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Invasive legume affects species and functional composition of mountain meadow plant communities

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Abstract Plant invasions are among the key drivers of global biodiversity and ecosystem change. They often cause reductions in native species richness and overall biodiversity. Nitrogen-fixing plants are problematic as they affect soil nutrient availability and outcompete species of nutrient-poor sites. Here we assessed the impacts of the legume *Lupinus polyphyllus* on species and functional diversity of mountain meadow communities in the UNESCO Biosphere Reserve Rhön. We compared species diversity (richness, evenness and effective species number), functional diversity (functional richness, evenness, divergence and dispersion) and similarity of plots in three characteristic vegetation types (*Nardus* grassland, mesic and wet mountain hay meadows) between different lupine cover classes. We calculated community weighted means (CWMs) of single plant traits and plotted them against lupine cover classes. The invasion of *L. polyphyllus* homogenizes vegetation composition since the similarity among plots of the different vegetation types increased with increasing lupine cover. It significantly affected species diversity in terms of richness and effective species number and the functional divergence of the vegetation. The trait set of species occurring together with lupine was shifted towards more competitive trait values. We demonstrate strongly negative impacts of *L. polyphyllus* on different mountain meadow vegetation types since *L. polyphyllus*, fosters the growth of competitive species and leads to overall more productive plant communities.

Keywords Plant functional traits · Functional indices · Diversity indices · Invasive plant species · Lupinus polyphyllus · Mountain grasslands

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Introduction

Plant invasions are considered one of the major drivers of ecosystem modification and biodiversity change at the global scale (Davis et al. 2011; Duraiappah et al. 2005; Hejda and Pyšek 2009; Keller et al. 2011). The immediate and long-term consequences of invasions may often be detrimental for the invaded ecosystems, as plant invasions have led to substantial declines in biodiversity and ecosystems functioning. Invasive plant species may also affect native plant communities through altered habitat structure and related changes in

light conditions (Otte and Maul 2005) or effects on water availability (Drenovsky et al. 2012) and nutrient supply (Ehrenfeld 2010). As a result, invasive species may alter the species composition of native communities (Hejda 2013; Otte and Maul 2005; Thiele et al. 2010). They are generally considered to reduce species richness or even erode whole gene pools by the extinction of endemics (Vilà et al. 2010). Consequently, dominance of invasive plants may lead to biotic homogenization of the resident communities, which manifests as an increase in genetic, taxonomic or functional similarity (Tordoni et al. 2019). However, Sax and Gaines (2003) pointed out that non-native species might also increase species richness at regional scales.

Species diversity, measured as species richness and species evenness, is related to productivity and population dynamics and, thus, ecosystems functions and services (Mace et al. 2012). Measuring changes in these indices therefore constitutes a first approach to assess impacts of invasive species on native communities. Functional traits reflect species interactions with the biotic and abiotic environment (Brym et al. 2018) and variation in traits is therefore strongly related to species composition (Tordoni et al. 2019). As invasive plant species may increase community similarity between invaded sites, they may also change the functional trait composition of invaded communities and thereby affect ecosystem functioning. A high functional diversity as "the range of the functional traits of the organisms in a given ecosystem" (Tilman 2001) may be beneficial for resistance to invasion (Mason et al. 2005). Functional diversity indices, calculated from plant traits, are thus tools that adequately reflect the different components of functional diversity and are, therefore, useful to detect impacts of plant invasions.

One of the most common alien invasive species in Europe is *Lupinus polyphyllus* Lindl. Introduced as an ornamental and for soil melioration, it has spread in many countries and has become dominant in various ecosystems. It has become invasive in several European countries like Norway, Lithuania, Latvia and Germany, but also on other continents e.g. in New Zealand (Fremstadt 2010). Further, *L. polyphyllus* is among the 15 most common plant invaders and listed on the blacklist of invasive species in Germany (Nehring et al. 2013). As a legume, it may increase the nitrogen availability of soils (Holdaway and

Sparrow 2006), which will deteriorate conditions for species adapted to nutrient poor sites. It may furthermore outcompete smaller species for light due to its tall stature (Otte and Maul 2005) and thus reduce species richness (e.g. Ramula and Pihlaja 2012).

In the study area, the Rhön UNESCO Biosphere reserve, *L. polyphyllus* was introduced in spruce forests in order to meliorate soil conditions. A change of the mowing regime due to the foundation of the Biosphere reserve in 1991 was followed by a rapid spread of *L. polyphyllus*. Today, it dominates the landscape, building stands with covers up to 90% on many meadows. Especially affected by the invasion are *Nardus* grasslands (Habitats Directive 92/43/EEC, habitat type 6230: species-rich *Nardus* grasslands) and mesic and wet mountain hay meadows (habitat type 6520: mountain hay meadows; Klinger et al. 2019; Otte and Maul 2005; Volz 2003), which constitute the typical vegetation types of the Biosphere reserve.

Assessing the impacts of plant invasions on the community level, but also on species and functional diversity of resident communities, is crucial in order to coordinate restoration efforts and utilize resources as efficient as possible (Hejda 2013; Vilà et al. 2010). Particularly in sensitive areas, which host many rare and endangered plant species and are hence vulnerable to biodiversity loss, information on the impacts of invasive plant species are necessary. While previous studies have mainly focused on the impacts of *L. polyphyllus* on species diversity and community composition (Hejda 2013; Otte and Maul 2005), the simultaneous effects of *L. polyphyllus* on species and functional diversity are still poorly understood. To our knowledge, few studies addressed potential habitat-specific responses to the invasive *L. polyphyllus* (Thiele et al. 2010).

Therefore, we present a comprehensive study testing the impacts of *L. polyphyllus* on community composition, species diversity and functional diversity of grasslands. Since the impact of invasive plants may vary among invaded plant communitites, and different communities may be driven by different environmental constraints, we explored the effects of *L. polyphyllus* on the vegetation separately for *Nardus* grasslands, mesic and wet mountain hay meadows.

We ask the following research questions:

a. Does *L. polyphyllus* affect the species composition of mountain meadows?

We hypothesize that *L. polyphyllus* will increase the similarity across plant communities of the different meadow types.

b. Does *L. polyphyllus* affect the species diversity of the mountain meadows?

We hypothesize that *L. polyphyllus* increases species diversity (expressed by species richness, evenness, and effective species number) at low cover of *L. polyphyllus* by creating new niches, while all three variables will decrease at high cover.

c. Does *L. polyphyllus* affect multivariate functional diversity as well as community-weighted means of single traits of mountain meadows?

We hypothesize that with increasing lupine cover, sites become more productive, which will be reflected by the respective plant traits (SLA, seed releasing height, LDMC, seed number, flowering duration, life persistence). Functional diversity as well as the proportion of certain plant traits in the vegetation types will decrease with increasing cover of *L. polyphyllus*.

