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

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Abstract

Aim: Experimental nitrogen (N) addition (fertilization) studies are commonly used to quantify the impacts of increased N inputs on plant biodiversity. However, given that plant community responses can vary considerably among individual studies, there is a clear need to synthesize and generalize findings with meta-analytical approaches. Our goal was to quantify changes in species richness and abundance in plant communities in response to N addition across different environmental contexts, while controlling for different experimental designs.

Location: Global.

Time period: Data range: 1985–2016; Publication years: 1990–2018.

Major taxa studied: Plants.

Methods: We performed a meta-analysis of 115 experiments reported in 85 studies assessing the effects of N addition on terrestrial natural and semi-natural plant communities. We quantified local-scale changes in plant biodiversity in relationship to N addition using four metrics: species richness (SR), individual species abundance (IA), mean species abundance (MSA) and geometric mean abundance (GMA).

Results: For all metrics, greater amounts of annual N addition resulted in larger declines in plant diversity. Additionally, MSA decreased more steeply with N that was applied in reduced (NH_4^+) rather than oxidized (NO_3^-) form. Loss of SR with increasing amounts of N was found to be larger in warmer sites. Furthermore, greater losses of SR were found in sites with longer experimental durations, smaller plot sizes and lower soil cation exchange capacity. Finally, reductions in the abundance of individual species were larger for N-sensitive plant life-form types (legumes and non-vascular plants).

Main conclusions: N enrichment decreases both SR and abundance of plants in N-addition experiments, but the magnitude of the response differs among biodiversity metrics and with the environmental and experimental context. This underlines the importance of integrating multiple dimensions of biodiversity and relevant modifying factors into assessments of biodiversity responses to global environmental change.

KEYWORDS
anthropogenic impacts, biodiversity, eutrophication, global change, GLOBIO, soil acidification, vegetation

1 | 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 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 (Perring, Diekmann, et al., 2018; Simkin et al., 2016; Vellend et al., 2017). 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); 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, because this might drive the composition and function of plant communities into different trajectories of change (Perring, Bernhardt-Römermann, et al., 2018).

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, & Gowing, 2010) or over a spatial gradient (e.g., Duprè et al., 2010; Jones et al., 2004). Observational gradient studies can benefit from existing datasets (e.g., Simkin et al., 2016) but need to correct for confounding site factors and cannot prove causality (Dise et al., 2011). Experimental studies, in contrast, allow for effects to be attributed directly to N addition. However, experimental studies typically assess relatively short-term responses only and often use higher levels of N addition compared with atmospheric deposition in the field. Furthermore, the results might be influenced by experimental design and local environmental conditions, which limit the possibilities for regional and global extrapolation (Hettelingh et al., 2015). The latter might be solved by setting up globally distributed experiments, such as the Nutrient Network (Borer et al., 2014; Firn et al., 2011), but also by synthesizing multiple N-addition experiments with a meta-analysis, allowing the derivation of a more general quantitative response of plant species diversity to N enrichment.

