

RESEARCH ARTICLE

Controlling the abundance of a native invasive plant does not affect species richness or functional diversity of wet grasslands

Marie-Therese Krieger¹  | Julia Ditton¹ | Harald Albrecht¹ | Barteline Martina Baaij^{1,2} | Johannes Kollmann^{1,3} | Leonardo Henrique Teixeira¹

¹Chair of Restoration Ecology, School of Life Sciences, Technical University of Munich, Freising, Germany

²Plant Ecology and Nature Conservation Group, Wageningen University & Research, Wageningen, The Netherlands

³Norwegian Institute of Bioeconomy Research (NIBIO), Ås, Norway

Correspondence

Marie-Therese Krieger, Chair of Restoration Ecology, School of Life Sciences, Technical University of Munich, Freising, Germany.

Email: marie-therese.krieger@tum.de

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Abstract

Aim: In this study, we tested plant community-based management methods to reduce the abundance of the invasive native plant *Jacobaea aquatica* (marsh ragwort). As *J. aquatica* mainly occurs in species-rich wet grasslands, our aim was to define management measures that do not reduce the conservation value of the resident communities.

Location: Data were collected from 20 independent sites which varied in productivity and management intensity across the pre-alpine Allgäu region (South Germany).

Methods: We monitored effects of temporary abandonment and decreased mowing intensity in very low- and low-productive sites, as well as of decreased mowing and fertilization at moderately productive sites. Abundances of *J. aquatica* and the co-occurring species were recorded at start and end of two experiments (2018–2021: very low- and low-productive conservation grasslands; 2017–2020: moderately productive agricultural grasslands), while functional traits data of all species were gathered from the literature and specific databases. Generalized linear mixed-effects models (GLMMs) were used to analyse the effects of management intensity on the abundance of *J. aquatica*, functional diversity and species richness of the resident communities.

Results: At all productivity levels, the abundance of *J. aquatica* declined under reduced management. Changes in community composition and species richness of the resident community were less pronounced than the reduction of *J. aquatica*, but species richness declined under lowest management intensities. Thus, moderate reduction in management intensity provided the most benefits in terms of reduction of *J. aquatica*, and maintenance of species richness and composition of the resident plant community.

Conclusions: Reducing management intensity in wet grasslands decreases the abundance of *J. aquatica* and thus is a suitable method to control this species. As plant community responses were only partially consistent, management plans must account for

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the productivity of invaded sites. To avoid negative effects on grassland biodiversity, only moderate suppression of *J. aquatica* is recommended.

KEYWORDS

community structure, cutting management, functional dispersion, functional redundancy, *Jacobaea aquatica*, marsh ragwort, native invader, plant diversity, weed control, wet grasslands

1 | INTRODUCTION

Species-rich wet grasslands have a high conservation value because they belong to the most threatened vegetation types in Europe (Čop et al., 2009). Historically originated under low-intensity mowing or grazing, these ecosystems are now declining due to agricultural intensification or abandonment (Dengler et al., 2014). Remnant wet grasslands suffer from declines in characteristic biodiversity (Joyce & Wade, 1998), expressed by a decrease in wetland-adapted plants, and a simultaneous increase of ruderal and weedy species (Prach, 2008). Such transformations of plant communities are often triggered by modified management regimes and shifts in resource availability (Poptcheva et al., 2009; Parepa et al., 2013), which creates opportunities for the establishment of alien plants as well as for the overabundance of certain native species (Valéry et al., 2009; Möhrle et al., 2021). Similar to alien plants, such native species can become dominant and spread within their range, sharing aspects of invasion by alien species (Valéry et al., 2008; Carey et al., 2012; Nackley et al., 2017). While some authors describe those as 'expansive species' (Sholto-Douglas et al., 2017; Haile et al., 2021), we follow the definition of Carey et al. (2012) using the term 'native invaders'.

Some of these species are detrimental as they reduce grassland yield and forage quality or can even be poisonous to livestock (DiTomaso, 2000). Examples from Central Europe are *Pteridium aquilinum* (common bracken), *Colchicum autumnale* (meadow saffron), and *Senecio* or *Jacobaea* sp. (ragworts), the latter containing toxic pyrrolizidine alkaloids (Stewart et al., 2008; Winter et al., 2014; Suttner et al., 2016). The rapid spread of such native species threatens resident communities through altered competition, leading to reduction or even local extinction of rare native species (Carey et al., 2012; Nackley et al., 2017). Yet, developing effective control measures is complicated due to the conflicting goals of reducing the native invader, while maintaining plant diversity of the resident community.

The most common practices to control unwanted grassland species include mowing, burning, manual removal and herbicides (DiTomaso, 2000). Such control methods are costly and time-consuming, and they can have – particularly in the case of chemical control – negative side effects (Power et al., 2013). Thus, several research groups tried to develop more sustainable management methods to suppress invaders (Frankow-Lindberg, 2012; Connolly et al., 2018; Möhrle et al., 2021). One of these approaches, i.e. the use of community-based biotic filters, showed that increasing plant density, biomass or diversity of the recipient community reduces

invader establishment and performance. The underlying mechanisms are based on three ecological principles: (i) density-dependent competition; (ii) differentiation of functional traits among resident plants leading to niche pre-emption; and (iii) further niche limitation through functional similarity between resident and invasive species (Hooper & Dukes, 2010; Möhrle et al., 2021). In other words, increasing the number of individuals or species in a community increases competition for light and nutrients, and weakens the performance of already established invaders (Naeem et al., 2000). Furthermore, communities displaying high functional-trait differentiation among resident plants and, thus, higher functional dispersion, can also have reduced probabilities of invasion and invader establishment due to a greater use of available resources (Hooper & Dukes, 2010). Such effects could be enhanced by resident species yielding similar functional traits to those of potential invaders (Funk et al., 2008; Yannelli et al., 2017).