Materials and methods

Study area

The study was carried out in the mountainous region of the UNESCO Rhön Biosphere Reserve in Central Germany, which was founded in 1991 and comprises an area of approx. 2400 km^2. Tertiary sands and clays shaped the geology by building an elevated shelf, which is covered by basaltic rocks (Klausing 1988). Soils over basaltic bedrocks are usually well supplied with cations. However, in the Rhön region, high precipitation and traditional land use resulted in low nutrient availability and low pH values (Puffe and Zerr 1988). The mean annual precipitation at the highest elevation in the area, Mt. Wasserkuppe (950 m a.s.l.), amounts to 1,135 mm (mean of 1981–2010; DWD 2019) and the mean annual temperature reaches no more than 5.5 °C (mean of 1981–2010; DWD 2019).

Traditional land-use such as regular mowing and pastoral sheep-herding in combination with low fertilizer input shaped the landscape and formed extended semi-natural grasslands with high conservation value (Otte and Maul 2005). The Rhön Biosphere Reserve comprises 8,900 ha of low-intensively used species-rich grasslands and thus plays an important role in nature conservation (Grebe 1995).

Vegetation data

Vegetation was sampled in *Nardus* grasslands, mesic mountain hay meadows and wet mountain hay meadows. These types are characterized by high abundance of the following plant species: mesic mountain meadows—*Geranium sylvaticum*, *Trisetum flavescens* and *Alchemilla monticola*; wet mountain meadows – *Persicaria bistorta*, *Trollius europaeus* and *Deschampsia cespitosa*; *Nardus* grasslands—*Nardus stricta*, *Potentilla erecta* and *Galium saxatile*. The vegetation types differ in productivity with *Nardus* grasslands usually yielding 3 t * ha^{-1}, while mountain hay meadows produce about 6 t * ha^{-1} annually (Dierschke et al. 2002). In total, we used 84 vegetation plots (5 m x 5 m) sampled during the growing season in 2014 and 2016. Within each vegetation type, we selected plots with four levels of *L. polyphyllus* cover (class 1: 0%, class 2: > 0–25%, class 3: > 25–75%, class 4: > 75–100%) with seven replicates, resulting in 84 sampled vegetation plots. Selection of the plots sampled in 2014 took place shortly before the sampling. Plots sampled in June 2016 were selected based on their lupine cover in September 2015, therefore, slight differences between the original estimation and the sampled lupine cover might occur. Plant species cover was estimated using the approach of Braun-Blanquet (1964) and converted it into percentage values for further analysis (r = 0.01%, + = 0.5%, 1 = 3.0%, 2 = 15%, 3 = 38%, 4 = 62.5%, 5 = 87.5%). Plant nomenclature follows (Jäger et al. 2017).

Data analysis

1. Community composition

To obtain the main floristic gradients, we performed a non-metric multidimensional scaling (NMDS) ordination. We chose NMDS as a robust, distance-based method that accurately displays the vegetation data. NMDS was calculated based on Bray-Curtis distances as dissimilarity measure with 20 random starts and three dimensions using the

metaMDS function as implemented in the R vegan package 2.5-5 (Oksanen et al. 2019). We included *L. polyphyllus* in the ordination (for an NMDS without *L. polyphyllus*, see Fig. 7 in "Appendix"). The vegetation types and the lupine cover classes were used as grouping variables in the NMDS analysis. To avoid noise in the dataset we excluded species with less than three occurrences. We included weighted Ellenberg L (light), N (nutrients), R (reaction) and M (moisture) indicator values (including *L. polyphyllus*) as well as species diversity indices in the analysis in order to further evaluate the effects *L. polyphyllus* has on the vegetation composition.

To quantify the effects of *L. polyphyllus* on the community composition in the NMDS, we calculated the average distance of all plots in one cover class to the respective cover class centroid and compared these distances among the cover classes. Furthermore, we compared the distances of lupine cover class centroids with each other. In order to determine whether increasing cover of *L. polyphyllus* homogenizes the community composition, we estimated the similarity based on quantitative Sörensen dissimilarity (similarity = 1 − Sörensen dissimilarity) between all vegetation types within the cover classes. In order to account for environmental effects on similarities, we analyzed environmental alongside lupine effects on the similarity by means of a random intercepts linear mixed effect model without interaction term using the lme4 package (Bates et al. 2015). We calculated multivariate Gower distances between environmental variables (topographic wetness index and topographic position index derived from a digital elevation model and pH measured in 2015) of each plot using the FD package (Laliberté and Legendre 2010). *L. polyphyllus* cover classes and environmental distances served as fixed effects, whereas plot, i.e. vegetation type combinations, constituted the random effect. Statistical significance was obtained via bootstrapped p values based on 500 bootstrap samples from likelihood ratio tests between the full model with effects in question against reduced models without the effects in question.

Additionally, we calculated permutation-based analysis of variance (PerMANOVA, adonis function, Oksanen et al. 2019) in order to test for differences in species composition between lupine cover classes. Additionally, we used pH, topographic wetness index and position index as covariates to account for potential environmental effects. Subsequently,

pairwise differences in the species composition of the different lupine cover classes in each of the three vegetation types were tested using the pairwise.adonis function (Martinez Arbizu 2020). We ran PerMANOVAs and following pairwise comparisons with 1000 permutations and Bray-Curtis distances as dissimilarity measure. We obtained adjusted p values using Bonferroni corrections for the pairwise comparisons.

2. Species diversity

To test for changes in species diversity among lupine cover classes, we calculated species richness, effective species number based on Shannon diversity (Jost 2006), and evenness (Hill 1973). After visually inspecting diagnostic plots (Zuur et al. 2010), differences in effective species number and evenness were tested through one-way ANOVAs separately for each vegetation type and Post-hoc Tukey tests. In the case of species richness, we computed generalized linear models (GLMs) for Poisson distributions for the single vegetation types and pairwise post-hoc Tukey tests.

3. Functional diversity and traits

We preselected 14 traits that we considered being responsive to changing lupine cover (life persistence, leaf dry matter content, seed number, flowering onset, end of flowering, reproduction type, leaf persistence, flowering duration, strategy type, life form, canopy height, releasing height, seed mass, specific leaf area). We obtained trait data from the open source trait databases LEDA and BIOLFLOR (Kleyer et al. 2008; Klotz et al. 2002). Several studies have shown that using trait data from databases provides valuable estimates and meaningful results (Bernhardt-Römermann et al. 2011; Bernhardt-Römermann et al. 2008; Busch et al. 2018; Hattermann et al. 2019). In order to gain a reduced set of traits, we performed a double canonical correspondence analysis (double CCA) following the approach of Kleyer et al. (2012), using lupine cover as environmental gradient. By visual inspection of the resulting ordination plots, we identified six traits that best reflected functional responses to increasing lupine cover: (1) seed releasing height as a proxy for plant height, (2) LDMC (leaf dry matter content), (3) seed number, (4) SLA (specific leaf area), (5) flowering duration and (6) life persistence. Missing trait values were either obtained from literature or the mean value of the whole genus was taken. This was necessary in 23 (5 times canopy height, 10 times

LDMC, 6 times seed releasing height, 2 times seed number) of 1020 cases. Four species (*Tephroseris helenitis, Ranunculus polyanthemos, Ranunculus nemorosus, Crepis mollis*) had to be omitted because of lacking data. In order to achieve normal distribution of the data, seed number was log-transformed.