Previous meta-analyses that addressed impacts of N on plant assemblages focused on species richness (SR) or biomass in specific ecosystems (i.e., Humbert et al., 2016; Limpens et al., 2011) or in specific geographical regions (i.e., Clark et al., 2007; Fu & Shen, 2016) or continents (i.e., De Schrijver et al., 2011; Soons et al., 2017). To our knowledge, a systematic meta-analysis covering multiple dimensions of biodiversity in multiple ecosystems across the globe is lacking. In addition to covering a large geographical extent, it is particularly important to consider metrics beyond SR, such as measures of species abundance, because different aspects of biodiversity may respond differently to environmental change (Dornelas et al., 2014; Schipper et al., 2016; Winfree, Fox, Williams, Reilly, & Cariveau, 2015). In this study, we synthesized a large number of N-addition studies worldwide, in order to reveal the overall effects of N addition on various metrics of local plant biodiversity and explore the role of potential experimental (amount of yearly N applied, experimental duration, type of fertilizer and plot size) and environmental [temperature, precipitation, soil pH, soil cation exchange capacity (CEC) and atmospheric N deposition] moderators (Figure 1a). We considered four metrics of biodiversity change to incorporate richness and abundance as two essential dimensions of biodiversity (Schipper et al., 2016) (Figure 1b): species richness (SR), individual species abundance (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 amounts of N addition 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 of N addition will occur in sites with low soil pH and low atmospheric N deposition, because 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 forms of N (NH_4^+) will result in higher impacts on plant diversity than oxidized forms (NO_3^-), because reduced N tends to acidify the soil strongly and disadvantage the nutrient uptake of N-poor-adapted species (Song et al., 2012; van den Berg, Peters, Ashmore, & Roelofs, 2008). We further hypothesized that species losses would be larger in larger experimental plots, because these have higher chances of including rare species, which may also be more likely to go extinct in the treatment plots. Higher impacts were also expected in sites with low soil CEC, because lower CEC indicates higher susceptibility to acidification in response to N addition (Clark et al., 2007; De Vries, Posch, & Kämäri, 1989). 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 mineralization rates, hence enhanced N availability after fertilization (Dise et al., 2011; Yang, Ryals, Cusack, & Silver, 2017).
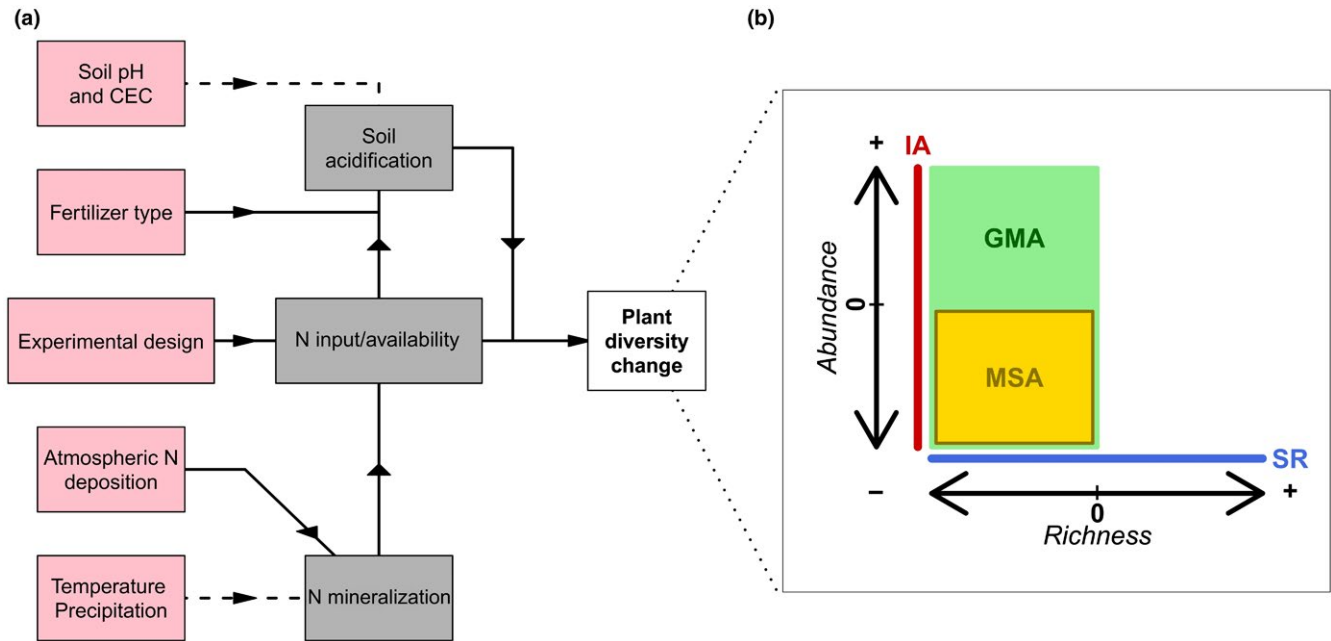
FIGURE 1 (a) Graphical representation of relationships between key factors (i.e., moderators; pink boxes) and fundamental processes (grey boxes) that trigger plant species responses in N-addition experiments. Solid arrows represent direct effects, whereas dashed arrows represent context-dependent effects (i.e., in the experiments, the extent of soil acidification and N mineralization may be positively or negatively affected by soil fertility and climatic conditions, respectively). (b) Graphical representation of 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. CEC = cation exchange capacity; GMA = geometric mean abundance; IA = individual species abundance; MSA = mean species abundance; SR = species richness. Note that the real values of MSA are limited between zero and one (see Figure 3c), with MSA = 1 indicating no change (i.e., "0" on the figure axes)

2 | METHODS

2.1 | 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 experiments and different dimensions of plant species diversity, for example ("nitrogen fertilization" OR "nitrogen addition") AND ("abundance" OR "composition" OR "number" OR "richness") (see the complete search strings in Supporting Information Appendix S1). We selected relevant studies based on the title and abstract, and then scanned their full texts and supporting materials to extract data on N-addition experiments. Where factorial treatment combinations were present, we retained data from control and N-addition plots alone to avoid confounding effects. Thus, we excluded data from plots where N addition was performed together with watering, temperature increase, litter removal, grazing or fire manipulation or where N was added in combination with other nutrients. We limited our selection to experiments conducted on natural or semi-natural vegetation, excluding studies conducted on crops, mono-cultures or where species were artificially introduced in plots. Finally, we removed studies that reported the same data as other studies already included in our database. To avoid over-representation, we

collected data on SR and abundance change at the final year of each experiment.