Management methods suitable to put the above-mentioned concepts into practice include different cutting intensities, delay of the first mowing event (Humbert et al., 2012), modified fertilization strategies (Oelmann et al., 2009), and re-seeding of vegetation gaps. Adaptation of mowing strategies was also found to reduce abundance and fecundity of native invaders (Winter et al., 2014; Bassler et al., 2016; Krieger et al., 2022). Nevertheless, such management practices may, apart from the desired suppression of the native invader, also negatively affect different aspects of community structure, such as species composition, evenness and richness (Chapin III et al., 2000). For example, delay of the first mowing event or mulching can shift the proportions of functional groups, e.g. from dicots to monocots (Seither & Elsässer, 2014; Bassler et al., 2016), raising concerns of maintaining the nature conservation value of those grasslands. In addition, other studies showed that within 3 years, cessation of mowing resulted in competitive shifts, including local exclusion of species (Joyce, 2014). In fact, abandonment as well as high fertilization levels can lead to dominance of tall-growing graminoids, while regular mowing in combination with a moderate nutrient supply benefits the establishment of weak competitors (Klimeš & Klimešová, 2002; Gerard et al., 2008). In the short term, however, losses in species numbers might be marginal, thus tolerable, while suppression of the native invader is more pronounced (Seither & Elsässer, 2014; Bassler et al., 2016). Hence, depending on the intensity and duration of the regulation measures and the productivity of the respective grassland systems, suppression effects on the native invader and its consequences for plant communities can vary (Poptcheva et al., 2009; Skurski et al., 2013; Bassler et al., 2016). Therefore, to obtain a comprehensive picture of management

success, regulation measures must be evaluated not only in terms of invader reduction but also with respect to their effect on resident plant diversity and community composition. Special attention needs to be given to the conservation of dicotyledons, as they contribute not only to plant diversity, but also to higher trophic levels including pollinators.

In this study, we tested community-based management methods to reduce the abundance and to prevent seed production of the invasive native marsh ragwort (*Jacobaea aquatica*). In the pre-alpine regions of Central Europe, overabundance of this species is an increasing problem on grazed areas and in forage as it contains toxic pyrrolizidine alkaloids. As *J. aquatica* mainly occurs in species-rich wet grasslands, suppression of this poisonous species must not affect the conservation value of these endangered resident communities. In our experiments, different mowing and fertilization intensities were tested covering a gradient from moderately to very low-productive sites, which represents the ecological amplitude of the study species. In two coordinated experiments, we monitored the effects of temporary abandonment and reduced mowing in low- and very low-productive sites, as well as of reduced mowing and less fertilization at moderately productive sites, on the abundance of *J. aquatica*, and on species richness and functional diversity of the wet grasslands.

We hypothesized that (i) lowest management intensities result in the most effective suppression of the early-successional *J. aquatica* at all productivity levels, and that (ii) species with similar growth forms to *J. aquatica* would experience similar suppression effects, thus leading to an overall reduction in dicots in relation to monocots. We further expected (iii) fewer effects on functional composition and species richness of resident communities due to delayed species turnover compared to rapid changes in species abundance. (iv) These effects would be smaller in magnitude than the suppression of *J. aquatica* but again most pronounced within the lowest management intensities.

2 | MATERIAL AND METHODS

2.1 | Study species

Jacobaea aquatica (marsh ragwort) is a biennial to short-lived perennial Asteraceae native to wet grasslands in Central Europe (Wagenitz, 1987). The species usually germinates in autumn or spring, hibernates as a rosette, and in its second year produces shoots with several yellow flower heads. Flowering occurs from late June till late August and, when cut, the plants quickly produce new lateral shoots and form new flowers (Bassler et al., 2017). Each flower head produces several hundred wind-dispersed seeds, which form persistent seed banks and germinate rapidly and frequently in favourable microsites (Suter & Lüscher, 2012).

As *J. aquatica* is an early-successional, light-demanding species, its occurrence and spread are supported by frequent disturbances and moderate nitrogen fertilization (Forbes, 1976; Suter & Lüscher, 2008). Moreover, drainage as well as re-wetting of drained

grasslands favours its occurrence by changing the local community or creating new ecological niches (Suter & Lüscher, 2008). In the past decades, *J. aquatica* has become more common in the pre-alpine grasslands of Austria, Germany and Switzerland (Suttner et al., 2016). As all parts of the plant contain pyrrolizidine alkaloids, which are toxic to livestock and humans (Gottschalk et al., 2018), local hotspots pose essential problems to farmers managing such grasslands. Previous studies already focused on practical control measures in agricultural grasslands (Sargent, 2011; Suter & Lüscher, 2011; Bassler et al., 2016), while management recommendations for ecologically valuable conservation grasslands are lacking.

2.2 | Field experiments and data collection

2.2.1 | Control experiment on very low- and low-productive grasslands

In 2018, different cutting regimes were established on 13 pre-alpine grassland sites invaded by *J. aquatica*. The grasslands were distributed across the Allgäu region in South Germany and split according to their estimated productivity and preceding usage ('very low-productive' nature conservation sites, $n = 6$; 'low-productive sites' with agricultural usage and conservation schemes, $n = 7$) to include a wide range of site conditions. Details on classification of the productivity levels are given in the supporting information (Appendix S1). Several management regimes consisting of different mowing times and frequencies were applied in treatment plots at each site from 2018 to 2021 (Table 1, Appendix S1). Management was reduced in the first years and adjusted over the course of the experiment, and regionally common management at each productivity level was used as reference (Table 1). Treatment plots were arranged in one row to ensure workability for farmers. Plots were 3.7 m × 6.0 m in size, which corresponds to the recommended area for vegetation sampling in grasslands (Dierßen, 1990).

Vegetation surveys were conducted in June 2018–2021, i.e. always before the first cut. On these occasions, relative percentage of individual species as well as the total cover of above-ground vascular vegetation, litter, open soil and mosses were estimated in each plot following Klapp (Voigtländer & Voss, 1979). Estimation of cover was chosen to allow the detection of subtle changes in species occurrence (Peratoner & Pötsch, 2015). Nomenclature follows World Flora Online (2020).