We calculated the diversity indices functional richness, i.e. the amount of niche space filled by the species in the community, functional evenness, i.e. the degree to which the biomass of a community is distributed in niche space, functional divergence, i.e. the degree of niche differentiation (Mason et al. 2005) as well as functional dispersion, i.e. the spread of the species in the trait space (Laliberté and Legendre 2010). Calculations were done using the dbFD function of the R package FD 1.0–12 (Laliberté et al. 2014) and included the most important dimensions of functional diversity (Mason et al. 2005). In order to test for differences in functional diversity indices between the lupine cover classes for each vegetation type, we performed ANOVAs and post-hoc Tukey tests after visual inspection of diagnostic plots (Zuur et al. 2010).

In addition, we examined if single traits were influenced by lupine cover through calculating the community weighted mean (CWM) for each trait, i.e. the averaged trait values, weighted by the relative abundance of each species (Garnier et al. 2015). In order to detect the direction of change within the single traits we plotted the CWMs against the lupine cover classes and added weighted linear least squares regression curves. We calculated linear models to assess the strength and significance of the relation between CWMs and *L. polyphyllus* cover.

Since we were furthermore interested in the proportions of functional groups on plots with different lupine cover we estimated the cover fractions of legumes (*Fabaceae*), separated into *L. polyphyllus* and other legumes, grasses (*Poaceae, Juncaceae, Cyperaceae*), and herbs (remaining species including some dwarf shrubs). For each vegetation type, we summarized the cover of all species belonging to each functional group within each vegetation type and cover class and used this as 100% cover, so that the results are represented as relative cover values of each functional group within each vegetation type.

All statistical analyses were carried out in the R statistical environment version 4.0.0 (R core team 2020).

Results

1. Community composition

The NMDS ordination plot (Fig. 1a) depicted floristic variation among and within the three main vegetation types. Across vegetation types, the centroid of lupine cover class 1 was closer to cover class 2 than to class 3 and 4, while the latter were situated very close together (Table 1).

In relation to the respective class centroid, mean distance of all single plots within each lupine cover class was largest in class 1 (0.789) and smallest in class 4 (0.297). One-way ANOVA showed significant differences in distances to centroids ($F_{3,80} = 21.1$; $p < 0.001$) among cover classes. Pairwise significant differences (Tukey test) between classes 1 and 2 ($p < 0.01$), 3 and 1 ($p < 0.001$), as well as 4 and 1 ($p < 0.001$) and 4 and 2 ($p < 0.01$) showed that the vegetation composition within the plots becomes more similar with higher lupine cover. In addition, the three vegetation types showed strong overlaps for plots with higher lupine cover (Fig. 1a). In *Nardus* grasslands, high lupine cover plots were less scattered than those with low cover (Fig. 1b). Richness and lupine cover correlated strongest with axis one (Richness: $R^2 = 24\%$, lupine cover: $R^2 = 61\%$). Effective species number and evenness on the other hand showed the strongest correlation with axis two (Effective species number: $R^2 = 24\%$, Evenness: $R^2 = 26\%$). In mesic hay meadows, high lupine cover plots were situated very closely together whereas low lupine cover plots were rather scattered (Fig. 1c). Effective species number and evenness in mesic hay meadows had an R^2 of 19% and 36%, respectively, and correlated with axis one, as did lupine cover and the N value ($R^2 = 68\%$, $R^2 = 38\%$, respectively). Mesic hay meadows had higher Ellenberg R and L values in plots with lower lupine cover. They correlated strongest with axis two ($R^2 = 50\%$, and 17% respectively). Species richness was also correlated with axis two ($R^2 = 19\%$). Similar to *Nardus* grasslands and mesic hay meadows also wet hay meadows showed a clear pattern, with plots with high lupine cover being located close together (Fig. 1d). Significant variables in wet hay meadows were Ellenberg indicator values N, R, L and M as well as lupine cover, all of which correlate with axis one (N:
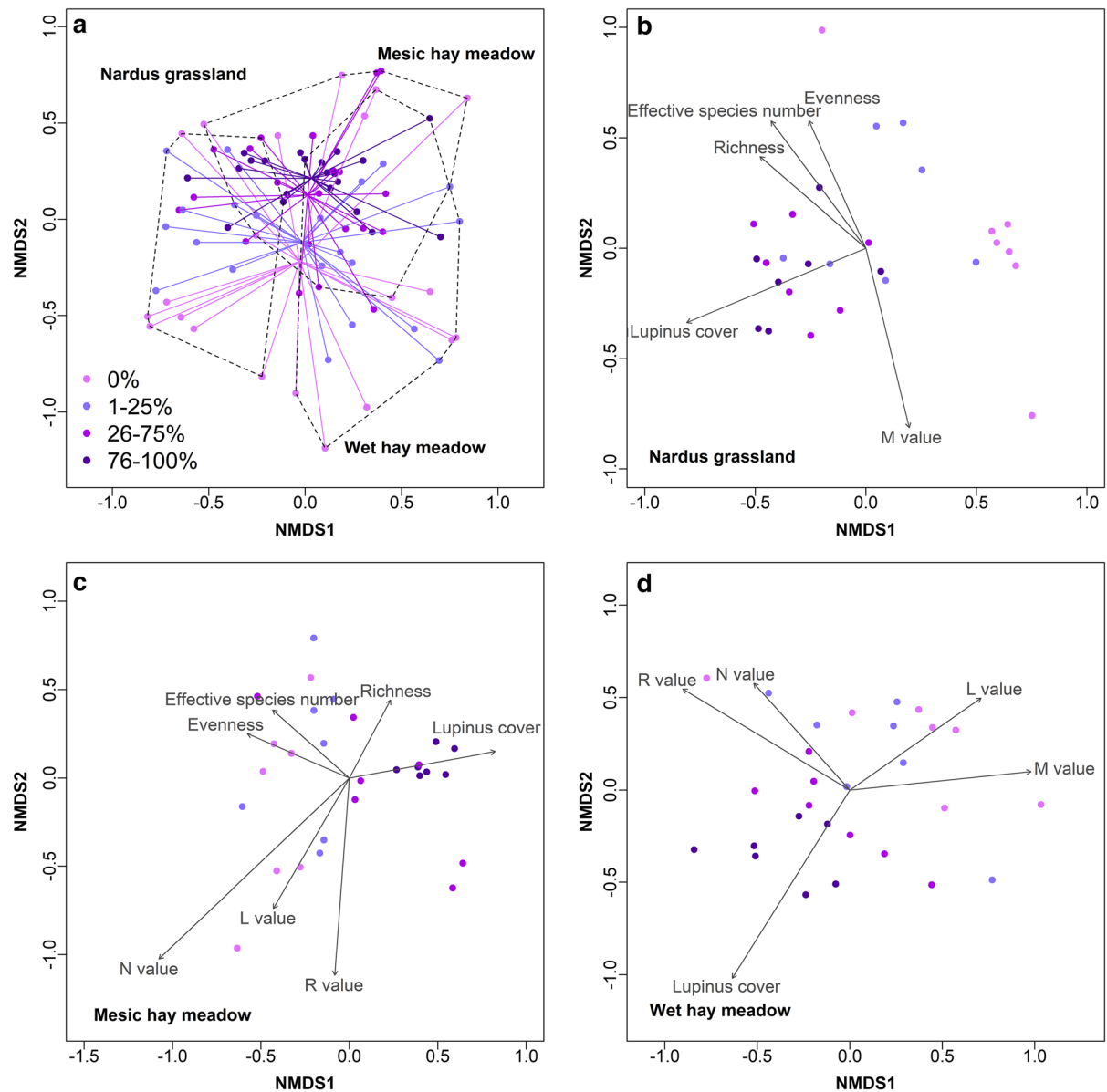
Fig. 1 NMDS ordination diagram of the main floristic gradients. The color scheme represents the lupinecover classes, the respective centroids of the classes are marked by a spider web. Vegetation types areencircled with dashed lines in (**a**). The arrows point in the direction of the strongest change in Ellenbergindicator values (light, reaction, moisture, nitrogen) and species diversity indices (species richness, effectivespecies number, species evenness) in (**b–d**). The length of the arrows represents the relationship betweenordination and gradient with a significance level of $p \leq 0.05$

