previous meta-

361   analyses (De Schrijver et al., 2011; Humbert et al., 2016). Soil acidity follows a negative linear

362   relationship with base saturation (exchangeable base cations) (Beery & Wilding, 1971). However,

363   the drop in base saturation is independent of initial soil pH, but it is dependent on soil cation exchange

364   capacity (CEC) when the soil pH ranges between 4-7 units, as in the case of our data (Helling,

365   Chesters & Corey, 1964, De Vries et al., 1989; Ulrich, 1986). This may explain why we found that

366   the response of species richness was not modified by initial soil pH, but instead was related to the soil

367   CEC, which reflects the ability of the soil to buffer N-induced acidification. Thus, in sites with higher

368   soil CEC, the negative impact of N addition through acidification is reduced by base cation exchange

369   in the soil, resulting in a lower species loss compared to sites with low CEC. Similar to our findings,

370   greater species loss has been associated with lower soil CEC across 23 N-addition experiments in

371   North America (Clark et al. 2007). Likely, soil CEC may also explain the small species richness

372   response observed in peatlands and bogs, where overall mean effect size was close to zero (Figure 4).

373   These ecosystems had the highest soil CEC values in our data (32 ± 3 cmol kg^{-1}), reflecting the high

374   organic matter content that characterizes peatland soils.

375   *Climate*

376   The best models selected for the abundance metrics retained main effects of the two climatic

377   moderators (Table 2), suggesting that overall larger abundance losses occur in sites with higher mean

378   annual temperature (for MSA) and precipitation (for IA and GMA). We also found evidence that the

379   slope of the dose-response relationship for species richness is dependent on mean annual temperature

380   at the site level, indicating that richness decreases more steeply with N dose in warmer sites. Similar

381   outcomes have been reported for species richness of mountain grasslands (Humbert et al. 2016) and

382   the abundance of *Sphagnum* mosses (Limpens et al. 2011), probably because N uptake tends to

383   increase with temperature (Cross, Hood, Benstead, Huryn, & Nelson, 2015). In grasslands, higher

384   temperature and precipitation have been found to amplify aboveground biomass growth in response

385   to N addition (Shaw et al., 2002; Zavaleta, Shaw, Chiariello, Mooney, & Field, 2003). Similarly, in

386   forests and tundra ecosystems, temperature has been shown to positively affect net primary

387   productivity following N addition (LeBauer and Treseder 2008). This in turn negatively influences

388   plant biodiversity, as increased biomass results in increased competition for light and in the loss of

389   rare species (Soons et al., 2017). In addition, higher precipitation could also lead to increased N

390   mineralisation (Yang et al. 2017) which, in the absence of increased N loss via leaching or gaseous

391   emissions, could result in higher N availability and increased biodiversity loss. Although in general

392   plant assemblage responses in our analysis were not very different among ecosystem types, the

393   modifying role of temperature and precipitation highlight the importance to account for

394   biogeographical and climatic gradients to assess the impacts of N enrichment on local plant diversity

395   across large geographical extents.

Individual responses of plant life-form types

397   We found that abundance losses were particularly large for legumes and non-vascular plants (mosses

398   and lichens). Indeed, both groups have been identified as the most sensitive to increased N inputs

399   (Bobbink et al., 2010; Craine et al., 2002). Previous studies showed that vascular plants are known to

400   outcompete mosses after N enrichment due to light competition (Malmer, Albinsson, Svensson, &

401   Wallen, 2003; van der Wal, Pearce, & Brooker, 2005), with a substantial decline of nonvascular plants

402 beyond 10-15 kg N ha^{-1}yr^{-1} (Bobbink et al., 2010). A large negative response of legumes was also

403 expected, as increased soil N availability represents a disadvantage for N fixation (Craine et al., 2002).

404 Long-term fertilization studies conducted on multiple sites in the USA found substantial declines in

405 N-fixers (Suding et al., 2005) and an overall large decline in total legume biomass was also detected

406 in previous systematic reviews (Fu and Shen, 2016; Humbert et al., 2016). In addition, we found the

407 abundance of individual graminoids decreased, on average, by half. This contradicts the general

408 hypothesis that graminoids tend to become dominant following N enrichment (see e.g. Bobbink et

409 al., 2010; Dise et al., 2011) and contrasts with previous meta-analyses of N addition studies that

410 reported significant increases in total biomass of grasses and sedges (De Schrijver et al., 2011; Fu

411 and Shen, 2016; Humbert et al., 2016). Such discrepancies with our results could reflect the fact that

412 grass encroachment following N input usually comes about by one or few species only (Bobbink et

413 al., 2010) while the rest of the graminoid species are progressively outcompeted in the treatment plots,

414 resulting, on average, in a loss of graminoids' individual abundance. Finally, the relatively small

415 impacts on woody species might be due to longer persistence in vegetation thanks to their longer life

416 span, which may exceed the typical duration of the experiments.

417 Further insight into the mechanisms behind community change with N enrichment, including

418 individual abundance responses, may be provided by trait analyses (see e.g. La Pierre & Smith, 2015;

419 Read, Henning, Classen & Sanders, 2018). However, analyses of changes in plant functional traits

420 (at both within- and among-species levels) were out of scope of our meta-analysis and the primary

421 studies analysed.

422 ***Concluding remarks***

423 We showed the importance of minimizing N enrichment in terrestrial ecosystems to reduce local plant

424 biodiversity loss. Compared to several previous studies that summarized the impacts of N-addition

425 experiments on plant biodiversity, we improved our understanding of the responses of plant

426 communities to N enrichment by including not only species richness but also abundance metrics,

427 which showed stronger responses and have been unexplored in meta-analyses so far. Further, we shed

428   more light on the roles of different moderators influencing the response of species richness and

429   abundance, thus showing how biodiversity loss is context-dependent and underlining the importance

430   to integrate multiple dimensions of biodiversity into assessments of biodiversity responses to global

431   environmental change.

References

Alkemade, R., van Oorschot, M., Miles, L., Nellemann, C., Bakkenes, M., & ten Brink, B. (2009). GLOBIO3: A Framework to Investigate Options for Reducing Global Terrestrial Biodiversity Loss. *Ecosystems*, *12*(3), 374–390. https://doi.org/10.1007/s10021-009-9229-5

Beery, M.; Wilding, L. P. (1971). The Relationship Between Soil pH and Base-Saturation Percentage for Surface and Subsoil Horizons of Selected Mollisols, Alfisols, and Ultisols in Ohio. *The Ohio Journal of Science 43-55* http://hdl.handle.net/1811/5590

Benítez-López, A., Alkemade, R., Schipper, A. M., Ingram, D. J., Verweij, P. A., Eikelboom, J. A. J., & Huijbregts, M. A. J. (2017). The impact of hunting on tropical mammal and bird populations. *Science*, *356*(6334), 180–183. https://doi.org/10.1126/science.aaj1891

Benítez-López, A., Alkemade, R., & Verweij, P. A. (2010). The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. *Biological Conservation*, *143*(6), 1307–1316. https://doi.org/10.1016/j.biocon.2010.02.009

Bernhardt-Römermann, M., Baeten, L., Craven, D., Frenne, P. de, Hédl, R., Lenoir, J.,. . . Verheyen, K. (2015). Drivers of temporal changes in temperate forest plant diversity vary across spatial scales. *Global Change Biology*, *21*(10), 3726–3737. https://doi.org/10.1111/gcb.12993

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M.,. . . de Vries, W. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis. *Ecological Applications*, *20*(1), 30–59. https://doi.org/10.1890/08-1140.1

Bobbink, R., & H. Hettelingh, J. P, (2011). *Review and revision of empirical critical loads and dose-response relationships: Proceedings of an expert workshop, Noordwijkerhout, 23-25 June 2010*: Rijksinstituut voor Volksgezondheid en Milieu RIVM. Retrieved from https://rivm.openrepository.com/rivm/bitstream/10029/260510/3/680359002.pdf

Borer, E. T., Harpole, W. S., Adler, P. B., Lind, E. M., Orrock, J. L., Seabloom, E. W., & Smith, M. D. (2014). Finding generality in ecology: a model for globally distributed experiments. *Methods in Ecology and Evolution*, *5*(1), 65-73. https://doi.org/10.1111/2041-210X.12125

Buckland, S. T., Magurran, A. E., Green, R. E., & Fewster, R. M. (2005). Monitoring change in biodiversity through composite indices. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, *360*(1454), 243–254. https://doi.org/10.1098/rstb.2004.1589

Buckland, S. T., Studeny, A. C., Magurran, A. E., Illian, J. B., & Newson, S. E. (2011). The geometric mean of relative abundance indices: A biodiversity measure with a difference. *Ecosphere*, *2*(9), 1–15. https://doi.org/10.1890/ES11-00186.1

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P.,. . . Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*(7401), 59. https://doi.org/10.1038/nature11148

Chase, J. M. (2010). Stochastic community assembly causes higher biodiversity in more productive environments. *Science*, 1187820. https://doi.org/10.1126/science.1187820

Clark, C. M., Cleland, E. E., Collins, S. L., Fargione, J. E., Gough, L., Gross, K. L.,. . . Grace, J. B. (2007). Environmental and plant community determinants of species loss following nitrogen enrichment. *Ecology Letters*, *10*(7), 596–607. https://doi.org/10.1111/j.1461-0248.2007.01053.x

Clark, C. M.; Tilman, D. (2008): Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature 451 (7179),* 712–715. https://doi.org/10.1038/nature06503.

Craine, J. M., Tilman, D., Wedin, D., Reich, P., Tjoelker, M., & Knops, J. (2002). Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Functional Ecology*, *16*(5), 563–574. https://doi.org/10.1046/j.1365-2435.2002.00660.x

Cross, W. F., Hood, J. M., Benstead, J. P., Huryn, A. D., & Nelson, D. (2015). Interactions between temperature and nutrients across levels of ecological organization. *Global Change Biology*, *21*(3), 1025–1040. https://doi.org/10.1111/gcb.12809

Dentener, F., Stevenson, D., Ellingsen, K., van Noije, T., Schultz, M., Amann, M.,. . . Zeng, G. (2006). The global atmospheric environment for the next generation. *Environmental science & technology*, *40*(11), 3586–3594. https://doi.org/10.1021/es0523845.