Our literature search yielded a total of 2,314 studies, of which we selected 85 relevant studies (published between March 1990 and January 2018) that reported data from 115 N-addition experiments performed between 1985 and 2016 in different geographical locations (Figure 2; Supporting Information Appendix S2, Table S2.1). Of the 85 studies, 48 reported data on SR, 15 on IA, and 22 on both SR and abundance (a list of the data sources is given in the Appendix: Data sources). We extracted the number of species and species-specific abundance data separately from treatment and control plots and calculated the four biodiversity metrics as described in Table 1. Abundance data were extracted for each species reported in both the treatment and control plots, for a total of 403 taxa. The majority of these were identified to species level, but 32 were indicated with the genus name only. Thus, the total number of species in our dataset might be slightly overestimated. We recorded a total of 220 pairwise comparisons for SR. At the species level, we included 871 IA comparisons, some across multiple N-fertilization levels within the same experiment, which resulted in 89 observations for MSA and GMA. Nitrogen-addition levels ranged from 3.75 to 572 kg N/ha/year in the SR dataset (mean = 124.8 kg/ha/year; median = 92 kg/ha/year), and from 7 to 480 kg N/ha/year in the species abundance dataset (mean = 96.5 kg N/ha/year; median = 70 kg N/ha/year).
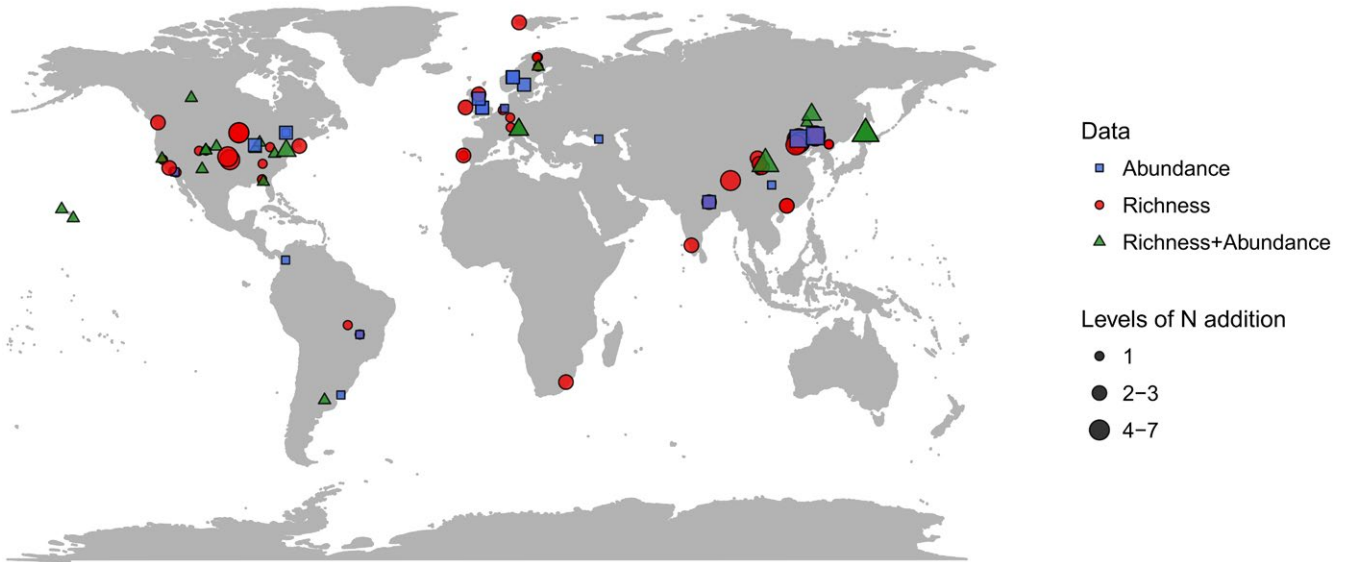
FIGURE 2 Geographical distribution of the studies included in the meta-analysis. Studies included experiments reporting on species richness only (= red circles); abundance only (= blue squares); or both species richness and abundance (= green triangles). Point size depicts the number of observations available (i.e., the number of N-addition level) from each experiment

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)[a]	$IA = \ln\left(\frac{\bar{A}_T}{\bar{A}_C}\right)$	Inverse of the sampling variance	Benítez-López et al. (2017)
Mean species abundance (MSA)	Mean of the individual species abundance response ratios (truncated at one if $A_T > A_C$). n is the number of species in each observation	$MSA = \frac{\sum_{\bar{A}_T < \bar{A}_C} \left(\frac{\bar{A}_T}{\bar{A}_C}\right) + \sum_{\bar{A}_T \geq \bar{A}_C} 1}{n}$	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 the number of species in each observation	$GMA = \exp\left(\frac{\sum [\ln(\bar{A}_T) - \ln(\bar{A}_C)]}{n}\right)$	Number of replicates	Buckland et al. (2011)
				Schipper et al. (2016)
				Santini et al. (2017)

[a]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 "Methods").

2.2 | Calculation of the effect sizes

We calculated four biodiversity metrics for the meta-analysis, including the SR ratio, IA ratio, MSA and GMA (Table 1). Both SR and IA were obtained by log-transforming the ratio between the SR and IA in each N-treatment plot and control plot, respectively (Hedges, Gurevitch, & Curtis, 1999). Some species had zero abundance in treatment plots, precluding log-transformation for IA calculation. Therefore, we transformed IA effect sizes using a modification of the transformation proposed by Smithson and Verkuilen (2006) to shrink the ratios and avoid zero values (Benítez-López et al., 2017) (Equation 1):

$$y_i = \frac{(y \times n + 0.5)}{n} \qquad (1)$$

where y is the ratio (A_T/A_C) of IA in the treatment (A_T) and control (A_C), and n is the number of observations in the IA dataset (n = 871). This resulted in a distribution of ratios (y_i) slightly displaced toward larger values (before transformation: [0, 82.5]; after transformation: [0.0006, 82.5006]). The new ratios were then log-transformed to obtain IA. Given that ratios A_T/A_C cannot be calculated when abundance in the control is equal to zero, we decided to exclude species that were present only in the treatments from the calculation of the IA and GMA metrics, following the definitions and approaches applied in previous studies (Table 1).

We calculated MSA as the mean of the ratios of IA in each treatment versus the corresponding control (Alkemade et al., 2009; Benítez-López, Alkemade, & Verweij, 2010). Following the definition of MSA, the individual ratios were truncated at one for species with a higher abundance in the treatment group compared with the control group (Table 1). Given that MSA captures losses 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, 2011) also combines abundance and SR into one index but allows for gains in the abundance dimension (Figure 1b).

2.3 | Moderators

Factors influencing plant community responses to N were selected a priori based on literature study (Figure 1a; Supporting Information Appendix S3, Table S3.1) and data availability. Nine moderators were considered in the analysis: (a) the annual amount of N added in the experiment (in kilograms of N per hectare per year); (b) the annual amount of background N deposition (in kilograms of N per hectare per year; i.e., the amount of N deposited from the atmosphere, which is independent of the experimental N addition); (c) mean annual temperature (in degrees Celsius); (d) mean annual precipitation (in millimetres per year); (e) duration of the experiment (number of years of N addition); (f) 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 Supporting Information Appendix S4, Table S4.1); (g) plot size (in square metres; i.e., the area of vegetation surveyed to estimate richness or abundance in each experiment); (h) initial soil pH at the experimental sites (estimated before N addition); and (i) soil CEC (in centimole kilograms). Additionally, we examined overall biodiversity responses among the ecosystem types 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 Supporting Information Appendix S4, Table S4.2). Furthermore, we categorized each taxon into plant life-form types (herbaceous forbs, graminoids, legumes, ferns, woody plants and non-vascular plants; see Supporting Information Appendix S4, Table S4.3) and used this to assess possible differences in the individual abundance response among different species groups.