$R^2 = 23\%$, R: $R^2 = 61\%$, L: $R^2 = 38\%$, M: $R^2 = 64\%$, lupine cover: $R^2 = 31\%$).

Mean similarity among vegetation types increased with increasing lupine cover, roughly doubling from plots without lupine to plots with $> 70\%$ cover (Fig. 2). Similarity was significantly affected by lupine cover (bootstrapped $p < 0.01$), while the environmental distance among the plots had no effect ($p = 0.93$).

Species composition between lupine cover classes differed significantly within the three vegetation types and these differences solely depended on *L. polyphyllus* cover classes across all vegetation types (PerMANOVA: *Nardus* grassland: $F_{3,27} = 3.5$, $p < 0.001$;

Table 1 Distances of NMDS *L. polyphyllus* cover class centroids to one another. With cover classes 1: 0%, 2: 1–25%, 3: 26–75%, 4: 76–100%

L. polyphyllus cover class	2	3	4
1	0.010	0.120	0.190
2		0.060	0.112
3			0.008
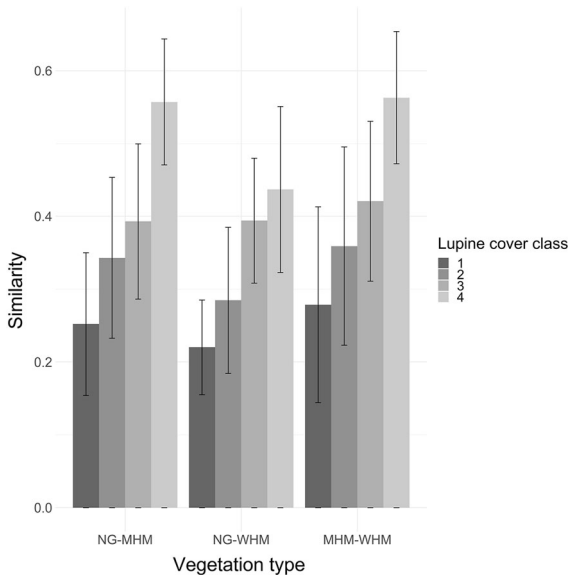
Fig. 2 Barplot of mean Sörensen similarity compared between vegetation types and lupine cover classes (1: 0%, 2: 1–25 %, 3: 26–75 %, 4: 76–100 %), where NG, Nardus grassland; MHM, mesic hay meadow, WHM, wet hay meadow. Bars show means ± standard error

mesic hay meadow: $F_{3,27} = 3.0$, $p < 0.001$; wet hay meadow: $F_{3,27} = 2.8$, $p < 0.001$), while environmental variables were not significant (*Nardus* grassland: cti: $F_{3,27} = 0.95$, $p = 0.44$, tpi: $F_{3,27} = 0.70$, $p = 0.75$; pH: $F_{3,27} = 1.15$, $p = 0.28$; mesic hay meadow: cti: $F_{3,27} = 1.19$, $p = 0.28$, tpi: $F_{3,27} = 1.27$, $p = 0.23$, pH: $F_{3,27} = 1,69$, $p = 0.09$; wet hay meadow: cti: $F_{3,27} = 0.72$, $p = 0.75$, tpi: $F_{3,27} = 1.10$, $p = 0.35$; pH: $F_{3,27} = 0.82$, $p = 0.61$). Pairwise comparisons of species composition differed significantly between cover classes 1 and 4 as well as 2 and 4 and 1 and 3 in *Nardus* grasslands, between cover classes 1 and 4 in as well as 2 and 4 in mesic hay meadows and between cover classes 1 and 4 as well as 1 and 3 and 2 and 4 in wet hay meadows (Table 2).

2. Species diversity

The 84 vegetation plots contained 173 plant species. Species richness ranged from 19 (*Nardus* grassland) to 57 (wet hay meadow) species per plot. Species richness and effective species number were significantly affected by *L. polyphyllus* in *Nardus* grasslands (richness: $F_{3,24} = 9.8$, $p < 0.001$; effective species number: $F_{3,24} = 7.8$, $p < 0.001$, Fig. 3a) and wet hay meadows (richness: $F_{3,24} = 3.4$, $p < 0.05$; effective species number: $F_{3,24} = 4.3$, $p < 0.05$, Fig. 3b). In both vegetation types, richness and effective species number were significantly higher at intermediate lupine cover classes than in plots without lupine. In mesic hay meadows, lupine cover had no significant effects on richness and effective species number (richness: $F_{3,24} = 2.3$, $p = 0.11$; effective species number: $F_{3,24} = 1.02$, $p = 0.40$; Fig. 3a, b). Evenness showed no clear pattern and did not vary significantly among lupine cover classes (*Nardus* grassland: $F_{3,24} = 0.90$, $p = 0.46$; mesic hay meadow: $F_{3,24} = 1.1$, $p = 0.38$; wet hay meadow: $F_{3,24} = 1.19$, $p = 0.33$; Fig. 3c).