2.2.2 | Control experiment on moderately productive grasslands

Another experiment was established on organic grasslands in the same region in 2017. Here, different combinations of mowing and fertilization were tested on seven grasslands with 3–4 cuts per year from 2017 until 2020 ('moderate productivity'; see Table 1, Appendix S1). The same plot design was used in this experiment, and

TABLE 1 Overview of the different mowing and fertilization regimes implemented at each grassland productivity level. The table includes the abbreviation used in the figures, treatments names, and a short description of the main focus of each treatment. Treatment names refer to the cutting regimes applied. More detailed information can be found in Appendix S1

	Abbreviation	Treatment name	Main focus of the treatment
Very low-productive sites	V-1	3-years fallow	Cessation of mowing for more than 1 year
	V-2	Fallow (1 year), late seasonal cut	Cessation of mowing for 1 year, followed by a yearly cut at the end of the vegetation period
	V-3	Fallow (1 year), early seasonal cut	Cessation of mowing for 1 year
	V-4	Late cut August	Delayed first cut and additional low fertilization
	V-ref	Reference treatment	Regionally specific mowing regime with cuts in July and September
Low-productive sites	L-1	Late cut October (3 year)	Off-season cut for 3 years
	L-2 ^a	2 years fallow	Cessation of mowing for two full years
	L-3 ^a	Fallow (1 year)	Cessation of mowing for two consecutive vegetation periods
	L-4	Late cut October (2 year)	Off-season cut for 2 years
	L-5	Late cut August	Delay of first cut to mid-season, skip of second cut
	L-6	Cut June with shift	Skip of second cut followed by a time-shift in the regionally specific mowing ^b
	L-7	Cut June	Skip of second cut
	L-ref	Reference treatment	Regionally specific mowing regime with cuts in June and August
	L-9	3-times cut	One additional cut during flowering season of <i>J. aquatica</i>
Moderately productive sites	M-1	Reduced cutting	Reduced mowing frequency (two instead of four cuts) with adapted fertilization ^b
	M-2	Skip of first seasonal cut	Reduced mowing frequency (three instead of four cuts), usual fertilization
	M-ref	Reference treatment	Regionally specific management with four cuts and 40 m ³ ha ⁻¹ slurry

^aPlots had to be split by sites as treatments could only be implemented on part of the sites (L2: $n = 4$; L3: $n = 3$).

^bDetails can be found in Appendix S1.

respective vegetation data were collected each year in May, before the first mowing.

In both experiments, information on climate, altitude, grassland productivity (BayernAtlas-plus, no date 2020; DWD – Deutscher Wetterdienst, no date 2020), and soil characteristics (analysis done by AGROLAB, Germany) was gathered and added to the description of the sites (Appendix S1).

2.3 | Plant functional traits and functional diversity calculation

Eighteen plant traits characterizing dispersal, establishment, growth and reproduction of all species, or indicating their competitive ability (Funk et al., 2008; Teixeira et al., 2020) were obtained from the databases 'Ecoflora' (Fitter & Peat, 1994), 'BioFlor' (Klotz et al., 2002) and 'LEDA' (Kleyer et al., 2008), using the TR8 package version 0.9.22 (Bocci, 2015) in R, version 4.0.2 (R Core Team, 2020). To reduce the number of missing values, trait information was obtained from LEDA files manually where possible; absent values were marked as 'NA' (Appendix S2). Additionally, species were characterized as graminoids, herbs or ferns. All traits were checked for correlation to

ensure unbiased calculation of functional indices via the exclusion of highly correlated traits (i.e. correlation coefficient > 0.75 ; Dormann et al., 2013) and indices were calculated using 15 of the obtained 19 traits (Appendix S2).

Functional dispersion (F_{dis}) and functional redundancy (F_{red}) at the start and end of the experiments were calculated using cover percentages and trait data of all species (excluding *J. aquatica*) occurring in those years. The F_{dis} index was calculated using the R package *FD* (Laliberté et al., 2014), while for calculation of the F_{red} index we used the function *uniqueness* (Ricotta et al., 2016). For the calculation of the indices, the nominal traits life form and vegetative reproduction method were first split into binary dummy variables, since species were often assigned to more than one category. Afterwards, those variables were weighted according to the number of categories used to ensure equal influence of all traits as suggested by Laliberté and Legendre (2010).

2.4 | Statistical analysis

To facilitate visual presentation, treatments implemented at all sites were categorized according to their management intensity and

plotted along an intensity gradient. To create a gradient for very low- and low-productive sites, each mowing event was weighted according to the time at which it occurred. Mowing earlier in the year was given a higher weight as it affects plant development more than late-seasonal mowing (Appendix S1).

Data from the start and the end of the four-year studies (2017–2020 and 2018–2021 respectively) were used, as we were interested in the total effects after 3 years of altered management regimes. Following exploratory data analysis, one extreme outlier was removed from the lowest-intensity treatment at the very low-productive sites. The respective experimental plot was dominated by *Filipendula ulmaria*, which accounted for 60% of the vegetation cover. The development of this plot was inverse to the overall pattern, because *F. ulmaria* occurred in large amounts at a nearby ditch. Therefore, including the information of this plot would distort the results.

Change of *J. aquatica* presence and community characteristics in response to reduced management were calculated using response ratios (Armas et al., 2004):

$$\text{Change} = \frac{(\text{Value}_{\text{final}} - \text{Value}_{\text{initial}})}{(\text{Value}_{\text{final}} + \text{Value}_{\text{initial}})}$$

Initial values were used as the reference level to which the final values were associated. The applied index symmetrizes the changes around zero (no changes) and can range from -1 (indicating total absence) to $+1$ (maximum increase observed). Dicot cover as well as species number were calculated excluding *J. aquatica*. Change values were individually assessed using generalized linear mixed-effects models (GLMMs) with Gaussian error distribution. Treatment was included as fixed factor and field site as random factor to account for potential spatial autocorrelation. Treatments following the typical regional management of the respective grasslands (Table 1) were considered as the reference conditions to which our altered mowing regimes were compared. Afterwards, a multiple-comparisons post-hoc test (i.e. emmeans with Dunnett adjustment) was applied to check for significant differences between treatments and its respective references (Lenth, 2022). The same calculations were performed for changes in F_{dis} and F_{red} . All statistical models were implemented using the R package *glmmTMB* (Brooks et al., 2017).

Differences in species richness between productivity levels and treatments at the start of the experiment were explored using Kruskal–Wallis tests. Additionally, differences in species richness per treatment between the start and the end of the experiment were evaluated using the paired Wilcoxon rank sum test. This was done to see if species numbers were similar at the start and if the numbers changed over time. In order to determine whether presence/absence and abundances of species were differently affected by management reduction over time, distance-based non-metric multidimensional scaling (NMDS) was performed. This was done by first calculating Bray–Curtis dissimilarities between samples and then iteratively ranking Euclidian distances between the sample scores (Legendre & Legendre, 2012) using the package *vegan* (Oksanen et al., 2022).