We collected from each study the location (geographical coordinates), experimental set-up (yearly amount of N addition, experimental duration, type of N fertilizer and plot size) and ecosystem type. Given that many studies did not report atmospheric N deposition levels, we collected these data from the global TM5 model for the year 2000 (Dentener et al., 2006). For the same reason, we extracted estimates of CEC and soil pH from the 250-m resolution global SoilGrids data (Hengl et al., 2014, 2017), by averaging values provided for soil depths of 0–5, 5–15 and 15–30 cm. Data on temperature and precipitation were derived from the global Climate Research Unit database, which comprises series of monthly meteorological data on a 0.5° × 0.5° grid (New, Hulme, & Jones, 1999). For each observation, we extracted data for the corresponding year and calculated the mean temperature and precipitation over the 12 monthly values.

2.4 | Data analysis

We performed the meta-analysis using multilevel mixed-effect models to control for non-independence in the data owing to multiple effect sizes per study and species (Nakagawa & Santos, 2012). We first fitted single meta-regression models using yearly N addition as the only moderator, in order to compare changes among the metrics for a given amount of N applied. Then, we fitted multiple meta-regression models by including other moderators and interaction terms between the amount of N addition and these other moderators. Except for mean annual temperature and soil pH, we log-transformed all continuous moderators, because the data showed strong positive skewness, and we scaled and centred all continuous variables. The only moderate correlation among moderators was between mean annual precipitation and soil pH (richness dataset ρ = −.75; abundance dataset ρ = −.68). Based on this, we decided not to exclude any moderators initially. We performed stepwise backward selection based on the Bayesian information criterion (BIC), whereby we excluded a moderator only if it was also dropped from the interaction term. We estimated the amount of heterogeneity reduced in the best models selected and by each moderator using the omnibus Wald-type test of moderators (Benítez-López et al., 2017).

We accounted for the correlation in the true effects, using experiments as the random effect in the models. For the IA metric, we used a crossed random effect structure, including both experiment and species as random components. We nested the individual estimates within the experiment grouping-level in the random structure of the models to account for the possibility that the underlying true effects within experiments are not homogeneous (Konstantopoulos, 2011). Because of non-independence of the effect sizes, we computed the variance–covariance matrix based on Lajeunesse (2011). For SR and IA, the models were fitted with the

rma.mv function of the R package "metafor" (Viechtbauer, 2010). Observations were weighted by the inverse of the sampling variance (Table 1), which we calculated from the standard deviation directly from papers or through personal contact with the authors. We imputed missing standard deviations using the coefficient of variation from all complete cases with the *impute_SD* function of the R package "metagear" (Lajeunesse, 2016). Given that MSA and GMA have a different structure compared with log-transformed response ratios, and standard deviations are not reported for these derived metrics, we used the number of replicates in each experiment to weight the observations (Soons et al., 2017). We fitted multi-level linear mixed-effect models for MSA and GMA with the *lme* function of the R package "nlme" (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017).

Finally, we used null models to estimate the weighted mean pooled effect size, namely the overall amount of plant diversity change across all experiments, independently from the amount of N addition. Based on these models, we also investigated publication bias with visual estimation of the funnel plots (Nakagawa & Santos, 2012). We tested the significance of asymmetry of the funnel plots with the Egger's test by fitting the residuals of the null model with observation precision (1/*SE* or the inverse of the number of replicates) as a moderator (Møller & Jennions, 2001; Nakagawa & Santos, 2012). Results of null models and publication bias are reported in Appendix S5. All analyses were performed in the R environment (version 3.4.2; R Core Team, 2017).

3 | RESULTS

We found that all metrics of plant diversity responded negatively to increasing yearly N addition (Figure 3). The single meta-regression models estimated different amounts of plant diversity loss per unit of N addition, depending on the metric considered. For example, with a yearly amount of 100 kg N/ha/year the models indicated a relative loss of SR by 17% and of individual abundance by 64%, whereas the MSA and GMA were estimated to be reduced by 34% and 36%, respectively, compared with the control plots. Only the GMA metric showed a nonlinear relationship with yearly N amounts, indicating that a small amount of N addition might lead to an increase in abundance or evenness (Figure 3d).

The multiple meta-regression models showed that the responses of plant biodiversity to N addition are influenced by various environmental and experimental covariates (Table 2; for detailed model outputs, see Supporting Information Appendix S6). Climatic moderators were found to influence the responses of the abundance metrics, indicating stronger declines in areas with greater mean annual precipitation (for IA and GMA) or higher mean annual temperature (for MSA). In addition, the lowest BIC model for SR retained a significant interaction between yearly amounts of N addition and mean annual temperature (Table 2), indicating that richness decreases more steeply with increasing N addition amounts in warmer sites. The SR decreased not only with yearly

amounts of N addition, but also with experimental duration, indicating cumulative effects over time. We also found that plot size was a relevant moderator for SR, with larger relative losses occurring in smaller plots. Additionally, we found that overall losses in SR were less pronounced in soils with higher CEC. For instance, after a 5-year experiment with an addition level of 100 kg N/ha/year, the model estimates 10% of SR loss for soils with a moderately high buffering capacity to acidification (CEC = 35 cmol/kg). However, estimated SR loss increases to 30% if the same experiment (i.e., same duration and yearly N addition) is conducted on a poorly buffered soil (CEC = 8 cmol/kg). The best model for MSA retained a significant interaction between yearly amount of N addition and fertilizer type, with stronger declines for N applied in a reduced form (NH_4^+ in urea or ammonium sulphate) compared with fertilizer containing oxidized N forms (NO_3^- in ammonium nitrate or alkali nitrates).