3. Functional diversity and traits

All indices varied largely within vegetation types and cover classes. Functional richness and functional evenness were not significantly affected by lupine cover (*Nardus* grasslands: FRichness: $F_{3,24} = 0.27$, $p = 0.85$, FEveness: $F_{3,24} = 0.12$, $p = 0.95$; mesic hay meadows: FRichness: $F_{3,24} = 0.36$, $p = 0.78$; FEveness: $F_{3,24} = 2.98$, $p = 0.06$, wet hay meadows: FRichness: $F_{3,24} = 1.67$, $p = 0.2$, FEveness: $F_{3,24} = 1.91$, $p = 0.16$; Fig. 4a and b). Functional divergence was significantly higher in cover class four than in cover class one, two and three in mesic hay meadows ($F_{3,24} = 8.98$; $p < 0.001$, Fig. 4c) and differed significantly between cover classes two and four in wet hay meadows ($F_{3,24} = 3.42$, $p < 0.05$, Fig. 4d). It showed similar but non-significant patterns in *Nardus* grasslands ($F_{3,24} = 2.5$, $p = 0.08$). Functional dispersion differed significantly between cover classes two and four in mesic hay meadows ($F_{3,24} = 3.3$, $p < 0.05$) and was insignificant in *Nardus* grasslands and wet hay meadows (*Nardus* grasslands: $F_{3,24} = 0.41$, $p = 0.75$; wet hay meadow: $F_{3,24} = 0.19$, $p = 0.91$).

Community weighted means of single traits showed different responses among vegetation types (Fig. 5). In *Nardus* grassland communities, LDMC ($R^2 = 0.52$)

Table 2 Results of pairwise PerMANOVA comparisons between plant species compositions of four *L. polyphyllus* cover classes (1: 0%, 2: 1–25%, 3: 26–75%, 4: 76–100%)

Pairs	*Nardus* grassland				Mesic hay meadow				Wet hay meadow			
	df	F	R^2	p. adj.	df	F	R^2	p. adj.	df	F	R^2	p. adj.
1 versus 2	1	2.26	0.16	0.090	1	1.07	0.08	1.000	1	1.51	0.11	0.702
1 versus 3	1	5.9	0.33	0.006 **	1	1.96	0.14	0.300	1	2.62	0.18	0.036 *
1 versus 4	1	6.33	0.35	0.006 **	1	6.79	0.36	0.006 **	1	4.85	0.29	0.006 **
2 versus 3	1	2.29	0.16	0.114	1	1.59	0.12	0.756	1	1.91	0.14	0.162
2 versus 4	1	3.08	0.20	0.024 *	1	5.98	0.33	0.006 **	1	4.27	0.26	0.006 **
3 versus 4	1	1.03	0.08	1.000	1	1.74	0.13	0.708	1	1.97	0.14	0.108

With df, degrees of freedom; F, F-statistic, R^2 and p. adj. = adjusted *p* value. Asterisks mark the significance level (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

decreased whereas releasing height ($R^2 = 0.784$) and SLA ($R^2 = 0.29$) increased significantly with increasing lupine cover. In mesic and wet hay meadows, releasing height was significantly affected, showing the same behavior as in *Nardus* grasslands. LDMC decreased with higher lupine cover in both vegetation types, but only significantly in mesic hay meadows.

In all three vegetation types, the proportion of grasses was considerably smaller (0.24–0.26) in the highest *L. polyphyllus* cover class than in the lowest cover class (0.34–0.50), whereas the fractions of herbs declined to a minor extent. Other legumes were only affected and reduced in mesic and wet hay meadows (Fig. 6).

Discussion

Our results suggest that the invasive *L. polyphyllus* has significant effects on species composition of mountain meadow communities. When *L. polyphyllus* becomes dominant, many species of the native communities drop out (e.g. Thiele et al. 2010). The similarity among different vegetation types increased, which was reflected in the ordination and through direct comparison of centroid distances. This homogenization of native vegetation communities after plant invasion has been reported in several studies (La Sorte et al. 2014). This is most probably because only a specific set of other plants are able to co-exist with dominant non-native species (Hejda 2013), because they have a certain suite of functional traits (see below) matching with the conditions created by the dominant species (mass ratio hypothesis, Grime 1998). In contrast to Ramula and Pihlaja (2012), who could not show an effect of *L. polyphyllus* on community composition, using pooled relevés from meadows, forests, road verges and wastelands, we found a homogenization of the vegetation with increasing cover of *L. polyphyllus* among vegetation types. Moreover, our results showed that the species composition differed significantly within the vegetation types as lupine cover increased.

In *Nardus* grassland and wet hay meadow, the Ellenberg M value was lower in sites with a dense lupine cover. As the species itself has an Ellenberg moisture indicator value of 5 (Ellenberg et al. 1992) and hence an ecological optimum on mesic sites, *L. polyphyllus* apparently prefers sites with lower moisture in *Nardus* grassland and wet hay meadows. In mesic and wet hay meadows Ellenberg L value was higher were lupine cover was lower. Due to its tall growth, it fosters shade-adapted species that have a rather low light indicator value (Otte and Maul 2005; Thiele et al. 2010). Accordingly, species with high light value occur only in low lupine cover sites, where illumination is relatively high. Surprisingly, also the N value was higher in low lupine cover stands, while one would expect a higher N value in dense lupine stands, since *L. polyphyllus* increases plant available nitrogen (Hiltbrunner et al. 2014). The supposed discrepancy between expected and actual N value may result from the calculation of weighted Ellenberg values since *L. polyphyllus* has not been assigned an Ellenberg N value. Other species that co-occur with lupine and show high covers in mesic and wet mountain hay
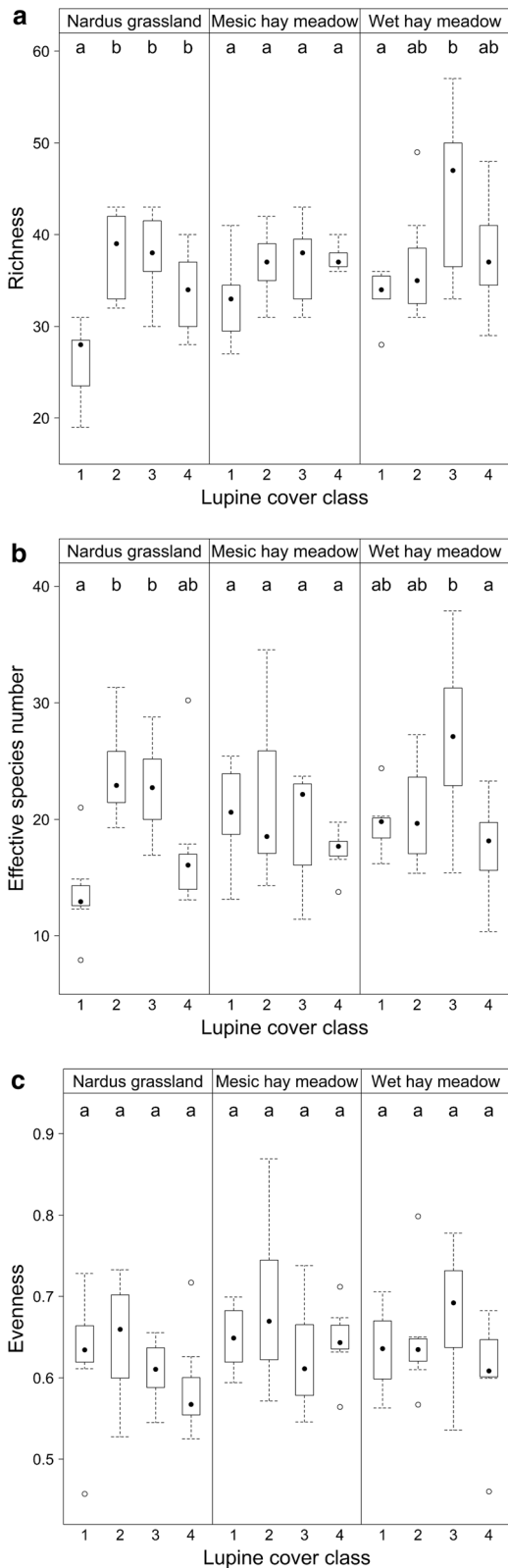
meadows have rather low or no N value, such as *Deschampsia cespitosa, Anthoxantum odoratum, Alopecurus pratensis, Cirsium palustre* or *Plantago lanceolata*. While our study was not designed to examine the soil conditions of lupine stands, these results may suggest that the change in vegetation composition is rather related to changing light and not soil conditions.