To understand the relationship between the investigated variables, we assessed their correlations using a Kendall correlation matrix. This correlation was chosen because it does not assume linear relationships between variables and is recommended for small sample sizes (Croux & Dehon, 2010). Throughout the results, significances lower than $p = 0.05$ are referred to in the text and mean values (\pm SE) are given to underline some findings; full results of the GLMM post-hoc analysis are provided in Appendix S3. All statistical analyses were done using R, version 4.0.2 (R Core Team, 2020) in the R-Studio environment.

3 | RESULTS

3.1 | Abundance of the native invader *Jacobaea aquatica*

As a result of the applied treatments, the abundance of *J. aquatica* decreased over time at all productivity levels: in very low-productive grasslands from $4.8 \pm 0.7\%$ to $1.5 \pm 0.5\%$ cover, in low-productive ones from $6.4 \pm 0.4\%$ to $3.7 \pm 0.5\%$ cover, and under moderate productivity from $4.2 \pm 0.6\%$ to $1.1 \pm 0.3\%$. At very low- and low-productivity, this decrease was significant (very low: $\chi^2 = 31.0$, $df = 4$, $p < 0.001$, $R^2 = 0.20$; low: $\chi^2 = 50.2$, $df = 8$, $p < 0.001$, $R^2 = 0.07$), with greater reduction at lowest management intensity (Figure 1a,b). Overall, relative reduction of *Jacobaea* abundance was highest in very low-productive sites. At those sites, the effect of all experimental treatments on *Jacobaea* abundance significantly differed from the effect of the reference management ($p < 0.05$; Appendix S3), while the reduction of *J. aquatica* was similar across treatments (V-1 to V-4).

In low-productive sites, a strong reduction of *J. aquatica* was observed for low intensities (L-1 to L-3), whereas only small effects were observed for management intensities similar to the reference level (L-4 to L-7; L-9). A significant reduction in *J. aquatica* abundance was observed for the treatments 'late cut October (3 year)' and 'fallow (1 year)' ($p < 0.01$; Figure 1b, Appendix S3).

In contrast, no significant differences in abundance were found between management intensities in moderately productive sites (moderately: $\chi^2 = 3.65$, $df = 2$, $p = 0.2$, $R^2 = 0.26$). Still, total abundance of *J. aquatica* decreased (Figure 1c).

3.2 | Functional composition of plant communities

Changing the management intensity also influenced the abundance of both dicots and monocots. In very low-productive sites, reduced mowing resulted in lower abundance of dicots compared to the reference (very low: $\chi^2 = 14.3$, $df = 4$, $p < 0.01$, $R^2 = 0.23$; Figure 2a). Treatment 'fallow (3 year)' (V-1) strongly reduced dicot abundance compared to the reference, which had the smallest changes (relative cover V-1: $19.8 \pm 4.7\%$ to $3.7 \pm 2.1\%$, V-ref: $16.5 \pm 4.3\%$ to $12.3 \pm 2.7\%$; $p < 0.01$; Appendix S3). Changes in the

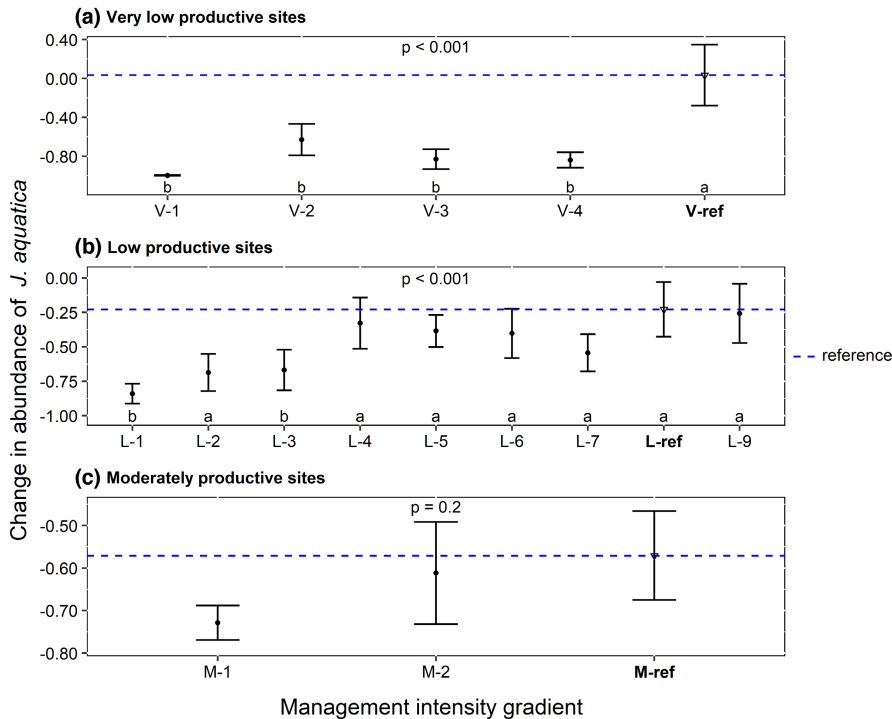


FIGURE 1 Effects of management intensities on changes in the abundance of the native invader *Jacobaea aquatica* in wet grasslands of (a) very low, (b) low and (c) moderate productivity. Changes in *J. aquatica* abundance were calculated as a standardized response (following Armas et al., 2004) after 3 years of modified management regimes, so that numbers indicate relative changes in species cover. Treatments are arranged according to increasing intensity; the treatment abbreviations are explained in Table 1. Given are mean \pm SE, the overall p value and differences to reference according to post-hoc analysis. The blue line indicates the reference mean; note the different y axes

abundance of monocots were not as pronounced and no statistical differences were found (very low: $\chi^2 = 6.44$, $df = 4$, $p = 0.2$, $R^2 = 0.06$; Figure 2b).