We did not find a significant interaction between N application and ecosystem type for any metric, indicating that the overall direction of biodiversity change with increasing yearly N addition was the same in all the ecosystem types considered (Figure 4). For plant life-form types, we did not find a significant interaction with N application either. A single regression model with life-form types as moderator indicated the largest mean losses for the most N-sensitive groups (−85% for legumes; −75% for non-vascular plants; Figure 5). The responses of woody species and ferns showed larger variation and were not significantly different from zero.

4 | DISCUSSION

4.1 | Nitrogen dose–response relationships

The biodiversity loss observed was strongly driven by the yearly amount of N addition. The higher the N addition to the soil, the larger the negative impact on local plant diversity, reflecting that the coexistence of different species is promoted by nutrient limitation (Harpole et al., 2011; Soons et al., 2017). Accumulation of N in the soil increases soil acidification, which progressively determines abundance loss up to the complete extirpation of species adapted to N-poor conditions (Bobbink et al., 2010). In addition, eutrophication caused by N enrichment causes plant diversity losses through enhanced light competition (Hautier, Niklaus, & Hector, 2009). The negative relationships between plant biodiversity and the amount of N addition agree with the results of previous meta-analyses conducted over a large geographical extent across multiple types of ecosystems (De Schrijver et al., 2011; Soons et al., 2017) and in mountain grasslands specifically (Humbert et al., 2016), although these studies did not consider species abundance. Abundance metrics and SR were found to decrease at different rates as N addition increased. The largest declines were observed for IA, possibly because at the assemblage level extremely negative responses of some species (such as full extirpation occurring in the treatment plot) might be buffered by positive responses of other species in the same plot.
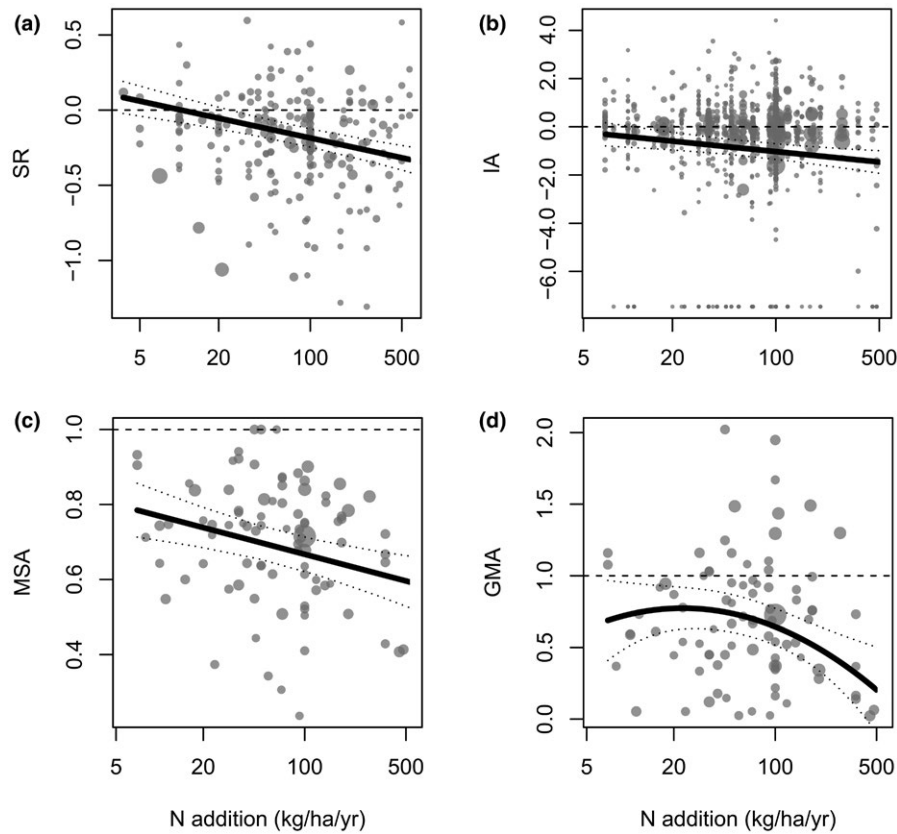
FIGURE 3 Effect of annual experimental amount of N addition (in kilograms of N per hectare per year) on the following plant biodiversity metrics: (a) species richness (SR); (b) individual species abundance (IA); (c) mean species abundance (MSA); and (d) geometric mean abundance (GMA). Continuous lines represent model predictions with log-transformed yearly N addition as a moderator only, allowing for inclusion of a quadratic term when significantly improving the goodness of fit (the dotted lines represent the corresponding 95% CI bounds). The dashed lines indicate no change in biodiversity compared with the control. Point size depicts observation weight

4.2 | Experimental duration and cumulative nitrogen enrichment

For SR, we found that experimental duration had a negative additive effect comparable in magnitude to the effect of the yearly amount of N addition (Table 2), in accordance with the results of Humbert et al. (2016). This suggests that plant communities respond in a similar manner to cumulative N application and cumulative atmospheric N deposition (Stevens et al., 2004; Duprè et al., 2010) and indicates that large diversity losses may occur even at low yearly N amounts when fertilization is protracted over a long time period (Clark & Tilman, 2008). In the short term, SR loss attributable to N application is likely to be buffered by species gain. However, species turnover tends to decline after several years of N addition (i.e., long experimental duration), when plant communities have become adapted to N inputs and populations of a few well-established N-tolerant species dominate the plots (Bobbink & Hettelingh, 2011; Dise et al., 2011). The absence of an effect of experimental duration on the responses of the species abundance metrics might reflect the fact that these metrics do not capture effects of species replacement, because they include only species that were already present in the controls. Furthermore, our models did not reveal a significant modifying influence of the background N deposition

on the biodiversity responses (Table 2). This might indicate that background annual N deposition rates were too low (0.7–46.3 kg N/ha/ year) compared with the amounts of N applied in the experiments. In addition, it might reflect that the data source used to retrieve the N deposition levels (50 km × 50 km resolution) was not detailed enough to capture the site-specific deposition rates adequately.