Many studies have shown that the character of the invaded community is decisive for the magnitude of the impact of invasive species (e.g. Hejda 2013; Mason et al. 2009). As pointed out by Thiele et al. (2010) especially *L. polypyllus* strongly interacts with the respective habitat type, which is in line with our findings. Species diversity was mainly affected in *Nardus* grasslands and wet hay meadows, where the introduction of *L. polyphyllus* increased the overall number of species. Similar results were found in studies conducted in Arizona (US), Australia and Uruguay, where exotic species increased local plant species diversity (Sax and Gaines, 2003 and see Davis, 2009). However, species richness and effective species numbers tended to decrease in the highest cover class, probably because small species will be shaded and outcompeted in the long term (Hejda 2013; Thiele et al. 2011). Mesic hay meadows were least affected by *L. polyphyllus*, as no significant impacts on species diversity indices were found. Species that co-occur here with lupine are often invasive in other regions of the world, such as *Anthoxantum odoratum, Trisetum flavescens, Festuca rubra* and *Holcus lanatus* (Gross et al. 2010; Hejda 2013). Thus, these species have high competitive abilities and can probably better cope with high lupine cover (Hejda 2013).

Multivariate functional diversity was not much affected by the lupine invasion. Functional divergence in mesic hay meadows and wet hay meadows showed increasing values in high lupine cover classes. This pattern of functional divergence may indicate a higher degree of niche differentiation in stands with high lupine cover (Funk et al. 2017) due to the increasing competition for light through lupine. Functional
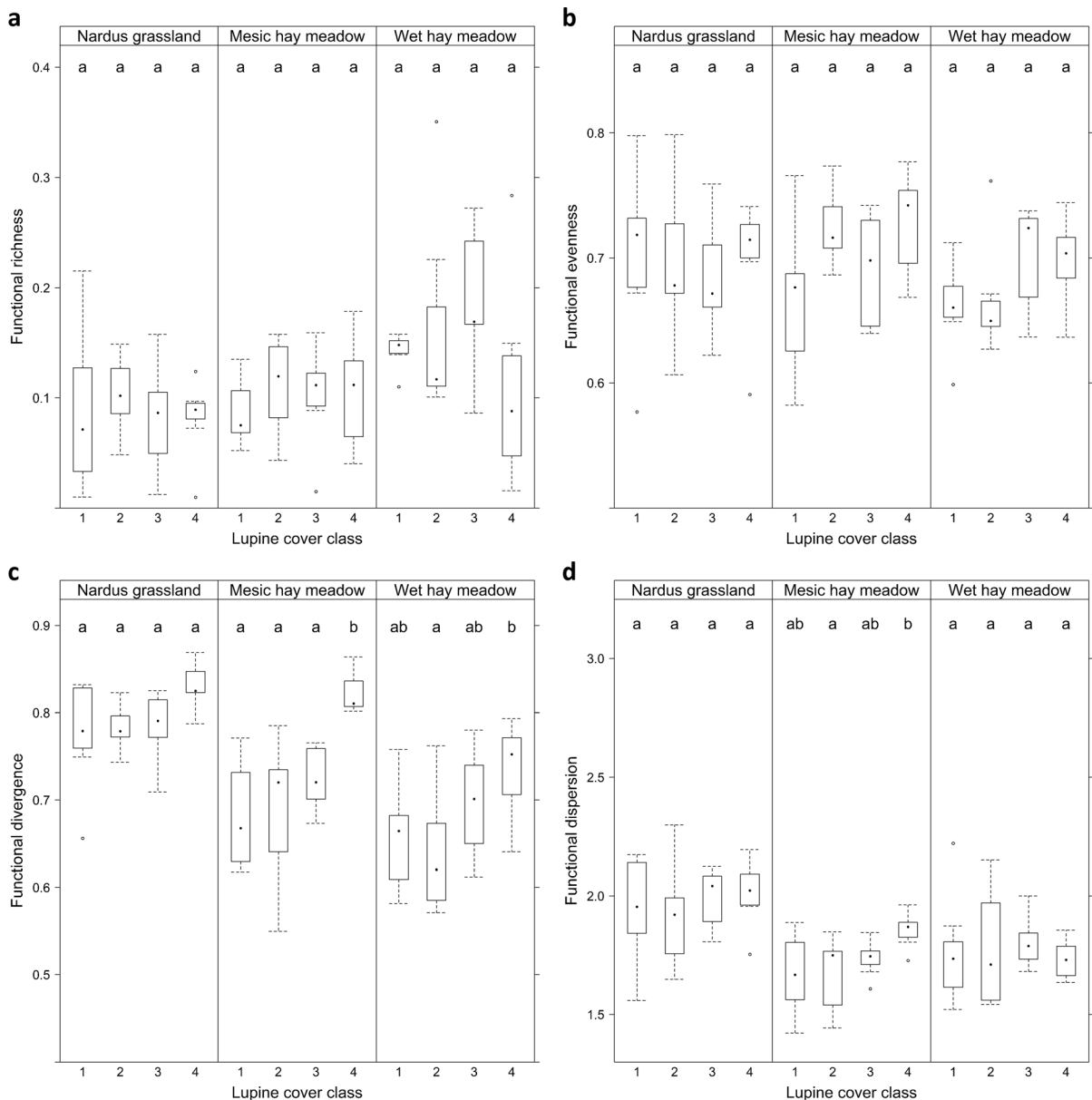
Fig. 4 Box whisker plots of the functional diversity indices, with dots representing outliers. Whiskers represent minimum and maximum of the data except for the outliers, the box upper and lower quartiles and the black dot the median. Equal letters indicate homogenous groups