De Schrijver, A. de, Frenne, P. de, Ampoorter, E., van Nevel, L., Demey, A., Wuyts, K., & Verheyen, K. (2011). Cumulative nitrogen input drives species loss in terrestrial ecosystems. *Global Ecology and Biogeography*, *20*(6), 803–816. https://doi.org/10.1111/j.1466-8238.2011.00652.x

Dias, T., Malveiro, S., Martins-Loução, M. A., Sheppard, L. J., & Cruz, C. (2011). Linking N-driven biodiversity changes with soil N availability in a Mediterranean ecosystem. *Plant and Soil*, *341*(1), 125–136. https://doi.org/10.1007/s11104-010-0628-3

Dise, N. B., M. Ashmore, S. Belyazid, A. Bleeker, R. Bobbink, W. de Vries,. . . C. J. Stevens. (2011). Nitrogen as a threat to European terrestrial biodiversity. In M. A. Sutton (Ed.), *The European nitrogen assessment. Sources, effects, and policy perspectives / edited by Mark A. Sutton ... [et al.]* (pp. 463–493). Cambridge: Cambridge University Press.

Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., & Magurran, A. E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science*, *344*(6181), 296–299. https://doi.org/10.1126/science.1248484

Duprè, C., Stevens, C. J., Ranke, T., Bleeker, A., Peppler-Lisbach, C., Gowing, D. J.,. . . Diekmann, M. (2010). Changes in species richness and composition in European acidic grasslands over the past 70 years: The contribution of cumulative atmospheric nitrogen deposition. *Global Change Biology*, *16*(1), 344–357. https://doi.org/10.1111/j.1365-2486.2009.01982.x

Erisman, J. W., Galloway, J. N., Seitzinger, S., Bleeker, A., Dise, N. B., Petrescu, A. M. R.,. . . de Vries, W. (2013). Consequences of human modification of the global nitrogen cycle. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, *368*(1621), 20130116. https://doi.org/10.1098/rstb.2013.0116

Firn, J., Moore, J. L., MacDougall, A. S., Borer, E. T., Seabloom, E. W., HilleRisLambers, J., ... & Prober, S. M. (2011). Abundance of introduced species at home predicts abundance away in herbaceous communities. *Ecology letters*, *14*(3), 274-281. https://doi.org/10.1111/j.1461-0248.2010.01584.x

Fu, G., & Shen, Z.-X. (2016). Response of Alpine Plants to Nitrogen Addition on the Tibetan Plateau: A Meta-analysis. *Journal of Plant Growth Regulation*, *35*(4), 974–979. https://doi.org/10.1007/s00344-016-9595-0

Galloway, J. N., Townsend, A. R., Erisman, J. W., Bekunda, M., Cai, Z., Freney, J. R.,. . . Sutton, M. A. (2008). Transformation of the Nitrogen Cycle: Recent Trends, Questions, and Potential Solutions. *Science*, *320*(5878), 889–892. https://doi.org/10.1126/science.1136674

Harpole W. S., Ngai, J. T., Cleland, E. E., Seabloom, E. W., Borer, E. T.,. . . Smith, J. E. (2011). Nutrient co-limitation of primary producer communities. *Ecology letters 14*(9), pp. 852–862. https://doi.org/10.1111/j.1461-0248.2011.01651.x

Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science*, 324(5927), 636-638. https://doi.org/10.1126/science.1169640

Hedges, L. V., Gurevitch, J., & Curtis, P. S. (1999). The Meta-Analysis of Response Ratios in Experimental Ecology. *Ecology*, 80(4), 1150. https://doi.org/10.2307/177062

Helling, C. S.; Chesters, G.; Corey, R. B. (1964). Contribution of Organic Matter and Clay to Soil Cation-Exchange Capacity as Affected by the pH of the Saturating Solution1. *Soil Science Society of America Journal 28 (4), 517*. https://doi.org/10.2136/sssaj1964.03615995002800040020x.

Hengl, Tomislav; Jesus, Jorge Mendes de; Heuvelink, Gerard B. M.; Gonzalez, Maria Ruiperez; Kilibarda, Milan; Blagotić, Aleksandar et al. (2017): SoilGrids250m. Global gridded soil information based on machine learning. *PLOS ONE* 12 (2). https://doi.org/10.2136/10.1371/journal.pone.0169748.

Hengl, Tomislav; Jesus, Jorge Mendes de; MacMillan, Robert A.; Batjes, Niels H.; Heuvelink, Gerard B. M.; Ribeiro, Eloi et al. (2014): SoilGrids1km—global soil information based on automated mapping. In *PloS one* 9 (8), e105992. https://doi.org/10.2136/10.1371/journal.pone.0105992.

Hettelingh, J.-P., Stevens, C. J., Posch, M., Bobbink, R., & de Vries, W. (2015). Assessing the Impacts of Nitrogen Deposition on Plant Species Richness in Europe. In W. de Vries, J. P. Hettelingh, & M. Posch (Eds.), *Environmental pollution, 1566-0745: volume 25. Critical loads and dynamic risk assessments. Nitrogen, acidity and metals in terrestrial and aquatic ecosystems / Wim de Vries, Jean-Paul Hettelingh, Maximilian Posch, editors* (pp. 573–586). Dordrecht: Springer. https://doi.org/10.1007/978-94-017-9508-1_23

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S.,. . . Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, 75(1), 3–35. https://doi.org/10.1890/04-0922

Humbert, J.-Y., Dwyer, J. M., Andrey, A., & Arlettaz, R. (2016). Impacts of nitrogen addition on plant biodiversity in mountain grasslands depend on dose, application duration and climate: A systematic review. *Global Change Biology*, 22(1), 110–120. https://doi.org/10.1111/gcb.12986

Jones, M. L. M., Wallace, H. L., Norris, D., Brittain, S. A., Haria, S., Jones, R. E.,. . . Emmett, B. A. (2004). Changes in Vegetation and Soil Characteristics in Coastal Sand Dunes along a Gradient of Atmospheric Nitrogen Deposition. *Plant Biology*, 6(5), 598–605. https://doi.org/10.1055/s-2004-821004

Kahmen, A., Renker, C., Unsicker, S. B., & Buchmann, N. (2006). Niche complementarity for nitrogen: an explanation for the biodiversity and ecosystem functioning relationship? *Ecology*, 87(5), 1244–1255. https://doi.org/10.1890/0012-9658(2006)87[1244:NCFNAE]2.0.CO;2

Kleijn, D., Bekker, R. M., Bobbink, R., Graaf, M. C. C. de, & Roelofs, J. G. M. (2008). In search for key biogeochemical factors affecting plant species persistence in heathland and acidic grasslands: A comparison of common and rare species. *Journal of Applied Ecology*, 45(2), 680–687. https://doi.org/10.1111/j.1365-2664.2007.01444.x

Konstantopoulos, S. (2011). Fixed effects and variance components estimation in three-level meta-analysis. *Research synthesis methods*, 2(1), 61–76. https://doi.org/10.1002/jrsm.35

La Pierre, K. J.; Smith, M.D. (2015). Functional trait expression of grassland species shift with short- and long-term nutrient additions. *Plant Ecology 216 2, 307–318*. https://doi.org/10.1007/s11258-014-0438-4.

Lajeunesse, M. J. (2011). On the meta-analysis of response ratios for studies with correlated and multi-group designs. *Ecology. 92 (11), 2049–2055*. https://doi.org/10.1890/11-0423.1.

Lajeunesse, M. J. (2016). Facilitating systematic reviews, data extraction and meta-analysis with the METAGEAR package for R. *Methods in Ecology and Evolution*, *7*(3), 323–330. https://doi.org/10.1111/2041-210X.12472

Limpens, J., Granath, G., Gunnarsson, U., Aerts, R., Bayley, S., Bragazza, L.,. . . Xu, B. (2011). Climatic modifiers of the response to nitrogen deposition in peat-forming Sphagnum mosses: A meta-analysis. *New Phytologist*, *191*(2), 496–507. https://doi.org/10.1111/j.1469-8137.2011.03680.x

LeBauer, D. S., & Treseder, K. K. (2008). Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology*, *89*(2), 371–379. https://doi.org/10.1890/06-2057.1

Maestre, F. T., Quero, J. L., Gotelli, N. J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M.,. . . Zaady, E. (2012). Plant Species Richness and Ecosystem Multifunctionality in Global Drylands. *Science*, *335*(6065), 214–218. https://doi.org/10.1126/science.1215442

Malmer, N., Albinsson, C., Svensson, B. M., & Wallen, B. (2003). Interferences between Sphagnum and vascular plants: Effects on plant community structure and peat formation. *Oikos*, *100*(3), 469–482. https://doi.org/10.1034/j.1600-0706.2003.12170.x

McGill, B. J., Dornelas, M., Gotelli, N. J., & Magurran, A. E. (2015). Fifteen forms of biodiversity trend in the Anthropocene. *Trends in ecology & evolution*, 30(2), 104-113. https://doi.org/10.1016/j.tree.2014.11.006

McKane, R. B., Johnson, L. C., Shaver, G. R., Nadelhoffer, K. J., Rastetter, E. B., Fry, B.,. . . Murray, G. (2002). Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*, *415*(6867), 68–71. https://doi.org/10.1038/415068a

Miller, A. E., & Bowman, W. D. (2002). Variation in nitrogen-15 natural abundance and nitrogen uptake traits among co-occurring alpine species: Do species partition by nitrogen form? *Oecologia*, *130*(4), 609–616. https://doi.org/10.1007/s00442-001-0838-8

Møller, A. P., & Jennions, M. D. (2001). Testing and adjusting for publication bias. *Trends in Ecology & Evolution*, *16*(10), 580–586. https://doi.org/10.1016/S0169-5347(01)02235-2

Nakagawa, S., & Santos, E. S. A. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology*, *26*(5), 1253–1274. https://doi.org/10.1007/s10682-012-9555-5

New, M., Hulme, M., & Jones, P. (1999). Representing Twentieth-Century Space-Time Climate Variability. Part I: Development of a 1961–90 Mean Monthly Terrestrial Climatology. *Journal of Climate*, *12*(3), 829–856. https://doi.org/10.1175/1520-0442(1999)012<0829:RTCSTC>2.0.CO;2