Mean reduction of dicots was higher in low-productive sites (-51%) compared to very low-productive sites (-10%). Nevertheless, as variation was high, no statistical differences between management intensities and reference treatment were observed (low: $\chi^2 = 11.4$, $df = 8$, $p = 0.2$, $R^2 = 0.08$; Figure 2c). By contrast, reduced mowing led to a significant increase in the abundance of monocots compared to the reference (low: $\chi^2 = 18.5$, $df = 8$, $p < 0.05$, $R^2 = 0.11$; Figure 2d). Again, most management intensities contained a high variation in monocot abundance, so that following the post-hoc analysis, only 'late cut October (3 year)' (L-1) significantly differed from the reference ($p < 0.05$; Appendix S3). In moderately productive sites, the abundance of dicots and monocots did not differ between treatments (dicots: $\chi^2 = 1.31$, $df = 2$, $p = 0.5$, $R^2 = 0.03$; monocots: $\chi^2 = 0.28$, $df = 2$, $p = 0.9$, $R^2 = 0.01$; Figure 2e,f).

Effects on the functional diversity of the sites were quite small and differed depending on the reduction in management intensity and the productivity of the sites. The analysis of changes in the functional diversity indices revealed an overall trend of decreased F_{dis} and a corresponding increase in F_{red} over time, independent of treatments in very low- and low-productive sites (Figure 3a–d). In very low-productive sites, on average, reduction of management intensity increased F_{dis} compared to the reference (F_{dis} : $\chi^2 = 10.6$, $df = 4$, $p < 0.05$, $R^2 = 0.26$; Figure 3a). Nevertheless, due to the high variation in the data and the small sample size, no statistical differences were observed in the post-hoc comparisons of individual treatments against the reference (Appendix S3). Changes in F_{red} were generally smaller and showed no differences between

individual treatments and reference (F_{red} : $\chi^2 = 4.90$, $df = 4$, $p = 0.3$, $R^2 = 0.08$; Figure 3b).

In low-productive sites, on average, reduction of management intensity did not induce significant changes in F_{dis} but increased F_{red} compared to the reference treatment (F_{dis} : $\chi^2 = 9.39$, $df = 8$, $p = 0.3$, $R^2 = 0.1$; Figure 3c; F_{red} : $\chi^2 = 17.1$, $df = 8$, $p < 0.05$, $R^2 = 0.12$). Specifically, the treatment 'cut June' (L-7) increased F_{red} ($p < 0.05$; Figure 3d; Appendix S3).

In moderately productive sites, F_{dis} and F_{red} did not differ between management intensities (F_{dis} : $\chi^2 = 4.55$, $df = 2$, $p = 0.1$, $R^2 = 0.15$; Figure 3e; F_{red} : $\chi^2 = 0.69$, $df = 2$, $p = 0.7$, $R^2 = 0.02$; Figure 3f). Nevertheless, the data showed a trend towards a stronger decrease in F_{dis} with stronger reduction in management intensity, while F_{red} showed the opposite trend (Figure 3e,f).

3.3 | Effects on plant species richness

Overall, species richness changed only slightly over time, with significant losses only at the most severe management reduction. At very low-productive sites, species number tended to decline in all treatments, while at low- to moderately productive sites, higher management intensity tended to increase species number.

At the start of the experiments, species numbers differed among productivity levels (very low productivity: 20 ± 1 spp.; low productivity: 18 ± 0 spp.; moderate productivity: 20 ± 1 spp.; Kruskal–Wallis test: $\chi^2 = 10.5$, $df = 2$, $p < 0.01$) but not among treatments within experiments (very low productivity: $\chi^2 = 0.76$, $df = 4$, $p = 0.9$; low productivity: $\chi^2 = 7.78$, $df = 8$, $p = 0.5$; moderate productivity: $\chi^2 = 2.45$, $df = 2$, $p = 0.3$).