dispersion showed a similar pattern in mesic hay meadows which may indicate a change of the spread of species in trait space (Laliberté and Legendre 2010) that may be caused by *L. polyphyllus* changing the location of the center of this trait space due to its high abundance. Concerning the CWMs of single traits, all three vegetation types were significantly influenced by *L. polyphyllus*. With high cover of lupine, they

harbored taller species with a lower LDMC. Large plant height implies high competition capacity (Bernhardt-Römermann et al. 2008), highlighting the increased competition capacity of co-occurring species in dense lupine stands. Species with low LDMC are associated with rather productive environments (Kleyer et al. 2008). In *Nardus* grasslands, lupine cover also significantly increased SLA, which may
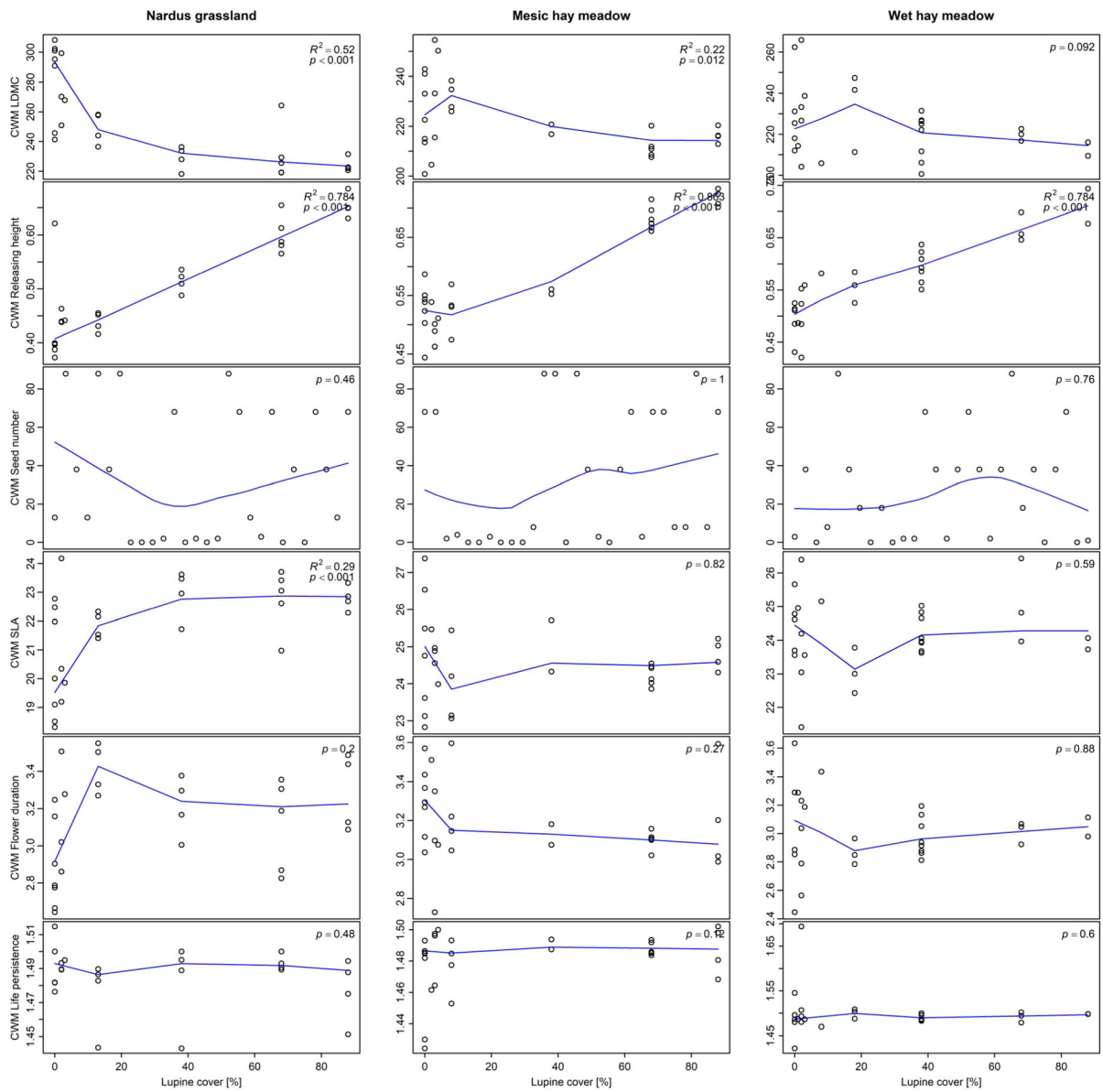
Fig. 5 Scatterplot of community weighted means (CWM) of single plant functional traits in relation to *L. polyphyllus* cover. The blue line indicates the weighted linear least squares regression curve (lowess). R^2 is given when *p* values are significant

indicate higher growth rates, higher leaf N concentrations (Westoby et al. 2002), and a higher productivity (Duru et al. 2014). Moreover species with a high SLA quickly invest nutrients in high-quality biomass and growth (Westoby et al. 2002). Taken together, increasing seed releasing height, decreasing LDMC in all high lupine cover vegetation types and increasing SLA in *Nardus* grasslands present evidence for higher productivity of lupine-dominated sites. In

accordance with Tordoni et al. (2019), our study suggests that a homogenization of the vegetation communities as well as significant shifts of single functional traits among the vegetation types occurred due to the *L. polyphyllus* invasion; yet the multivariate functional space itself was not affected. We suggest that since *L. polyphyllus* originates from mountain meadows (Starfinger and Kowarik 2003) it might, generally, have a similar set of functional traits as the