4.3 | Scale dependence

There is evidence that the effects of experimental N addition on local SR are scale dependent. For example, Lan et al. (2015) found that the proportional loss after N addition was significantly higher in larger plots (> 8 m²). Contrary to these findings, we found overall larger loss of SR in smaller plot sizes (1 m × 1 m or less) compared with larger ones (3 m × 3 m or more; see Supporting Information Appendix S6, Figure S6.1c). Possibly, in larger plots the chances are greater to survey a few remaining individuals of the same species, decreasing the chance of full extirpation from the sampled area. We have not observed any influence of plot size on species abundance metrics analysed, probably because in the species abundance dataset there was much less variation in plot size (from 0.04 to 4 m²; CV = 107%) compared with the SR dataset (from 0.0625 to 225 m²; CV = 558%).

TABLE 2 Standardized coefficients (slope estimates) of terms retained in the best meta-regression models based on the Bayesian information criterion (BIC)

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	.001	10.5 (1)	.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	.542	–	–
	Nadd:MAT	−0.049	0.019	−2.599	−0.085	−0.012	.009	6.7 (1)	.009
								76.9 (6)	< .0001
Individual species abundance (IA)	Nadd	−0.275	0.081	−3.389	−0.434	−0.116	.001	11.5 (1)	.001
	MAP	−0.441	0.146	−3.011	−0.728	−0.154	.002	9.1 (1)	.002
								18.5 (2)	< .0001
Mean species abundance (MSA)	Nadd:NO$_3$	−0.014	0.014	−0.958	−0.042	0.014	.014	6.5 (1)	.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	.025	5.2 (1)	.047
								26.0 (2)	< .0001
Geometric mean abundance (GMA)	Nadd	−0.103	0.037	−2.796	−0.175	−0.030	.008	6.8 (1)	.012
	MAP	−0.181	0.059	−3.079	−0.295	−0.065	.004	9.5 (1)	.004
								16.3 (3)	< .0001

Note. CEC = cation exchange capacity; duration = duration of the experiment; MAP = mean annual precipitation; MAT = mean annual temperature; Nadd = amount of yearly N addition; 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); plot size = size of the plot. 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 the event of an interaction, the omnibus test is reported for the interaction term only. See Supporting Information Appendix S6 for detailed model outputs.
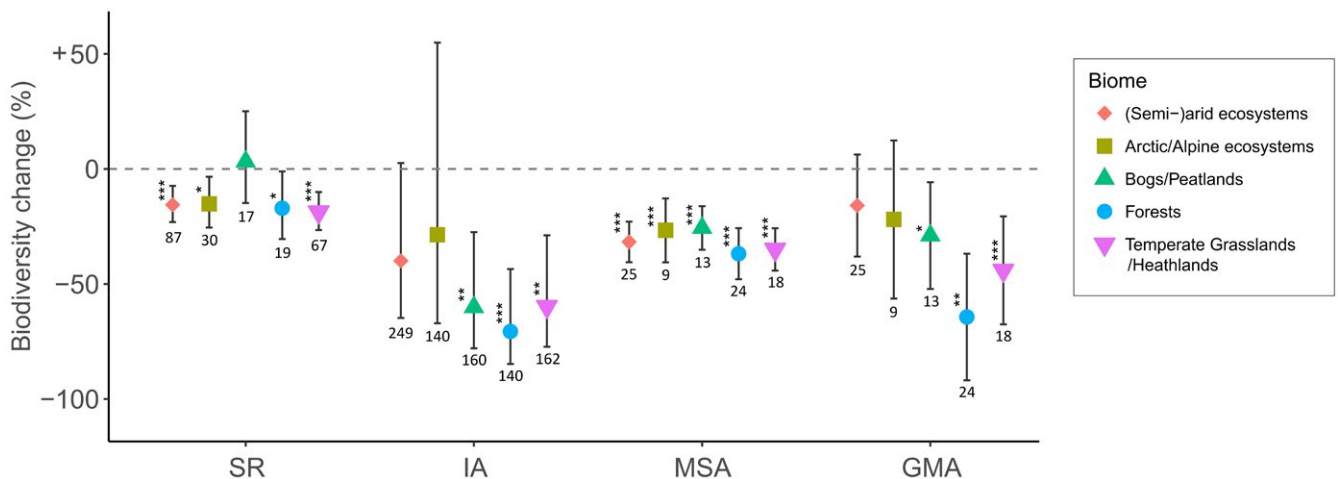

FIGURE 4 Mean pooled biodiversity change (and 95% CI) per ecosystem type, expressed as the percentage of change in N-addition plots compared with control plots. Biodiversity change is quantified with species richness (SR), individual species abundance (IA), mean species abundance (MSA) and geometric mean abundance (GMA). Values are obtained by fitting the models without the intercept term, to estimate the mean pooled effect of each level. The significance level (*p < .01; **p < .001; ***p < .0001) and number of observations are provided for each estimate