Pardo, L. H., Fenn, M. E., Goodale, C. L., Geiser, L. H., Driscoll, C. T., Allen, E. B.,. . . Dennis, R. L. (2011). Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. *Ecological Applications*, *21*(8), 3049–3082. https://doi.org/10.1890/10-2341.1

Paulissen, M.P.C.P., van der Ven, P.J.M., Dees, A. J., & Bobbink, R. (2004). Differential effects of nitrate and ammonium on three fen bryophyte species in relation to pollutant nitrogen input. *New Phytologist*, *164*(3), 451–458. https://doi.org/10.1111/j.1469-8137.2004.01196.x

Perring, M. P., Diekmann, M., Midolo, G., Costa, D. S., Bernhardt-Römermann, M., Otto, J. C., ... & Verheyen, K. (2018). Understanding context dependency in the response of forest understorey

607   plant communities to nitrogen deposition. *Environmental Pollution, 242*, 1787-1799. Advance

608   online publication. https://doi.org/10.1016/j.envpol.2018.07.089 [a]

609 Perring, M. P., Bernhardt-Römermann, M., Baeten, L., Midolo, G., Blondeel, H., Depauw, L.,. . .
610   Verheyen, K. (2018). Global environmental change effects on plant community composition
611   trajectories depend upon management legacies. *Global Change Biology, 24*(4), 1722-1740.
612   https://doi.org/10.1111/gcb.14030 [b]

613 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2017). nlme: Linear and Nonlinear
614   Mixed Effects Models. R package version 3.1-131 <URL: https://CRAN.R-
615   project.org/package=nlme>.

616 Quijas, S., Jackson, L. E., Maass, M., Schmid, B., Raffaelli, D., & Balvanera, P. (2012). Plant
617   diversity and generation of ecosystem services at the landscape scale: Expert knowledge
618   assessment. *Journal of Applied Ecology*, *49*(4), 929–940. https://doi.org/10.1111/j.1365-
619   2664.2012.02153.x

620 R Core Team. (2017). R: A language and environment for statistical computing. R Foundation for
621   Statistical Computing, Vienna, Austria. <URL https://www.R-project.org/>.

622 Read, Q. D.; Henning, J. A.; Classen, A. T.; Sanders, N. J. (2018). Aboveground resilience to
623   species loss but belowground resistance to nitrogen addition in a montane plant community. In
624   *Journal of Plant Ecology 11 (3) 351–363*. https://doi.org/10.2136/10.1093/jpe/rtx015.

625 Sala, O. E., Chapin, F. S., III, Armesto, J. J., Berlow, E., Bloomfield, J.,. . . Wall, D. H. (2000).
626   Global Biodiversity Scenarios for the Year 2100. *Science*, *287*(5459), 1770–1774.
627   https://doi.org/10.1126/science.287.5459.1770

628 Santini, L., Belmaker, J., Costello, M. J., Pereira, H. M., Rossberg, A. G., Schipper, A. M.,. . .
629   Rondinini, C. (2017). Assessing the suitability of diversity metrics to detect biodiversity change.
630   *Biological Conservation*, *213*, 341–350. https://doi.org/10.1016/j.biocon.2016.08.024

631 Schipper, A. M., Belmaker, J., Miranda, M. D., Navarro, L. M., Böhning‑Gaese, K., Costello, M.
632   J.,. . . Pereira, H. M. (2016). Contrasting changes in the abundance and diversity of North
633   American bird assemblages from 1971 to 2010. *Global Change Biology*, *22*(12), 3948–3959.
634   https://doi.org/10.1111/gcb.13292

635 Shaw, M. R., Zavaleta, E. S., Chiariello, N. R., Cleland, E. E., Mooney, H. A., & Field, C. B.
636   (2002). Grassland responses to global environmental changes suppressed by elevated CO2.
637   *Science*, *298*(5600), 1987–1990. https://doi.org/10.1126/science.1075312

638 Simkin, S. M., Allen, E. B., Bowman, W. D., Clark, C. M., Belnap, J., Brooks, M. L.,. . . Waller, D.
639   M. (2016). Conditional vulnerability of plant diversity to atmospheric nitrogen deposition across
640   the United States. *Proceedings of the National Academy of Sciences*, *113*(15), 4086–4091.
641   https://doi.org/10.1073/pnas.1515241113

642 Smith, N. G., Schuster, M. J., & Dukes, J. S. (2016). Rainfall variability and nitrogen addition
643   synergistically reduce plant diversity in a restored tallgrass prairie. *Journal of Applied Ecology*,
644   *53*(2), 579–586. https://doi.org/10.1111/1365-2664.12593

645 Smithson, M., & Verkuilen, J. (2006). A better lemon squeezer? Maximum-likelihood regression
646   with beta-distributed dependent variables. *Psychological methods*, *11*(1), 54–71.
647   https://doi.org/10.1037/1082-989X.11.1.54

648 Song, M.-H., Yu, F.-H., Ouyang, H., Cao, G.-M., Xu, X.-L., & Cornelissen, J. H. C. (2012).
649   Different inter-annual responses to availability and form of nitrogen explain species coexistence

in an alpine meadow community after release from grazing. *Global Change Biology*, *18*(10), 3100–3111. https://doi.org/10.1111/j.1365-2486.2012.02738.x

Soons, M. B., Hefting, M. M., Dorland, E., Lamers, L. P.M., Versteeg, C., & Bobbink, R. (2017). Nitrogen effects on plant species richness in herbaceous communities are more widespread and stronger than those of phosphorus. *Biological Conservation*, *212*, 390–397. https://doi.org/10.1016/j.biocon.2016.12.006

Stevens, C. J., Duprè, C., Dorland, E., Gaudnik, C., Gowing, D. J. G., Bleeker, A.,. . . Dise, N. B. (2010). Nitrogen deposition threatens species richness of grasslands across Europe. *Environmental pollution (Barking, Essex : 1987)*, *158*(9), 2940–2945. https://doi.org/10.1016/j.envpol.2010.06.006

Stevens, C. J., Manning, P., van den Berg, L. J. L., Graaf, M. C. C. de, Wamelink, G. W. W., Boxman, A. W.,. . . Dorland, E. (2011). Ecosystem responses to reduced and oxidised nitrogen inputs in European terrestrial habitats. *Environmental pollution (Barking, Essex : 1987)*, *159*(3), 665–676. https://doi.org/10.1016/j.envpol.2010.12.008

Stevens, C. J., Thompson, K., Grime, J. P., Long, C. J., & Gowing, D. J. G. (2010). Contribution of acidification and eutrophication to declines in species richness of calcifuge grasslands along a gradient of atmospheric nitrogen deposition. *Functional Ecology*, *24*(2), 478–484. https://doi.org/10.1111/j.1365-2435.2009.01663.x

Suding, K. N., Collins, S. L., Gough, L., Clark, C., Cleland, E. E., Gross, K. L.,. . . Pennings, S. (2005). Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(12), 4387–4392. https://doi.org/10.1073/pnas.0408648102

Ulrich, B. (1986). Natural and anthropogenic components of soil acidification. In *Zeitschrift für Pflanzenernährung und Bodenkunde 149 (6), 702–717.* https://doi.org/10.2136/10.1002/jpln.19861490607.

van den Berg, L. J. L., Peters, C. J. H., Ashmore, M. R., & Roelofs, J. G. M. (2008). Reduced nitrogen has a greater effect than oxidised nitrogen on dry heathland vegetation. *Environmental Pollution*, *154*(3), 359–369. https://doi.org/10.1016/j.envpol.2007.11.027

van der Wal, R., Pearce, I. S. K., & Brooker, R. W. (2005). Mosses and the struggle for light in a nitrogen-polluted world. *Oecologia*, *142*(2), 159–168. https://doi.org/10.1007/s00442-004-1706-0

Vellend, M., Baeten, L., Becker-Scarpitta, A., Boucher-Lalonde, V., McCune, J. L., Messier, J.,. . . Sax, D. F. (2017). Plant Biodiversity Change Across Scales During the Anthropocene. *Annual review of plant biology*, *68*, 563–586. https://doi.org/10.1146/annurev-arplant-042916-040949

Vellend, M., Baeten, L., Myers-Smith, I. H., Elmendorf, S. C., Beauséjour, R., Brown, C. D., ... & Wipf, S. (2013). Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences*, 201312779. https://doi.org/10.1073/pnas.1312779110

Vries, W. de; Posch, M.; Kämäri, J. (1989). Simulation of the long-term soil response to acid deposition in various buffer ranges. In *Water Air Soil Pollut 48 (3-4), 349–390.* https://doi.org/10.1007/BF00283336.

Viechtbauer, W. (2010). Conducting Meta-Analyses in R with the metafor Package. *Journal of Statistical Software*, *36*(1), 1–48. https://doi.org/10.18637/jss.v036.i03

693   Winfree, R., Fox, J. W., Williams, N. M., Reilly, J. R., & Cariveau, D. P. (2015). Abundance of
694   common species, not species richness, drives delivery of a real-world ecosystem service.
695   *Ecology Letters*, *18*(7), 626–635. https://doi.org/10.1111/ele.12424

696   Yang, W. H., Ryals, R. A., Cusack, D. F., & Silver, W. L. (2017). Cross-biome assessment of gross
697   soil nitrogen cycling in California ecosystems. *Soil Biology and Biochemistry*, *107*, 144-155.
698   https://doi.org/10.1016/j.soilbio.2017.01.004

699   Zavaleta, E. S., Shaw, M. R., Chiariello, N. R., Mooney, H. A., & Field, C. B. (2003). Additive
700   effects of simulated climate changes, elevated CO2, and nitrogen deposition on grassland
701   diversity. *Proceedings of the National Academy of Sciences of the United States of America*,
702   *100*(13), 7650–7654. https://doi.org/10.1073/pnas.0932734100

703   **Table 1**: Summary table of the metrics and weights used to quantify biodiversity change in the meta-analysis.