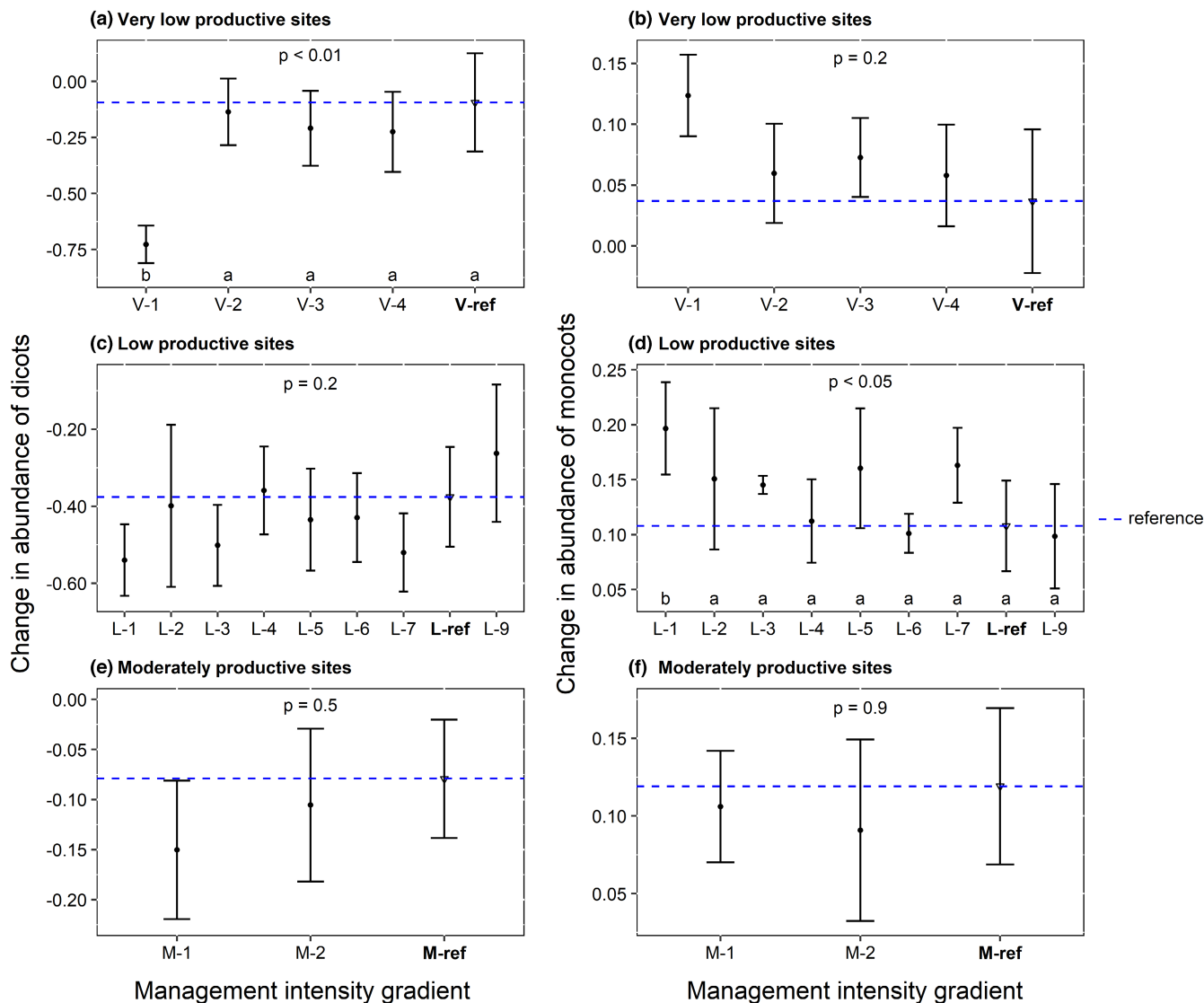


FIGURE 2 Effects of management intensities on abundance of dicots (left) and monocots (right) in wet grasslands of (a, b) very low, (c, d) low and (e, f) moderate productivity. Changes in abundance of dicots and monocots were calculated as a standardized response after 3 years of modified management regimes, so that numbers indicate relative changes in functional group cover. Treatments are arranged according to increasing intensity; the treatment abbreviations are explained in Table 1. Given are mean \pm SE, the overall p value and differences to reference according to post-hoc analysis. The blue line indicates the reference mean; note the different y axes

During the experiment, species richness changed only slightly (Appendix S4). Only under high management intensity at moderately productive sites species numbers significantly increased (paired Wilcoxon test, $p < 0.05$; Reference treatme: 20 ± 1 increased to 23 ± 1 spp.). NMDS calculation, however, showed a shift in vegetation composition in response to management reduction, especially when species abundances were included as compared to when only presence/absence data were assessed. Effects were more pronounced on the very low = and low-productive sites (Appendix S4, Figure A1).

Nevertheless, management intensity differentially influenced the shifts in number of species over time. In all treatments, at very low-productive sites, species richness decreased over time ($\chi^2 = 16.0$, $df = 4$, $p < 0.01$, $R^2 = 0.5$; Figure 4a), with a significant reduction in species numbers in the treatment 'fallow (3 year)' (V-1: 12 ± 1 species; -39%) compared to the reference treatment (V-ref: 18 ± 3

species; -4% ; $p < 0.05$; Appendix S3). While in low-productive sites, reduction of management intensity did not change species richness ($\chi^2 = 10.8$, $df = 8$, $p = 0.2$, $R^2 = 0.22$; Figure 4b), it did in moderately productive sites; especially reduced cutting (M-1) decreased the number of species significantly ($\chi^2 = 8.72$, $df = 2$, $p < 0.05$, $R^2 = 0.08$; Figure 4c; post-hoc comparison: $p < 0.05$; Appendix S3).

3.4 | Relationship between the abundance of the native invader and plant community responses

At all productivity levels, changes in the abundances of monocots versus dicots, as well as changes in functional dispersion versus functional redundancy had strong negative relationships [Kendall tau (τ) > -0.44 , $p < 0.01$; Appendix S5]. In very low-productive sites