Fig. 6 Proportion of the plant functional groups within vegetation types and *L. polyphyllus* cover classes
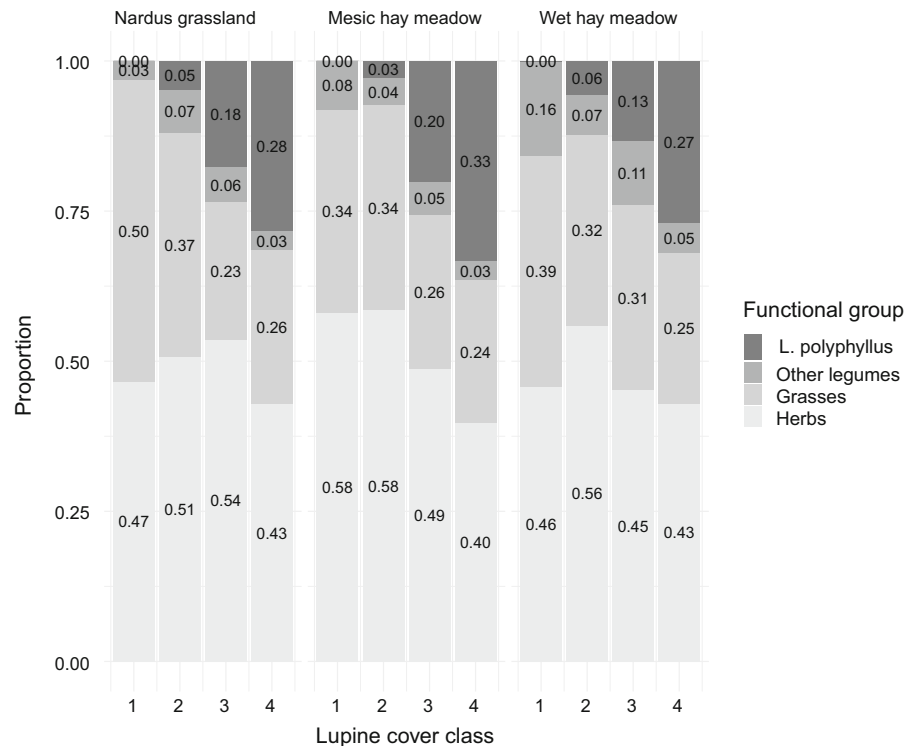
invaded community pool. Hence, *L. polyphyllus* does not change the dispersion of traits around the community mean in multivariate space, but it does promote a change of the mean value itself of certain traits, as it changes species composition and fosters the growth of competitive co-occurring species.

Our results showed that the proportion of functional plant groups changed substantially and consistently in all vegetation types with increasing *L. polyphyllus* cover. In unfertilized one-cut meadows the fraction of legumes is typically 10% (Voigtländer and Jacob 1987), while grasses and herbs have both a fraction of 45%. In the present study, the total proportion of legumes rose considerably with increasing *L. polyphyllus* cover, mainly to the disadvantage of grasses, which strongly declined. All three vegetation types hosted more than 30% of legumes and are thereby outside the range of unfertilized farmed grassland (Voigtländer and Jacob 1987). The changes of functional groups induced by *L. polyphyllus* again mirrors its shaping and homogenizing of the vegetation types.

Conclusions

Increasing cover of *L. polyphyllus* changed community composition and led to a homogenization of all three vegetation types. However, plots with low cover of lupine showed higher local species diversity. The primary effect of the *L. polyphyllus* invasion on functional diversity was a significant shift of certain species' traits to a more competitive suite of traits. Compared to mountain grasslands without lupine, the proportion of grasses dropped significantly in plots dominated by *L. polyphyllus*, whereas legumes increased. Since the study comprises vegetation types of high conservation value, hosting many rare and endangered species, measures to control the invasion and reduce the *L. polyphyllus* number are urgently needed.
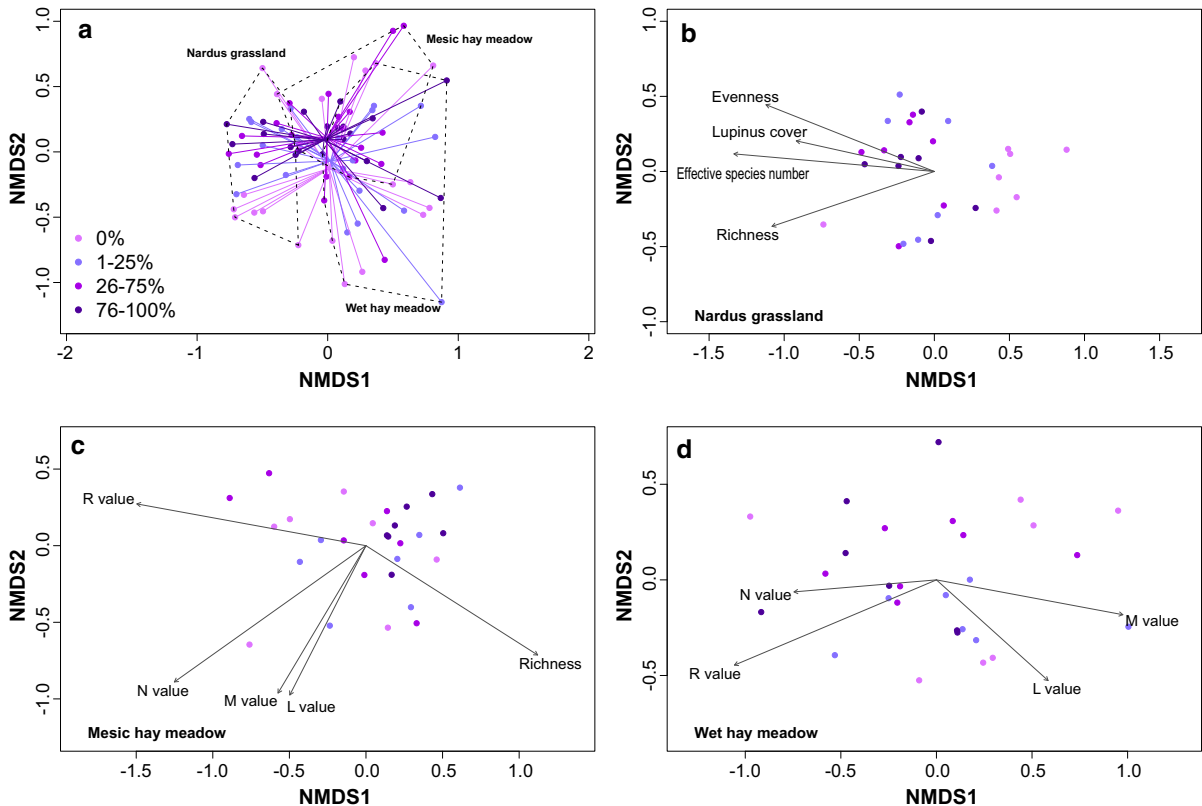
Compliance with ethical standards

Conflict of interest We declare that we have no conflict of interest.

Appendix

Fig. 7 NMDS ordination diagram of the main floristic gradients and excluding *L. polyphyllus*. The color scheme represents the lupine cover classes, the respective centroids of the classes are marked by a spider web. Vegetation types are encircled with dashed lines in (**a**). The arrows point in the direction of the strongest change in Ellenberg indicator values (light, reaction, moisture, nitrogen) and species diversity indices (species richness, effective species number, species evenness) in (**b–d**). The length of the arrows represents the relationship between ordination and gradient with a significance level of $p \leq 0.05$

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