Effect size	Description	Calculation	Weight	References
Species richness (SR)	Log-transformed response ratio of mean species richness in the treatment (S_T) and control (S_C)	$SR = \ln\left(\frac{\bar{S}_T}{\bar{S}_C}\right)$	Inverse of the sampling variance	De Schrijver et al. (2011) Bernhardt-Römermann et al. (2015) Humbert et al. (2016)
Individual species abundance (IA)	Log-transformed response ratio of mean individual abundance of species in the treatment (A_T) and control (A_C) *	$IA = \ln\left(\frac{\bar{A}_T}{\bar{A}_C}\right)$	Inverse of the sampling variance	Benítez-López et al. (2017)
Mean species abundance (MSA)	Mean of the individual species abundance response ratios (truncated at 1 if $A_T > A_C$). N is number of species in each observation.	$MSA = \dfrac{\sum_{\bar{A}_T < \bar{A}_C}\left(\frac{\bar{A}_T}{\bar{A}_C}\right) + \sum_{\bar{A}_T \geq \bar{A}_C} 1}{N}$	Number of replicates	Alkemade et al. (2009) Benítez-López et al. (2010)
Geometric mean abundance (GMA)	Mean of log-transformed response ratios of mean individual abundance. N is number of species in each observation.	$GMA = \exp\left(\dfrac{\sum(\ln(\bar{A}_T) - \ln(\bar{A}_C))}{N}\right)$	Number of replicates	Buckland et al. (2011) Schipper et al. (2016) Santini et al. (2017)

704   * Before log-transformation, the ratio was first transformed following Smithson and Verkuilen (2006) to shrink the data and avoid zero values in the treatment. See
705   'Methods'

Table 2: Standardized coefficients (slope estimates) of terms retained in the best meta-regression models based on the Bayesian information criterion (BIC). Nadd = amount of yearly N addition; duration = duration of the experiment; CEC = cation exchange capacity; plot size = size of the plot; Nadd:MAT = interaction term between Nadd and MAT; Nadd:NO_3 / Nadd:NH_4 = interaction term (slope) of responses to Nadd depending on fertilizer used in the experiment (containing NO_3 or NH_4 only, respectively); MAP = mean annual precipitation; MAT = mean annual temperature. The omnibus test statistics (Q_M and P_Q) indicate the amount of residual heterogeneity explained for each individual moderator and for the whole model. In case of an interaction, the omnibus test is reported for the interaction term only. See Appendix S6 for detailed model outputs.

Effect size	Fixed effect (moderators)	Estimate	SE	Z-value	LCI	UCI	P-value	Q_M (d.f.)	P_Q
Species richness (SR)	Nadd	-0.111	0.016	-6.855	-0.142	-0.079	<.0001	-	-
	duration	-0.093	0.024	-3.909	-0.140	-0.046	<.0001	15.7 (1)	<.0001
	CEC	0.076	0.023	3.237	0.030	0.122	0.001	10.5 (1)	0.001
	plot size	0.101	0.024	4.168	0.054	0.149	<.0001	17.4 (1)	<.0001
	MAT	-0.015	0.024	-0.610	-0.062	0.033	0.542	-	-
	Nadd:MAT	-0.049	0.019	-2.599	-0.085	-0.012	0.009	6.7 (1)	0.009
								76.9 (6)	< .0001
Individual species abundance (IA)	Nadd	-0.275	0.081	-3.389	-0.434	-0.116	0.001	11.5 (1)	0.001
	MAP	-0.441	0.146	-3.011	-0.728	-0.154	0.002	9.1 (1)	0.002
								18.5 (2)	< .0001
Mean species abundance (MSA)	Nadd:NO_3	-0.014	0.014	-0.958	-0.042	0.014	0.014	6.5 (1)	0.014
	Nadd:NH_4	-0.072	0.022	-2.552	-0.145	0.000	-	-	-
	MAT	-0.050	0.023	-2.314	-0.092	-0.008	0.025	5.2 (1)	0.047
								26.0 (2)	< .0001
Geometric mean abundance (GMA)	Nadd	-0.103	0.037	-2.796	-0.175	-0.030	0.008	6.8 (1)	0.012
	MAP	-0.181	0.059	-3.079	-0.295	-0.065	0.004	9.5 (1)	0.004
								16.3 (3)	< .0001

712
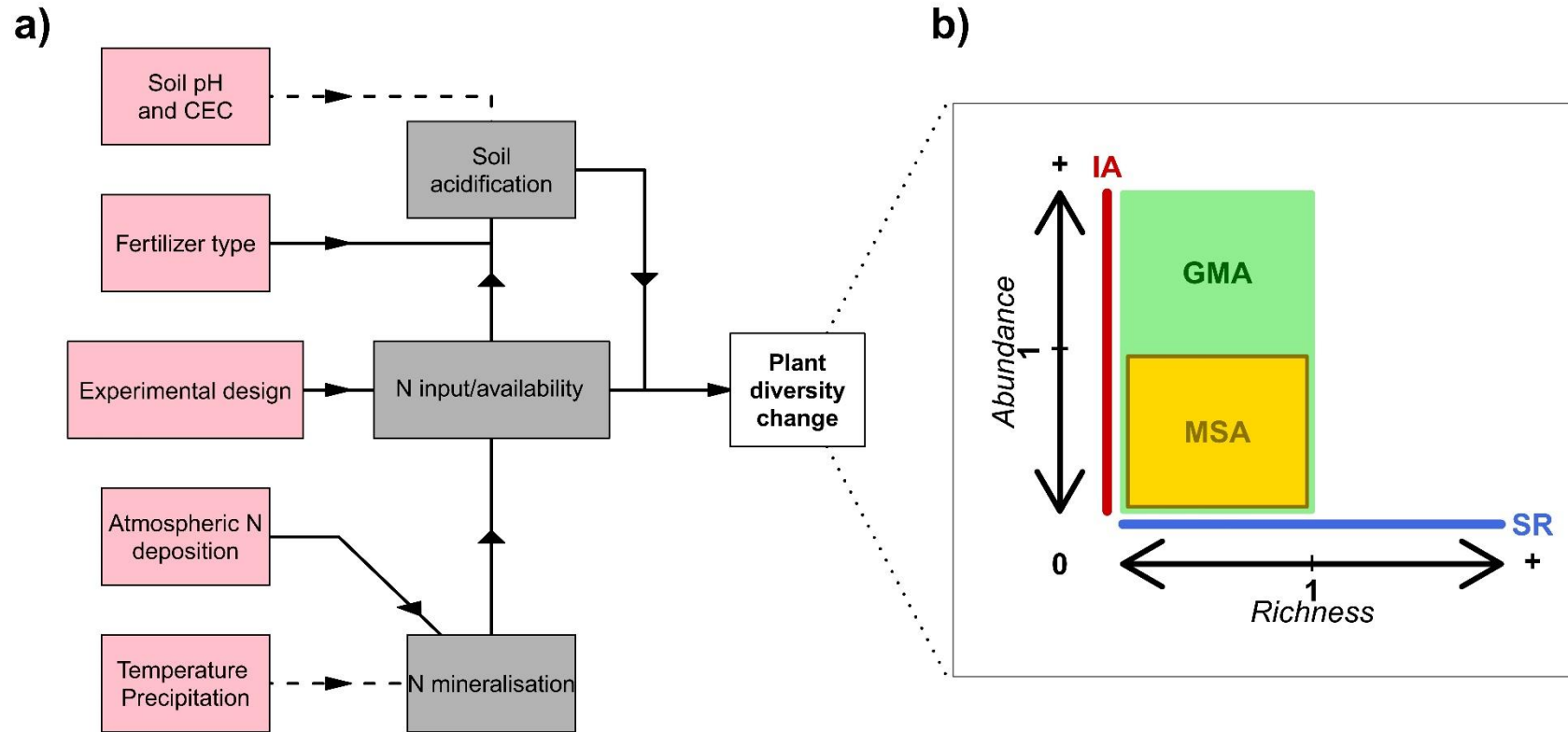
Figure 1: Graphical representation of **a)** relationships between key factors (i.e. moderators; pink boxes) and fundamental processes (grey boxes) that trigger plant species responses in N-addition experiments. Solid arrows represent direct effects, while dashed arrows represent context-dependent effects (i.e. in the experiments, the extent of soil acidification and N mineralisation may be positively or negatively affected by soil fertility and climatic conditions, respectively), and **b)** the linkages between the changes in biodiversity metrics considered in this study. Richness and abundance represent the two dimensions of biodiversity affected by N addition, with '-', '0' and '+' on the axes indicating loss, no change and increase, respectively. SR = species richness, IA = individual species abundance, MSA = mean species abundance, and GMA = geometric mean abundance.

719
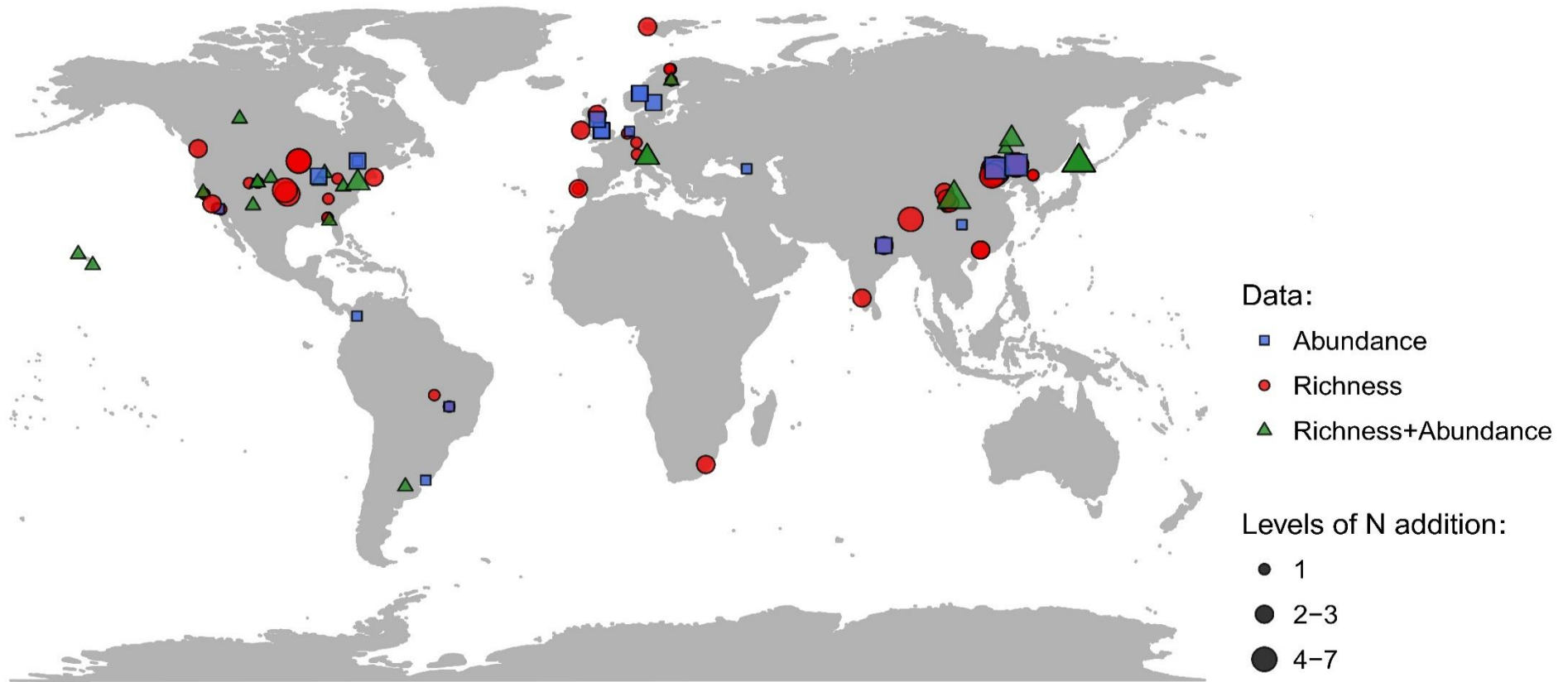
Figure 2: Geographical distribution of the studies included in the meta-analysis. Studies included experiments reporting on species richness only (=