Given that we studied effects on local or site-level biodiversity only, we cannot make inferences on the impacts of N on plant biodiversity at larger extents. Trends in local biodiversity have implications for changes in biodiversity at larger scales, but the mechanisms involved in these links are not yet fully understood (McGill, Dornelas, Gotelli, & Magurran, 2015). Chase (2010) found that higher beta diversity (specifically, spatial turnover) in more productive mesocosms yielded higher overall (gamma) diversity at greater nutrient levels.
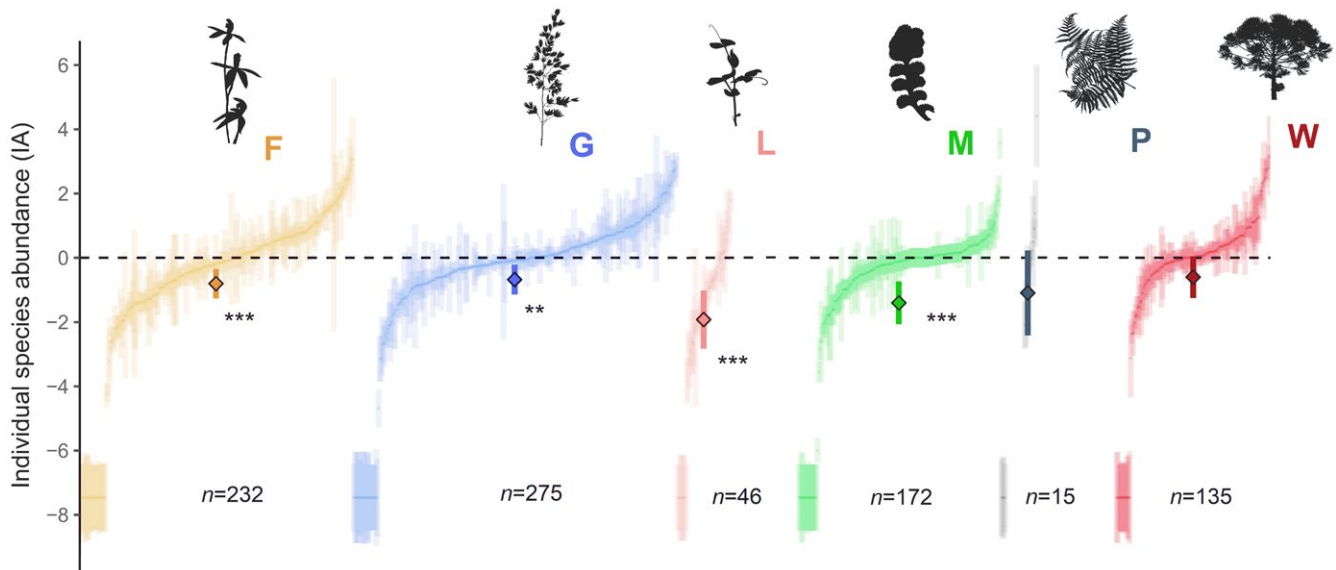
FIGURE 5 Individual species abundance ratios (and 95% CI) for forbs (F), graminoids (G), leguminosae (L), non-vascular plants (M), ferns (P) and woody species (W) (*n* = number of observations of each plant life-form type). Extremely negative effect sizes indicate the extirpation of species in the treatment plots. Diamonds represent the overall weighted mean effect size estimate for each group (and 95% CI). Significance levels are provided for each mean estimate (***p < .001; ****p < .0001). The values were obtained by running the model without the intercept term to estimate the mean pooled effect of each level

However, the extent to which such effects will also occur in response to atmospheric N deposition remains elusive, because atmospheric deposition levels are lower than typical experimental N addition doses and because responses may be confounded by influences of other environmental pressures. This might also explain why previous analyses of temporal changes in site-level plant diversity revealed no clear trends in SR (Vellend et al., 2017, 2013), despite increasing atmospheric N deposition levels occurring in the last century.

4.4 | Effect of N fertilizer type

In our analysis, fertilizer type itself did not induce a significant response in any of the metrics considered, indicating similar overall impacts of the two types of N fertilizer. However, we found that MSA decreased more strongly when N was added as urea or ammonium nitrate (containing only NH_4^+) rather than ammonium nitrate or alkali nitrate (fertilizers also containing NO_3^-). In general, differences in the chemical form of fertilizer applied are very often neglected in the experimental design of N-addition studies (but see Dias, Malveiro, Martins-Loução, Sheppard, & Cruz, 2011; Song et al., 2012). Nevertheless, evidence suggests that plant species occurring in the same community differ in their ability to take up NO_3^- and NH_4^+ forms, implying that plant community composition and abundance might depend strongly on the partitioning of differentially available soil N forms (Kahmen, Renker, Unsicker, & Buchmann, 2006; McKane et al., 2002; Miller & Bowman, 2002). Various studies in Northern Europe suggest that larger species losses are expected with increasing NH_4^+ deposition owing to increased acidification, especially in the case of oligotrophic ecosystems that are sensitive to NH_4^+:NO_3^- increase, such as heathlands, bogs and acidic grasslands

(Kleijn, Bekker, Bobbink, de Graaf, & Roelofs, 2008; Paulissen, van der Ven, Dees, & Bobbink, 2004), whereas acidification tends to be less severe when NO_3^- fertilizers are applied instead (van den Berg et al., 2008). Future nutrient-addition experiments should account for the type of fertilizer applied to elucidate such differences better.

4.5 | Soil properties

Soil acidification is one of the major processes to drive biodiversity loss after atmospheric N enrichment (Stevens et al., 2011). Nevertheless, we did not find any evidence of soil pH modifying the relationship between local plant biodiversity and N addition, similar to the results of previous meta-analyses (De Schrijver et al., 2011; Humbert et al., 2016). Soil acidity follows a negative linear relationship with base saturation (exchangeable base cations) (Beery & Wilding, 1971). However, the drop in base saturation is independent of initial soil pH, but it is dependent on soil CEC when the soil pH ranges between 4 and 7 units, as in the case of our data (De Vries et al., 1989; Helling, Chesters, & Corey, 1964; Ulrich, 1986). This might explain why we found that the response of SR was not modified by initial soil pH, but instead was related to the soil CEC, which reflects the ability of the soil to buffer N-induced acidification. Thus, in sites with higher soil CEC, the negative impact of N addition through acidification is reduced by base cation exchange in the soil, resulting in a lower species loss compared with sites with low CEC. Similar to our findings, greater species loss has been associated with lower soil CEC across 23 N-addition experiments in North America (Clark et al., 2007). It is likely that soil CEC might also explain the small SR response observed in peatlands and bogs, where the overall mean effect size was close to zero (Figure 4). These ecosystems had the

highest soil CEC values in our data (32 ± 3 cmol/kg), reflecting the high organic matter content that characterizes peatland soils.