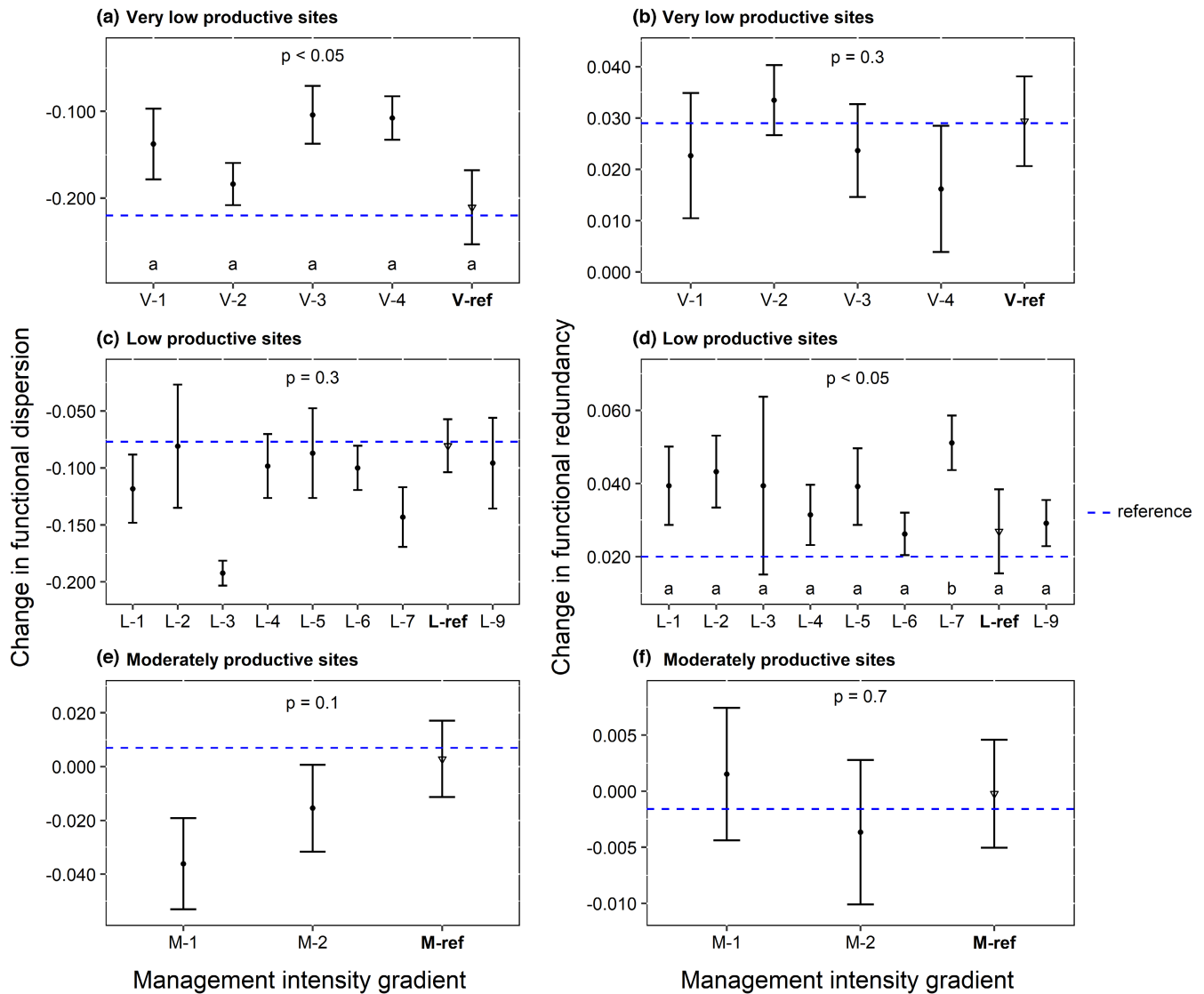


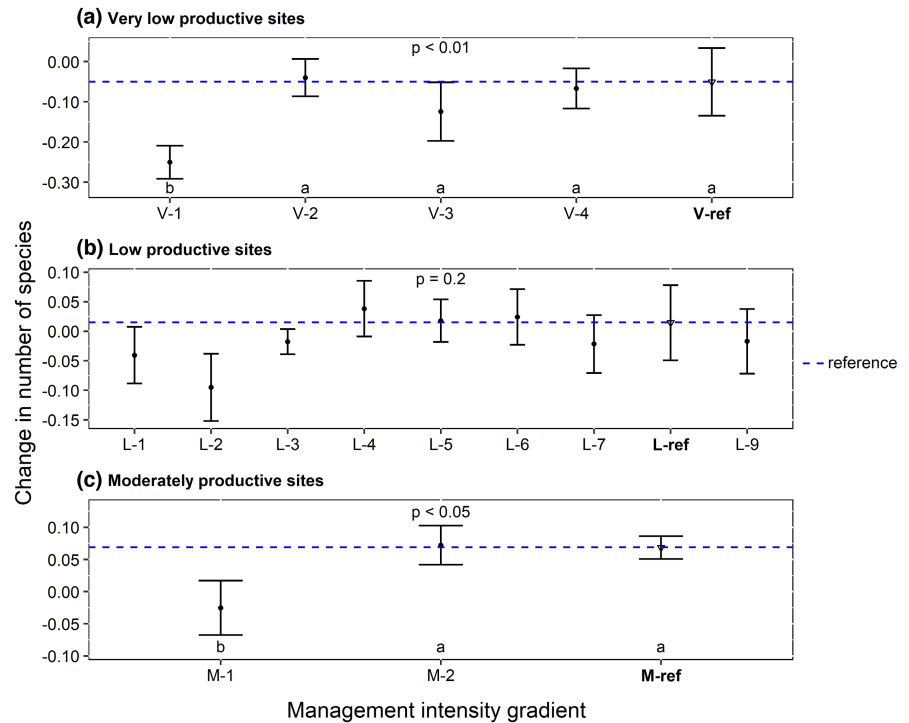
FIGURE 3 Effects of management intensities on functional dispersion (left) and functional redundancy (right) in wet grasslands of (a, b) very low, (c, d) low and (e, f) moderate productivity. Changes in functional dispersion (F_{dis}) and functional redundancy (F_{red}) were calculated as a standardized response after 3 years of modified management regimes, so that numbers indicate relative changes in functional diversity. Treatments are arranged according to increasing intensity; the treatment abbreviations are explained in Table 1. Given are mean \pm SE, the overall p values and differences to reference according to post-hoc analysis. The blue line indicates the reference mean; note the different y axes

species number was positively related to the abundance of dicots ($\tau = 0.51$, $p < 0.001$) and negatively to the abundance of monocots ($\tau = -0.33$, $p < 0.05$; Appendix S5). The number of species in low-productive sites was positively related to the abundance of *J. aquatica* ($\tau = 0.25$, $p < 0.01$) and functional redundancy ($\tau = 0.24$, $p < 0.01$), and negatively to functional dispersion ($\tau = -0.25$, $p < 0.01$; Appendix S5). Furthermore, the abundance of monocots was positively related to functional redundancy ($\tau = 0.26$, $p < 0.001$) and negatively to functional dispersion ($\tau = -0.23$, $p < 0.05$). Additionally, in low-productive sites, abundance of *J. aquatica* positively correlated to the abundance of dicots ($\tau = 0.20$, $p < 0.05$). In moderately productive sites, abundance of *J. aquatica* was positively related to functional dispersion ($\tau = 0.33$, $p < 0.05$) and negatively to functional redundancy ($\tau = -0.28$, $p < 0.05$; Appendix S5).

4 | DISCUSSION

The main results of the two four-year grassland experiments showed that the effects of reduced management were more pronounced on the abundance of the native invader *J. aquatica* than on the resident communities. Moreover, we observed that reducing management increased the abundance of monocots, whereas the abundance of dicots decreased. Similarly, functional dispersion declined and functional redundancy increased, accompanied by a decline in species richness under reduced management. All changes in community composition were more pronounced at lower management intensities. Furthermore, changes were higher at very low-productive sites, and negative relations in the correlation matrix indicated that reduced management applied to control *J. aquatica* directly affected resident communities.

FIGURE 4 Effects of management intensities on the number of species in wet grasslands of (a) very low, (b) low and (c) moderate productivity. Changes in species number were calculated as a standardized response after 3 years of modified management regimes, so that numbers indicate relative changes. Treatments are arranged according to increasing intensity; the treatment abbreviations are explained in Table 1. Given are mean \pm SE, the overall p value and differences to reference according to post-hoc analysis. The blue line indicates the reference mean; note the different y axes



4.1 | Suppression of the native invader

Abundance of *J. aquatica* in the studied wet grasslands was negatively affected by reduced management at all productivity levels, with greater changes at lower management intensities. This supports our first hypothesis that a strong reduction in management intensity would be the best option to suppress the early-successional native invader. Our results are in line with those of Suter and Lüscher (2011) who reported a reduction of *J. aquatica* following a repeated late-seasonal mowing instead of bi-annual mowing in grasslands of different productivity levels. Generally, competition for light reduced *J. aquatica* growth and the number of individuals; the latter due to dying rosettes and less reproduction (Suter & Lüscher, 2011; Bassler et al., 2016; Krieger et al., 2022).