red circles); abundance only (= blue squares); or both species richness and abundance (= green triangles). Point size depicts the number of observations

available (i.e. the number of N addition level) from each experiment.

723

724
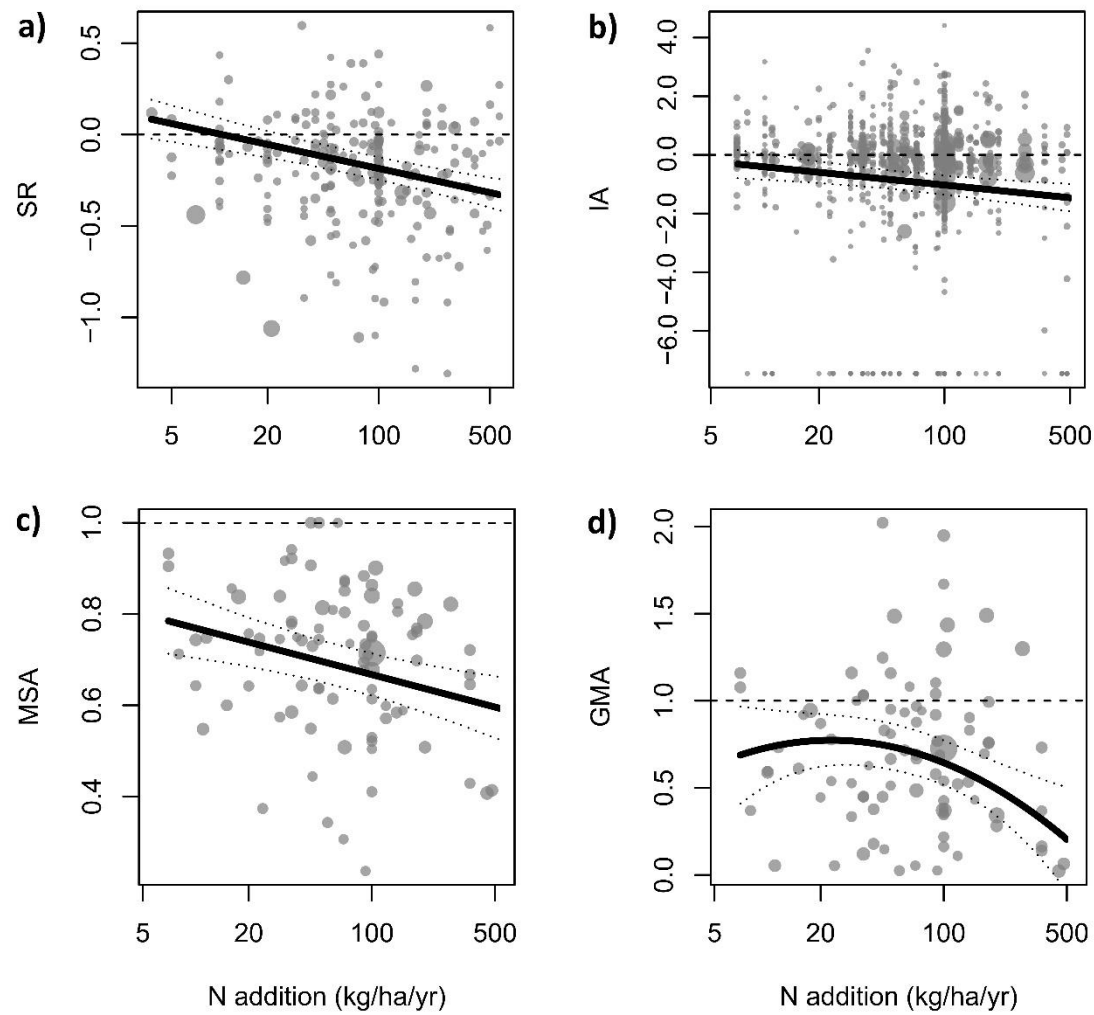
Figure 3: Effect of yearly N addition amount (kg N ha^{-1}yr^{-1}) on plant biodiversity metrics: a) species richness (SR); b) individual species abundance (IA); c) mean species abundance (MSA); and d) geometric mean abundance (GMA). Solid lines represent model predictions with log-transformed yearly N addition as moderator only, allowing for quadratic term inclusion when significantly improving the goodness of fit (the dotted lines represent the corresponding 95% CI bounds). The dashed lines indicate no biodiversity change compared to the control. Point size depicts observation weight.

731

732
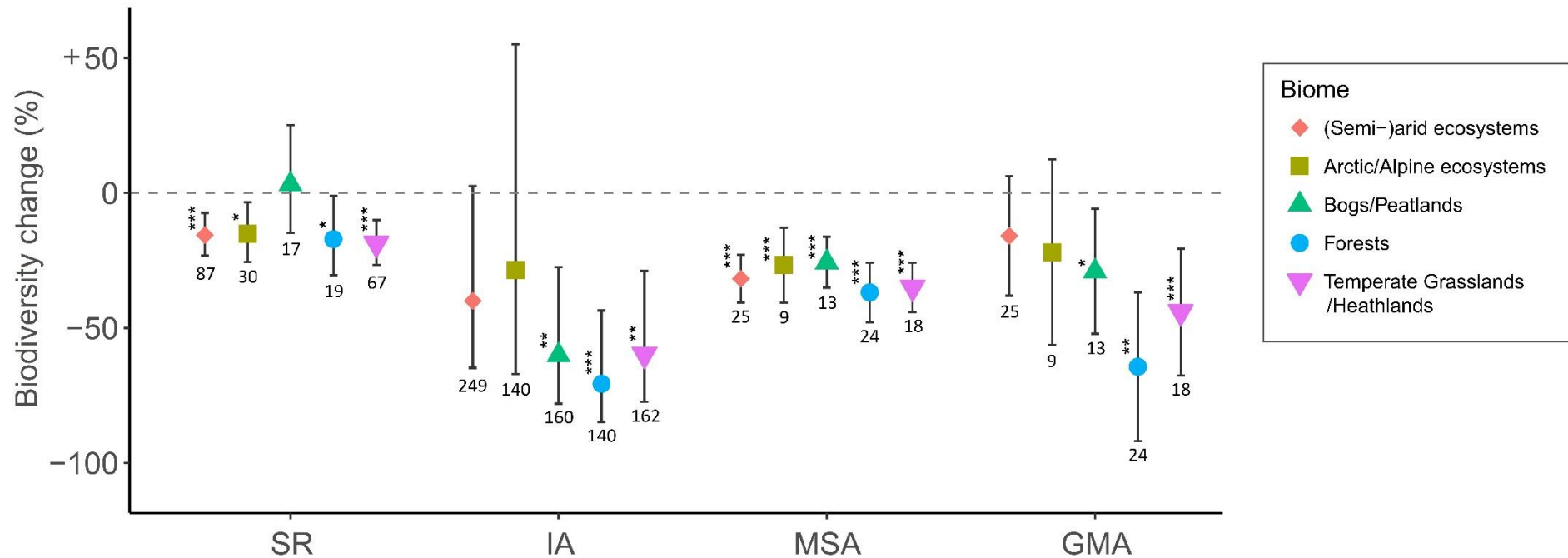
Figure 4: Mean pooled biodiversity change (and 95% CI) per ecosystem type, expressed as percentage of change in N addition plots compared to

control plots. Biodiversity change is quantified with species richness (SR), individual species abundance (IA), mean species abundance (MSA), and

geometric mean abundance (GMA). Values are obtained by fitting the models without the intercept term, to estimate the mean pooled effect of each

level. Significance level (*$P < 0.01$; **$P < 0.001$; ***$P < 0.0001$) and number of observation is provided for each estimate.