4.6 | Climate

The best models selected for the abundance metrics retained main effects of the two climatic moderators (Table 2), suggesting that overall, larger abundance losses occur in sites with higher mean annual temperature (for MSA) and precipitation (for IA and GMA). We also found evidence that the slope of the dose–response relationship for SR is dependent on mean annual temperature at the site level. Similar outcomes have been reported for SR of mountain grasslands (Humbert et al., 2016) and the abundance of *Sphagnum* mosses (Limpens et al., 2011), probably because N uptake tends to increase with temperature (Cross, Hood, Benstead, Huryn, & Nelson, 2015). In grasslands, higher temperature and precipitation have been found to amplify aboveground biomass growth in response to N addition (Shaw et al., 2002; Zavaleta, Shaw, Chiariello, Mooney, & Field, 2003). Likewise, in forests and tundra ecosystems, temperature has been shown to affect net primary productivity positively after N addition (LeBauer & Treseder, 2008). This, in turn, negatively influences plant biodiversity, because increased biomass results in increased competition for light and in the loss of rare species (Soons et al., 2017). In addition, higher precipitation could also lead to increased N mineralization (Yang et al., 2017) which, in the absence of increased N loss via leaching or gaseous emissions, could result in higher N availability and increased biodiversity loss. Although, in general, plant assemblage responses in our analysis were not very different among ecosystem types, the modifying role of temperature and precipitation highlights the importance of accounting for biogeographical and climatic gradients to assess the impacts of N enrichment on local plant diversity across large geographical extents.

4.7 | Individual responses of plant life-form types

We found that abundance losses were particularly large for legumes and non-vascular plants (mosses and lichens). Indeed, both groups have been identified as the most sensitive to increased N inputs (Bobbink et al., 2010; Craine et al., 2002). Previous studies showed that vascular plants outcompete mosses after N enrichment owing to light competition (Malmer, Albinsson, Svensson, & Wallen, 2003; van der Wal, Pearce, & Brooker, 2005), with a substantial decline of non-vascular plants beyond 10–15 kg N/ha/year (Bobbink et al., 2010). A large negative response of legumes was also expected, because increased soil N availability represents a disadvantage for N fixation (Craine et al., 2002). Long-term fertilization studies conducted on multiple sites in the USA found substantial declines in N fixers (Suding et al., 2005), and an overall large decline in total legume biomass was also detected in previous systematic reviews (Fu & Shen, 2016; Humbert et al., 2016). In addition, we found that the abundance of individual graminoids decreased, on average, by half. This contradicts the general hypothesis that graminoids tend to become dominant after N enrichment (see e.g., Bobbink et al., 2010; Dise et al., 2011)

and contrasts with previous meta-analyses of N-addition studies that reported significant increases in total biomass of grasses and sedges (De Schrijver et al., 2011; Fu & Shen, 2016; Humbert et al., 2016). Such discrepancies with our results could reflect the fact that grass encroachment after N input usually comes about by one or a few species only (Bobbink et al., 2010), while the rest of the graminoid species are progressively outcompeted in the treatment plots, resulting, on average, in a loss of individual abundance of graminoids. Finally, the relatively small impacts on woody species might be attributable to longer persistence in vegetation thanks to their longer life span, which may exceed the typical duration of the experiments.

Further insight into the mechanisms behind community change with N enrichment, including individual abundance responses, may be provided by trait analyses (see e.g., La Pierre & Smith, 2015; Read, Henning, Classen, & Sanders, 2018). However, analyses of changes in plant functional traits (at both within- and among-species levels) were outside the scope of our meta-analysis and the primary studies analysed.

4.8 | Concluding remarks

We showed the importance of minimizing N enrichment in terrestrial ecosystems to reduce local plant biodiversity loss. Compared with several previous studies that summarized the impacts of N-addition experiments on plant biodiversity, we improved our understanding of the responses of plant communities to N enrichment by including not only SR but also abundance metrics, which showed stronger responses and have been unexplored in meta-analyses so far. Furthermore, we shed more light on the roles of different moderators influencing the response of SR and abundance, thus showing how biodiversity loss is context dependent and underlining the importance of integrating multiple dimensions of biodiversity into assessments of biodiversity responses to global environmental change.

The response relationships resulting from our study can be used to improve integrated modelling frameworks aiming to describe the response of biodiversity to anthropogenic pressures, such as the GLOBIO framework (Alkemade et al., 2009). The GLOBIO model is routinely used in (large-scale) biodiversity assessments of the present and future state of biodiversity to provide support for policy-makers (e.g., Kok et al., 2018). Our results will be implemented in the next versions of GLOBIO, next to response relationships for land-use change, climate change and fragmentation. Our results might also be of use for other models of biodiversity and ecosystem services, such as PREDICTS (Newbold et al., 2015) or InVEST (Sharp et al., 2018).

DATA ACCESSIBILITY

Data used in this study are available at the GLOBIO website (www. globio.info).

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BIOSKETCH

GABRIELE MIDOLO is a PhD student interested in the response of plant communities and functional traits to environmental change. His co-authors are interested in the factors that determine species distributions and abundance at multiple scales, how anthropogenic impacts disrupt these patterns and how this knowledge can be applied to aid ecosystem management and conservation.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

APPENDIX

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

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