Nonetheless, changes in the abundance of *J. aquatica* plants varied among the three productivity levels, with reduction of *J. aquatica* being most effective under reduced management at very low-productive sites. At low to moderate productivity, reducing the mowing frequency resulted in minor changes in abundance of the native invader, with less reduction under intermediate management intensity. At low-productive sites, lower sward density may have mediating effects as previously reported (Bassler et al., 2016). Density effects in the very low-productive sites were achieved through additional fertilization or via cessation of mowing. This is in line with findings of Rosenthal (2010), who showed that in fallow treatments, strong light reduction together with nutrient limitation were the main cause of changes in abundance, leading to a complete extinction of *J. aquatica* within a few years. As competition for light is enhanced by the rapid growth of tall species (Hautier et al., 2009), shading effects on *J. aquatica* remained strong even under low fertilizer application.

4.2 | Impacts of altered management on diversity of resident communities

At all productivity levels, reducing management intensity also changed the functional composition of grassland communities. Overall, abundance of dicots declined, while monocots increased. Those changes indicate that species similar to *J. aquatica* in phylogeny and growth form likewise experienced suppression. Decreased management selects for a tall and dense vegetation (Seifan et al., 2010), while regionally specific management maintains the plant community composition, especially at low-productive sites (Pavlů et al., 2011). In fact, a reduced cutting frequency benefits tall grasses and leads to a competitive exclusion of small forb species (Pavlů et al., 2011; Conradi et al., 2017). Overall, under moderate management intensities, we observed only small changes in forb abundance. Since this group is functionally more diverse, highly competitive or shade-tolerant species might be less suppressed than low-growing species, such as stoloniferous or rosette species (Rosenthal, 2010; Boob et al., 2021).

Contrastingly, alterations in abundance of functionally dissimilar species appeared to balance changes in the functional indices (Rosenthal, 2010; Simons et al., 2017). Changes in F_{dis} and F_{red} showed higher variation but greater magnitude (F_{dis} : very low: -0.15, low: -0.11, moderate: -0.016; F_{red} : very low: 0.025, low: 0.036, moderate: -0.0008) at very low- and low-productive sites in comparison to moderately productive sites. Similarly, other studies reported such inconsistent responses of functional dispersion, e.g. to grazing at different productivity levels, due to different plant adaptation or avoidance strategies (Laliberté et al., 2013; Zuo et al., 2018).

Furthermore, changes in species richness were small but significantly different among management intensities at very low- and moderately productive sites. Species richness declined under all management intensities at very low-productive sites. In contrast, species richness increased at intermediate management intensity in low- to moderately productive sites. Again, lowest management intensities had the highest negative effects within each productivity level. These findings are in line with those of van Klink et al. (2017) and Tälle et al. (2018) who report that a moderate or only slightly reduced management intensity combined with fertilization could maintain or increase plant species richness. In contrast, an extreme reduction in management intensity with mowing cessation for more than 1 year had a negative impact on the number of species (Pykälä et al., 2005; Römermann et al., 2009), which was also observed at our grasslands.

4.3 | Management implications

Our results indicate the need to differentiate among productivity levels of wet grasslands when controlling invasive plants. Within these levels, efficiency in suppressing *J. aquatica* as well as the changes observed in the diversity of resident communities varied across management intensities. Although reduced management resulted in a stronger suppression of the native invader, moderate intensities should be preferred to avoid losses of plant diversity in wet grasslands, especially for sites with high conservation priority. Management plans should not only account for site productivity, but the management goals need to be well defined, because at sites with high *J. aquatica* abundance, where agricultural use is threatened, more severe measures might be required to control the species. Finally, intermediate management intensities are recommended for grasslands that are susceptible to invasions, thus avoiding future problems (Catford et al., 2012; Kershaw & Mallik, 2013).

5 | CONCLUSION

Based on grasslands with different soil conditions and management, there are some consistent responses of the native invader and the resident grasslands to the control management. This allows controlling the native invasive plant without negatively affecting plant species and functional diversities of wet grasslands with high conservation value. Overall, management effects on the abundance of *J. aquatica* are higher than effects on the functional composition and species richness of the resident communities. Therefore, in terms of biodiversity, a moderate suppression of this poisonous species is recommended, which would have little impact on the resident community. Yet, besides the intensity of the control measures, management plans must account for site productivity as this can change the effectiveness of measures applied.

AUTHOR CONTRIBUTIONS

Johannes Kollmann, Harald Albrecht, Marie-Therese Krieger and Julia Ditton designed the research; Marie-Therese Krieger and Julia Ditton collected the field data; Marie-Therese Krieger, Barteline Martina Baaij and Leonardo Henrique Teixeira worked on the plant traits data; Leonardo Henrique Teixeira designed the statistical analyses; Marie-Therese Krieger, Barteline Martina Baaij and Leonardo Henrique Teixeira processed and analysed the data; Marie-Therese Krieger, Johannes Kollmann, Harald Albrecht and Leonardo Henrique Teixeira discussed the results; Marie-Therese Krieger, with contributions from Johannes Kollmann, Harald Albrecht, and Leonardo Henrique Teixeira, wrote the manuscript, supported by all co-authors.

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DATA AVAILABILITY STATEMENT

All data included in this manuscript will be deposited at MediaTUM; those derived from public sources are available upon request.

ORCID

Marie-Therese Krieger  <https://orcid.org/0000-0001-7701-8629>

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SUPPORTING INFORMATION

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

Appendix S1. Overview of site characteristics and experimental treatments.

Appendix S2. Plant traits obtained from the literature.

Appendix S3. Post-hoc statistics of the generalized linear mixed-effects models (GLMMs).

Appendix S4. Information on changes in species richness.

Appendix S5. Correlation matrices of all analysed variables.

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