737
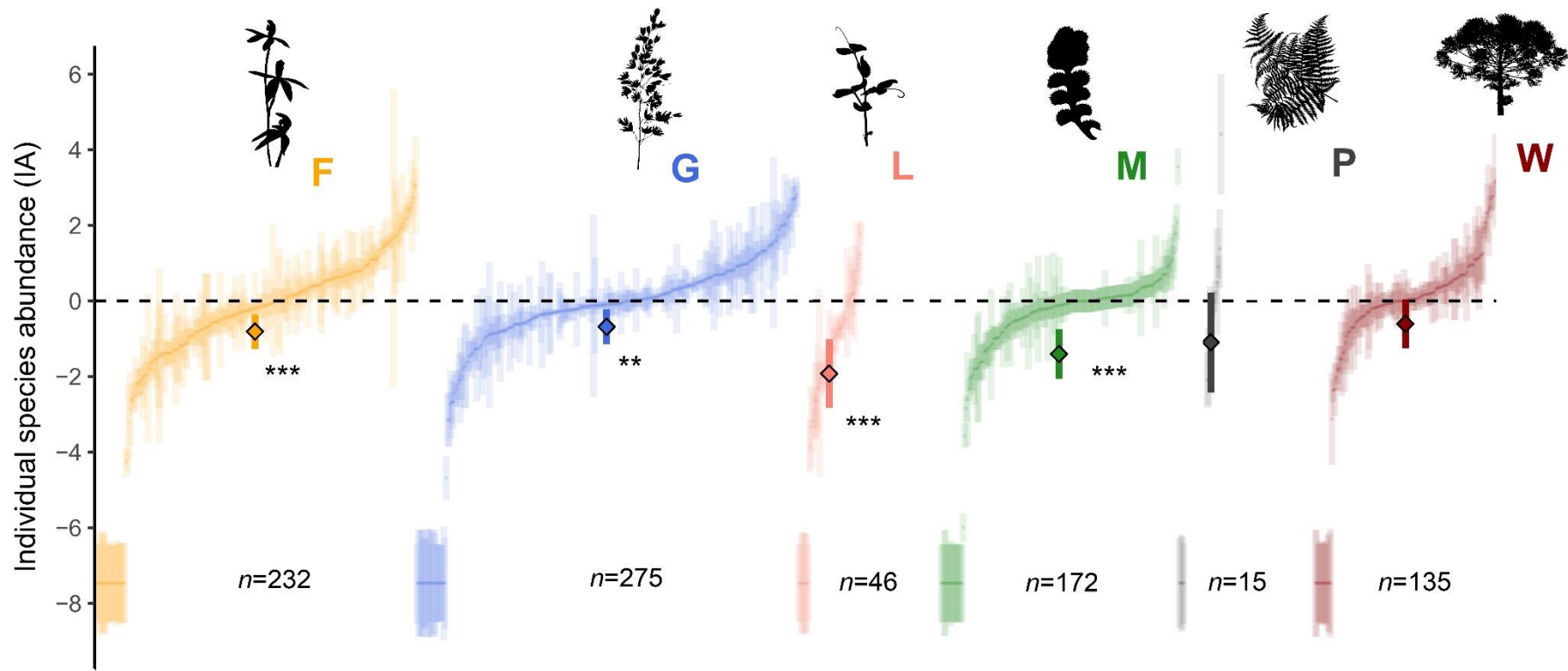
Figure 5: Individual species abundance ratios (and 95% CI) for forbs (F), graminoids (G), leguminosae (L), non-vascular plants (M), ferns (P) and woody species (W) (*n* = number of observations of each plant life-form type). Extremely negative effect sizes indicate the extirpation of species in the treatment plots. Diamonds represent overall weighted mean effect size estimate for each group (and 95% CI). Significance levels are provided for each mean estimate (**$P < 0.001$; ***$P < 0.0001$). The values are obtained by running the model without the intercept term to estimate the mean pooled effect of each level.

Appendix A – Data Sources

Alatalo, J. M., Little, C. J., Jägerbrand, A. K., & Molau, U. (2015). Vascular plant abundance and diversity in an alpine heath under observed and simulated global change. *Scientific reports*, 5, 10197. https://doi.org/10.1038/srep10197

Bai, Z., Gao, Y., Xing, F., Sun, S., Jiao, D., Wei, X.,. . . Michalet, R. (2015). Responses of two contrasting saline-alkaline grassland communities to nitrogen addition during early secondary succession. *Journal of Vegetation Science*, 26(4), 686–696. https://doi.org/10.1111/jvs.12282

Beck, J. J., Hernández, D. L., Pasari, J. R., & Zavaleta, E. S. (2015). Grazing maintains native plant diversity and promotes community stability in an annual grassland. *Ecological Applications*, 25(5), 1259–1270. https://doi.org/10.1890/14-1093.1

Bird, E. J., & Choi, Y. D. (2017). Response of native plants to elevated soil nitrogen in the sand dunes of Lake Michigan, USA. *BIOLOGICAL CONSERVATION*, 212, 398–405. https://doi.org/10.1016/j.biocon.2016.12.001

Borer, E. T., Seabloom, E. W., Mitchell, C. E., & Cronin, J. P. (2014). Multiple nutrients and herbivores interact to govern diversity, productivity, composition, and infection in a successional grassland. *OIKOS*, 123(2), 214–224. https://doi.org/10.1111/j.1600-0706.2013.00680.x

Bowman, W. D., Theodose, T. A., Schardt, J. C., & Conant, R. T. (1993). Constraints of Nutrient Availability on Primary Production in Two Alpine Tundra Communities. *ECOLOGY*, 74(7), 2085–2097. https://doi.org/10.2307/1940854

Brancaleoni, L., & Gerdol, R. (2014). Habitat-dependent interactive effects of a heatwave and experimental fertilization on the vegetation of an alpine mire. *Journal of Vegetation Science*, 25(2), 427–438. https://doi.org/10.1111/jvs.12085

Britton, A. J., & Fisher, J. M. (2007). Interactive effects of nitrogen deposition, fire and grazing on diversity and composition of low-alpine prostrate Calluna vulgaris heathland. *Journal of Applied Ecology*.

Bustamante, M. M. C., Brito, D. Q. de, Kozovits, A. R., Luedemann, G., de Mello, Thiago R. B., Siqueira Pinto, A. de,. . . Takahashi, F. S. C. (2012). Effects of nutrient additions on plant biomass and diversity of the herbaceous-subshrub layer of a Brazilian savanna (Cerrado). *Plant Ecology*, 213(5), 795–808. https://doi.org/10.1007/s11258-012-0042-4

Carpenter, A. T., Moore, J. C., Redente, E. F., & Stark, J. C. (1990). Plant community dynamics in a semi-arid ecosystem in relation to nutrient addition following a major disturbance. *PLANT AND SOIL*, 126(1), 91–99. https://doi.org/10.1007/BF00041373

Carroll, J.A., Caporn, S.J.M., Johnson, D., Morecroft, M.D., & Lee, J.A. (2003). The interactions between plant growth, vegetation structure and soil processes in semi-natural acidic and calcareous grasslands receiving long-term inputs of simulated pollutant nitrogen deposition. *ENVIRONMENTAL POLLUTION*, 121(3), 363–376. https://doi.org/10.1016/S0269-7491(02)00241-5

Chapman, S. K., Devine, K. A., Curran, C., Jones, R. O., & Gilliam, F. S. (2016). Impacts of Soil Nitrogen and Carbon Additions on Forest Understory Communities with a Long Nitrogen Deposition History. *Ecosystems*, 19(1), 142–154. https://doi.org/10.1007/s10021-015-9922-5

Chen, W., Zhang, Y., Mai, X., & Shen, Y. (2016). Multiple mechanisms contributed to the reduced stability of Inner Mongolia grassland ecosystem following nitrogen enrichment. *PLANT AND SOIL*, 409(1-2), 283–296. https://doi.org/10.1007/s11104-016-2967-1

Clark, C. M., & Tilman, D. (2008). Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature*, 451(7179), 712–715. https://doi.org/10.1038/nature06503

Dias, T., Malveiro, S., Martins-Loução, M. A., Sheppard, L. J., & Cruz, C. (2011). Linking N-driven biodiversity changes with soil N availability in a Mediterranean ecosystem. *PLANT AND SOIL*, 341(1), 125–136. https://doi.org/10.1007/s11104-010-0628-3

Du, E. (2017). Integrating species composition and leaf nitrogen content to indicate effects of nitrogen deposition. *ENVIRONMENTAL POLLUTION*, *221*, 392–397. https://doi.org/10.1016/j.envpol.2016.12.001

Fang, Y., Xun, F., Bai, W., Zhang, W., & Li, L. (2012). Long-Term Nitrogen Addition Leads to Loss of Species Richness Due to Litter Accumulation and Soil Acidification in a Temperate Steppe. *PLOS ONE*, *7*(10), e47369. https://doi.org/10.1371/journal.pone.0047369

Faust, C., Storm, C., & Schwabe, A. (2012). Shifts in plant community structure of a threatened sandy grassland over a 9-yr period under experimentally induced nutrient regimes: Is there a lag phase? *Journal of Vegetation Science*, *23*(2), 372–386. https://doi.org/10.1111/j.1654-1103.2011.01355.x

Foster, B. L., & Gross, K. L. (1998). Species richness in a successional grassland: Effects of nitrogen enrichment and plant litter. *(None)*. Retrieved from https://kuscholarworks.ku.edu/bitstream/1808/16489/1/FosterB_Ecology_79%288%292593.pdf

Fremstad, E. L.I., Paal, J., & Möls, T. (2005). Impacts of increased nitrogen supply on Norwegian lichen-rich alpine communities: A 10-year experiment. *Journal of Ecology*, *93*(3), 471–481. https://doi.org/10.1111/j.1365-2745.2005.00995.x

Gasarch, E. I., & Seastedt, T. R. (2016). Plant community response to nitrogen and phosphorus enrichment varies across an alpine tundra moisture gradient. *Plant Ecology & Diversity*, *8*(5-6), 739–749. https://doi.org/10.1080/17550874.2015.1123317

Gilliam, F. S., Hockenberry, A. W., & Adams, M. B. (2006). *Effects of atmospheric nitrogen deposition on the herbaceous layer of a central Appalachian hardwood forest*. Retrieved from https://www.fs.fed.us/nrs/pubs/jrnl/2006/nrs_2006_gilliam_001.pdf

Gornish, E. S., & Miller, T. E. (2015). Plant community responses to simultaneous changes in temperature, nitrogen availability, and invasion. *PLOS ONE*, *10*(4), e0123715. https://doi.org/10.1371/journal.pone.0123715

Hardpole, W. S., Potts, D. L., & Suding, K. N. (2007). Ecosystem responses to water and nitrogen amendment in a California grassland. *Global Change Biology*, *13*(11), 2341–2348. https://doi.org/10.1111/j.1365-2486.2007.01447.x

He, F., & Barclay, H. J. (2000). Long-term response of understory plant species to thinning and fertilization in a Douglas-fir plantation on southern Vancouver Island, British Columbia. *Canadian Journal of Forest Research*, *30*(4), 566–572. https://doi.org/10.1139/x99-237

Heijmans, Monique M. P. D., Berendse, F., Arp, W. J., Masselink, A. K., Klees, H., Visser, W. de, & van Breemen, N. (2001). Effects of elevated carbon dioxide and increased nitrogen deposition on bog vegetation in the Netherlands. *Journal of Ecology*, *89*(2), 268–279. https://doi.org/10.1046/j.1365-2745.2001.00547.x

Huang, Y., Kang, R., Mulder, J., Zhang, T., & Duan, L. (2015). Nitrogen saturation, soil acidification, and ecological effects in a subtropical pine forest on acid soil in southwest China. *Journal of Geophysical Research: Biogeosciences*, *120*(11), 2457–2472. https://doi.org/10.1002/2015JG003048

Jacobson, T. K. B., Bustamante, M. M. d. C., & Kozovits, A. R. (2011). Diversity of shrub tree layer, leaf litter decomposition and N release in a Brazilian Cerrado under N, P and N plus P additions. *Environmental pollution (Barking, Essex : 1987)*, *159*(10), 2236–2242. https://doi.org/10.1016/j.envpol.2010.10.019

Kirkman, L. K., Giencke, L. M., Taylor, R. S., Boring, L. R., Staudhammer, C. L., & Mitchell, R. J. (2016). Productivity and species richness in longleaf pine woodlands: Resource-disturbance influences across an edaphic gradient. *ECOLOGY*, *97*(9), 2259–2271. https://doi.org/10.1002/ecy.1456

Kwak, J.-H., Chang, S. X., & Naeth, M. A. (2018). Eleven years of simulated deposition of nitrogen but not sulfur changed species composition and diversity in the herb stratum in a boreal forest in western Canada. *Forest Ecology and Management*, *412*, 1–8. https://doi.org/10.1016/j.foreco.2018.01.049

838 Ladwig, L. M., Collins, S. L., Swann, A. L., Xia, Y., Allen, M. F., & Allen, E. B. (2012). Above- and
839   belowground responses to nitrogen addition in a Chihuahuan Desert grassland. *OECOLOGIA*, *169*(1),
840   177–185. https://doi.org/10.1007/s00442-011-2173-z

841 Lan, Z., Jenerette, G. D., Zhan, S., Li, W., Zheng, S., & Bai, Y. (2015). Testing the scaling effects and
842   mechanisms of N-induced biodiversity loss: Evidence from a decade-long grassland experiment. *Journal*
843   *of Ecology*, *103*(3), 750–760. https://doi.org/10.1111/1365-2745.12395

844 Lezama, F., & Paruelo, J. M. (2016). Disentangling grazing effects: Trampling, defoliation and urine
845   deposition. *APPLIED VEGETATION SCIENCE*, *19*(4), 557–566. https://doi.org/10.1111/avsc.12250

846 Li, J., Zhang, C., Yang, Z., Guo, H., Zhou, X., & Du, G. (2017). Grazing and fertilization influence plant
847   species richness via direct and indirect pathways in an alpine meadow of the eastern Tibetan Plateau.
848   *GRASS AND FORAGE SCIENCE*, *72*(2), 343–354. https://doi.org/10.1111/gfs.12232

849 Li, W., Wen, S., Hu, W., & Du, G. (2011). Root–shoot competition interactions cause diversity loss after
850   fertilization: A field experiment in an alpine meadow on the Tibetan Plateau. *Journal of Plant Ecology*,
851   *4*(3), 138–146. https://doi.org/10.1093/jpe/rtq031

852 Lu, X., Mo, J., Gilliam, F. S., Yu, G., Zhang, W., Fang, Y., & Huang, J. (2011). Effects of experimental
853   nitrogen additions on plant diversity in tropical forests of contrasting disturbance regimes in southern
854   China. *Environmental pollution (Barking, Essex : 1987)*, *159*(10), 2228–2235.
855   https://doi.org/10.1016/j.envpol.2010.10.037

856 Madan, N. J., Deacon, L. J., & Robinson, C. H. (2006). Greater nitrogen and/or phosphorus availability
857   increase plant species' cover and diversity at a High Arctic polar semidesert. *Polar Biology*, *30*(5), 559.
858   https://doi.org/10.1007/s00300-006-0213-7

859 Massad, T. J., Balch, J. K., Davidson, E. A., Brando, P. M., Mews, C. L., Porto, P.,. . . Trumbore, S. E.
860   (2013). Interactions between repeated fire, nutrients, and insect herbivores affect the recovery of diversity
861   in the southern Amazon. *OECOLOGIA*, *172*(1), 219–229. https://doi.org/10.1007/s00442-012-2482-x

862 Neill, C., Wheeler, M. M., Loucks, E., Weiler, A., Holle, B. von, Pelikan, M., & Chase, T. (2015). Influence
863   of soil properties on coastal sandplain grassland establishment on former agricultural fields. *Restoration*
864   *Ecology*, *23*(5), 531–538. https://doi.org/10.1111/rec.12196

865 Nilsson, M.-C., Wardle, D. A., Zackrisson, O., & Jäderlund, A. (2002). Effects of alleviation of ecological
866   stresses on an alpine tundra community over an eight-year period. *OIKOS*, *97*(1), 3–17.
867   https://doi.org/10.1034/j.1600-0706.2002.970101.x

868 Nishimura, A., & Tsuyuzaki, S. (2015). Plant responses to nitrogen fertilization differ between post-mined
869   and original peatlands. *Folia Geobotanica*, *50*(2), 107–121. https://doi.org/10.1007/s12224-015-9203-2

870 Niu, D., Yuan, X., Cease, A. J., Wen, H., Zhang, C., Fu, H., & Elser, J. J. (2018). The impact of nitrogen
871   enrichment on grassland ecosystem stability depends on nitrogen addition level. *SCIENCE OF THE*
872   *TOTAL ENVIRONMENT*, *618*, 1529–1538. https://doi.org/10.1016/j.scitotenv.2017.09.318

873 Nohrstedt, H.-Ö. (1998). Residual effects of N fertilization on soil-water chemistry and ground vegetation in
874   a Swedish Scots pine forest. *ENVIRONMENTAL POLLUTION*, *102*(1), 77–83.
875   https://doi.org/10.1016/S0269-7491(98)80018-3

876 Ostertag, R., & Verville, J. H. (2002). Fertilization with nitrogen and phosphorus increases abundance of
877   non-native species in Hawaiian montane forests. *Plant Ecology*, *162*(1), 77–90.
878   https://doi.org/10.1023/A:1020332824836

879 Pan, J. J., Widner, B., Ammerman, D., & Drenovsky, R. E. (2010). Plant community and tissue chemistry
880   responses to fertilizer and litter nutrient manipulations in a temperate grassland. *Plant Ecology*, *206*(1),
881   139–150. https://doi.org/10.1007/s11258-009-9630-3

882 Pan, Q., Bai, Y., Wu, J., & Han, X. (2011). Hierarchical Plant Responses and Diversity Loss after Nitrogen
883   Addition: Testing Three Functionally-Based Hypotheses in the Inner Mongolia Grassland. *PLOS ONE*,
884   *6*(5), e20078. https://doi.org/10.1371/journal.pone.0020078

885 Pauli, D., Peintinger, M., & Schmid, B. (2002). Nutrient enrichment in calcareous fens: Effects on plant
886   species and community structure. *Basic and Applied Ecology*, *3*(3), 255–266.
887   https://doi.org/10.1078/1439-1791-00096

888 Piper, J. K., Billings, D. N., & Leite, V. J. (2005). Effects of nitrogen fertilizer on the composition of two
889   prairie plant communities. *Community Ecology*, *6*(1), 93–100. https://doi.org/10.1556/ComEc.6.2005.1.10

890 Quan, Q., Nianpeng, H., Zhen, Z., Yunhai, Z., & Yang, G. (2015). Nitrogen enrichment and grazing
891   accelerate vegetation restoration in degraded grassland patches. *Ecological Engineering*, *75*, 172–177.
892   https://doi.org/10.1016/j.ecoleng.2014.11.053

893 Roem, W. J., Klees, H., & Berendse, F. (2002). Effects of nutrient addition and acidification on plant species
894   diversity and seed germination in heathland. *Journal of Applied Ecology*, *39*(6), 937–948.
895   https://doi.org/10.1046/j.1365-2664.2002.00768.x

896 Sheppard, L. J., Leith, I. D., Mizunuma, T., Neil Cape, J., Crossley, A., Leeson, S.,. . . Fowler, D. (2011).
897   Dry deposition of ammonia gas drives species change faster than wet deposition of ammonium ions:
898   Evidence from a long-term field manipulation. *Global Change Biology*, *17*(12), 3589–3607.
899   https://doi.org/10.1111/j.1365-2486.2011.02478.x

900 Smith, N. G., Schuster, M. J., Dukes, J. S., & Diamond, S. (2016). Rainfall variability and nitrogen addition
901   synergistically reduce plant diversity in a restored tallgrass prairie. *Journal of Applied Ecology*, *53*(2),
902   579–586. https://doi.org/10.1111/1365-2664.12593

903 Song, L., Bao, X., Liu, X., Zhang, Y., Christie, P., Fangmeier, A., & Zhang, F. (2011). Nitrogen enrichment
904   enhances the dominance of grasses over forbs in a temperate steppe ecosystem. *Biogeosciences*, *8*(8),
905   2341–2350. https://doi.org/10.5194/bg-8-2341-2011

906 Song, M.-H., Yu, F.-H., Ouyang, H., Cao, G.-M., Xu, X.-L., & Cornelissen, J. H.C. (2012). Different inter-
907   annual responses to availability and form of nitrogen explain species coexistence in an alpine meadow
908   community after release from grazing. *Global Change Biology*, *18*(10), 3100–3111.
909   https://doi.org/10.1111/j.1365-2486.2012.02738.x

910 Soudzilovskaia, N. A., & Onipchenko, V. G. (2005). Experimental Investigation of Fertilization and
911   Irrigation Effects on an Alpine Heath, Northwestern Caucasus, Russia. *Arctic, Antarctic, and Alpine*
912   *Research*, *37*(4), 602–610. https://doi.org/10.1657/1523-0430(2005)037[0602:EIOFAI]2.0.CO;2

913 Souza, L., Zelikova, T. J., & Sanders, N. J. (2016). Bottom-up and top-down effects on plant communities:
914   Nutrients limit productivity, but insects determine diversity and composition. *OIKOS*, *125*(4), 566–575.
915   https://doi.org/10.1111/oik.02579

916 Srinivasan, M. P., Gleeson, S. K., & Arthur, M. A. (2012). Short-term impacts of nitrogen fertilization on a
917   montane grassland ecosystem in a South Asian biodiversity hotspot. *Plant Ecology & Diversity*, *5*(3),
918   289–299. https://doi.org/10.1080/17550874.2012.727486

919 Sun, X., Yu, K., Shugart, H. H., & Wang, G. (2016). Species richness loss after nutrient addition as affected
920   by N:C ratios and phytohormone GA3 contents in an alpine meadow community. *Journal of Plant*
921   *Ecology*, *9*(2), 201–211. https://doi.org/10.1093/jpe/rtv037

922 Sundqvist, M. K., Liu, Z., Giesler, R., & Wardle, D. A. (2014). Plant and microbial responses to nitrogen and
923   phosphorus addition across an elevational gradient in subarctic tundra. *ECOLOGY*, *95*(7), 1819–1835.
924   https://doi.org/10.1890/13-0869.1

925 Tilman, D. (1993). Species Richness of Experimental Productivity Gradients: How Important is Colonization
926   Limitation? *ECOLOGY*, *74*(8), 2179–2191. https://doi.org/10.2307/1939572

927 Tognetti, P. M., & Chaneton, E. J. (2015). Community disassembly and invasion of remnant native
928   grasslands under fluctuating resource supply. *Journal of Applied Ecology*, *52*(1), 119–128.
929   https://doi.org/10.1111/1365-2664.12349

930 Urbina, J. C., & Benavides, J. C. (2015). Simulated Small Scale Disturbances Increase Decomposition Rates
931   and Facilitates Invasive Species Encroachment in a High Elevation Tropical Andean Peatland.
932   *Biotropica*, *47*(2), 143–151. https://doi.org/10.1111/btp.12191

933 Verhoeven, J.T.A., Beltman, B., Dorland, E., Robat, S. A., & Bobbink, R. (2011). Differential effects of
934   ammonium and nitrate deposition on fen phanerogams and bryophytes. *APPLIED VEGETATION*
935   *SCIENCE*, *14*(2), 149–157. https://doi.org/10.1111/j.1654-109X.2010.01113.x

936 Verma, P., Sagar, R., Verma, H., Verma, P., & Singh, D. K. (2015). Changes in species composition,
937   diversity and biomass of herbaceous plant traits due to N amendment in a dry tropical environment of
938   India. *Journal of Plant Ecology*, *8*(3), 321–332. https://doi.org/10.1093/jpe/rtu018

939 Verma, P., Verma, P., & Sagar, R. (2013). Variations in N mineralization and herbaceous species diversity
940   due to sites, seasons, and N treatments in a seasonally dry tropical environment of India. *Forest Ecology*
941   *and Management*, *297*, 15–26. https://doi.org/10.1016/j.foreco.2013.02.006

942 Vourlitis, G. L. (2017). Chronic N enrichment and drought alter plant cover and community composition in a
943   Mediterranean-type semi-arid shrubland. *OECOLOGIA*, *184*(1), 267–277.
944   https://doi.org/10.1007/s00442-017-3860-1

945 Vourlitis, G. L., & Pasquini, S. C. (2009). Experimental dry-season N deposition alters species composition
946   in southern Californian mediterranean-type shrublands. *ECOLOGY*, *90*(8), 2183–2189.
947   https://doi.org/10.1890/08-1121.1

948 Wang, J., Knops, J. M. H., Brassil, C. E., & Mu, C. (2017). Increased productivity in wet years drives a
949   decline in ecosystem stability with nitrogen additions in arid grasslands. *ECOLOGY*, *98*(7), 1779–1786.
950   https://doi.org/10.1002/ecy.1878

951 Wang, M., Larmola, T., Murphy, M. T., Moore, T. R., & Bubier, J. L. (2016). Stoichiometric response of
952   shrubs and mosses to long-term nutrient (N, P and K) addition in an ombrotrophic peatland. *PLANT AND*
953   *SOIL*, *400*(1-2), 403–416. https://doi.org/10.1007/s11104-015-2744-6

954 Ward, D., Kirkman, K., & Tsvuura, Z. (2017). An African grassland responds similarly to long-term
955   fertilization to the Park Grass experiment. *PLOS ONE*, *12*(5).
956   https://doi.org/10.1371/journal.pone.0177208

957 Wardle, D. A., Gundale, M. J., Jäderlund, A., & Nilsson, M.-C. (2013). Decoupled long-term effects of
958   nutrient enrichment on aboveground and belowground properties in subalpine tundra. *ECOLOGY*, *94*(4),
959   904–919. https://doi.org/10.1890/12-0948.1

960 Wilson, S. D., & Tilman, D. (1991). Interactive effects of fertilization and disturbance on community
961   structure and resource availability in an old-field plant community. *OECOLOGIA*, *88*(1), 61–71.
962   https://doi.org/10.1007/BF00328404

963 Xu, D., Fang, X., Zhang, R., Gao, T., Bu, H., & Du, G. (2015). Influences of nitrogen, phosphorus and
964   silicon addition on plant productivity and species richness in an alpine meadow. *AoB PLANTS*, *7*.
965   https://doi.org/10.1093/aobpla/plv125

966 Xu, X., Liu, H., Song, Z., Wang, W., Hu, G., & Qi, Z. Response of aboveground biomass and diversity to
967   nitrogen addition along a degradation gradient in the Inner Mongolian steppe, China. *Scientific reports*, *5*,
968   10284. https://doi.org/10.1038/srep10284

969 Xu, Z., Ren, H., Cai, J., Wang, R., He, P., Li, M.-H.,. . . Jiang, Y. (2015). Antithetical effects of nitrogen and
970   water availability on community similarity of semiarid grasslands: Evidence from a nine-year
971   manipulation experiment. *PLANT AND SOIL*, *397*(1), 357–369. https://doi.org/10.1007/s11104-015-
972   2634-y

973 Xu, Z., Wan, S., Ren, H., Han, X., Li, M.-H., Cheng, W., & Jiang, Y. (2012). Effects of Water and Nitrogen
974   Addition on Species Turnover in Temperate Grasslands in Northern China. *PLOS ONE*, *7*(6), e39762.
975   https://doi.org/10.1371/journal.pone.0039762

976 Yang, H., Li, Y., Wu, M., ZHANG, Z. H.E., Li, L., & Wan, S. (2011). Plant community responses to
977   nitrogen addition and increased precipitation: The importance of water availability and species traits.
978   *Global Change Biology*, *17*(9), 2936–2944. https://doi.org/10.1111/j.1365-2486.2011.02423.x

979 Yu, L., Song, X.-L., Zhao, J.-N., Wang, H., Bai, L., & Yang, D.-l. (2015). Responses of plant diversity and
980   primary productivity to nutrient addition in a Stipa baicalensis grassland, China. *Journal of Integrative*
981   *Agriculture*, *14*(10), 2099–2108. https://doi.org/10.1016/S2095-3119(14)61001-7

982 Zavaleta, E. S., Shaw, M. R., Chiariello, N. R., Thomas, B. D., Cleland, E. E., Field, C. B., & Mooney, H. A.
983   (2003). Grassland responses to three years of elevated temperature, CO2, precipitation, and N deposition.
984   *Ecological Monographs*, *73*(4), 585–604. https://doi.org/10.1890/02-4053

985 Zeng, D.-H., Li, L.-J., Fahey, T. J., Yu, Z.-Y., Fan, Z.-P., & Chen, F.-S. (2010). Effects of nitrogen addition
986   on vegetation and ecosystem carbon in a semi-arid grassland. *Biogeochemistry*, *98*(1), 185–193.
987   https://doi.org/10.1007/s10533-009-9385-x

988 Zhang, T., Guo, R., Gao, S., Guo, J., & Sun, W. (2015). Responses of Plant Community Composition and
989   Biomass Production to Warming and Nitrogen Deposition in a Temperate Meadow Ecosystem. *PLOS*
990   *ONE*, *10*(4), e0123160. https://doi.org/10.1371/journal.pone.0123160

991 Zhang, X., Liu, W., Bai, Y., Zhang, G., & Han, X. (2011). Nitrogen deposition mediates the effects and
992   importance of chance in changing biodiversity. *Molecular ecology*, *20*(2), 429–438.
993   https://doi.org/10.1111/j.1365-294X.2010.04933.x

994 Zhou, X., Wang, Y., Zhang, P., Guo, Z., Chu, C., & Du, G. (2016). The effects of fertilization on the trait–
995   abundance relationships in a Tibetan alpine meadow community. *Journal of Plant Ecology*, *9*(2), 144–
996   152. https://doi.org/10.1093/jpe/rtv043

997 Zong, N., Shi, P., Song, M., Zhang, X., Jiang, J., & Chai, X. (2016) [A]. Nitrogen Critical Loads for an Alpine
998   Meadow Ecosystem on the Tibetan Plateau. *Environmental management*, *57*(3), 531–542.
999   https://doi.org/10.1007/s00267-015-0626-6

1000 Zong, S., Jina, Y., Xu, J., Wu, Z., He, H., Du, H., & Wang, L. (2016) [B]. Nitrogen deposition but not climate
1001   warming promotes Deyeuxia angustifolia encroachment in alpine tundra of the Changbai Mountains,
1002   Northeast China. *SCIENCE OF THE TOTAL ENVIRONMENT*, *544*, 85–93.
1003   https://doi.org/10.1016/j.scitotenv.2015.11.144

1004

1005 **Supporting Information**

1006 **Appendix S1:** Search string for primary studies collection

1007 **Appendix S2:** Summary of primary studies included in the meta-analysis

1008 **Appendix S3:** Influencing factors on plant diversity response to N addition

1009 **Appendix S4:** Description of categorical variables (ecosystem types, fertilizers and plant life-form

1010 types)

1011 **Appendix S5:** Mean pooled effect sizes and funnel plots of the null-model residuals

1012 **Appendix S6:** Detailed model outputs of best meta-regression models