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RESEARCH ARTICLE

Constraints in the restoration of mountain meadows invaded by the legume *Lupinus polyphyllus*

Wiebke Hansen[1,2], Yves P. Klinger[1], Annette Otte[1], Rolf L. Eckstein[3], Kristin Ludewig[4]

Semi-natural grasslands invaded by the legume *Lupinus polyphyllus* need the introduction of target species in order to promote highly endangered native target plant communities. However, which techniques are best suited to achieve both invader control and the introduction of target species at the same time? Few studies have investigated restoration techniques that support native plant communities in mountain meadows and control the invader simultaneously. We employed the restoration techniques seed bank activation and green hay transfer in combination with manual removal of the invasive *L. polyphyllus* on three types of grassland (*Nardus* grassland, mesic and wet mountain hay meadows) in the low mountain ranges of the Rhön UNESCO Biosphere Reserve in central Germany. Vegetation reacted differently to specific measures depending on the type of grassland. *L. polyphyllus* cover could be effectively reduced by *L. polyphyllus* removal in *Nardus* grassland and mesic hay meadow sites, but not in wet meadows. In *Nardus* grassland, the cover of target species was lowered by the application of green hay. The target species cover of wet mountain hay meadows declined in response to seed bank activation. When restoring mountain meadows, restoration practitioners should thus first consider the specific vegetation types. As our study indicates that target mountain meadow species may react negatively to restoration measures in the short term, the long-term effects of the application of green hay should be studied.

Key words: green hay transfer, invader management, invasive *Lupinus polyphyllus*, mountain-meadow restoration, seed-bank activation

Implications for Practice

- Green hay application might not be a suitable tool for restoring *Nardus* grassland since small species might not be able to grow through the plant material layer; in that case it should be removed before the following growing season.
- *Lupinus polyphyllus* cover on restoration sites can be reduced by manual removal of all parts of the plants, but a lasting reduction requires at least repeated applications.
- Reinvasion of *Lupinus polyphyllus* into restoration sites must be prevented with an appropriate management, e.g. early and/or repeated mowing.
- Active restoration through seed bank activation failed to promote mountain meadow target species and reduced the cover of wet mountain hay meadow target species.

Introduction

Semi-natural grassland ecosystems are among the most species-rich habitats in Central Europe (Habel et al. 2013). Semi-natural mountain meadows, in particular, provide habitats for many rare and endangered species. They are of high conservation value for both plant and animal species (Müller et al. 2014) but threatened by land use change and abandonment. Especially, land abandonment and deficient management might foster the spread of invasive species (Matus et al. 2003).

Since invasive species often act as ecosystem engineers, they may change environmental conditions and gain competitive advantages leading to the local disappearance of native plant species (Vilà et al. 2011; Lee et al. 2017). Consequently, they are regarded as a threat to biodiversity (Gallardo & Aldridge 2013). In many regions, invasive species massively complicate biodiversity and nature conservation efforts (Vilà et al. 2010) and invasive species control is hence a priority in the execution of many restoration projects (D'Antonio & Meyerson 2002).

Among the most common invasive species in Europe is *Lupinus polyphyllus* Lindl. (Nentwig et al. 2017). Being a tall-growing legume, *L. polyphyllus* has the potential to change the nutrient flows of ecosystems and to act as an ecosystem

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[1]Institute of Landscape Ecology and Resource Management, Research Centre for Biosystems, Land Use and Nutrition (IFZ), Justus Liebig University Giessen, Heinrich-Buff-Ring 26-32, Giessen, DE-35392, Germany
[2]Address correspondence to W. Hansen, email wiebke.hansen@umwelt.uni-giessen.de
[3]Department of Environmental and Life Sciences—Biology, Karlstad University, Universitetsgatan 2, Karlstad, SE-65188, Sweden
[4]Department of Biology, Faculty of Mathematics, Informatics and Natural Sciences, Institute of Plant Science and Microbiology, Applied Plant Ecology, University of Hamburg, Ohnhorststr. 18, Hamburg, DE-22609, Germany

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engineer. Thus, it meets the IUCN criteria for invasive species and is listed on the blacklist of invasive species in Europe (Nehring et al. 2013). Originating in Pacific North America, *L. polyphyllus* was brought to Europe in the nineteenth century to be grown as green manure and for ornamental purposes. However, it escaped from gardens and fields and is nowadays a common sight in road ditches, riverbanks, and meadows of European low mountain ranges (Valtonen et al. 2006). In the UNESCO Rhön Biosphere Reserve, the invasion of semi-natural species-rich mountain meadows by *L. polyphyllus* has been observed during the last three decades (Volz 2003; Otte & Maul 2005; Klinger et al. 2019). Located in central Germany, the Rhön Mountains are among the last refuges for Central European semi-natural mountain meadow ecosystems and their associated plant species. The ongoing spread of *L. polyphyllus* poses a serious threat to these mountain meadow species (Volz 2003; Otte & Maul 2005). *L. polyphyllus* was introduced to ameliorate soils of Rhön spruce afforestations in the 1940s. In recent years, it has spread and invaded the surrounding mountain meadows, probably due to changes in the traditional mowing regime (Volz 2003; Klinger et al. 2019). The UNESCO Biosphere Reserve Rhön was founded in 1991 in order to protect, among others, the largest Central European population of Black Grouse (*Tetrao tetrix*; Müller et al. 2007). To this end, annual mowing, traditionally carried out in July, was delayed to August or September. While early mowing had inhibited the spread and establishment of *L. polyphyllus* in the meadows, the shift to a later mowing date gave it opportunity to reproduce and disperse ripe seeds before mowing. Over time, this altered management for conservation resulted in a strong increase of *L. polyphyllus* cover. Nowadays many meadows in the nature conservation area are heavily invaded by *L. polyphyllus*. As it forms stands with up to 90% cover, it shades and outcompetes small-stature light-demanding species (Thiele et al. 2010) and thereby alters the vertical vegetation structure (Otte & Maul 2005). Moreover, tall-growing competitive species that benefit from *L. polpyhyllus* invasion homogenize the diversity within and among the different vegetation types (Hansen et al. 2020). To address this issue, since 2015 the mowing dates have been gradually brought forward again (T. Kirchner, personal communication, 2017).

Generally, in order to control invasive plant species in grassland ecosystems, different management techniques have proven successful, e.g. grazing, mowing, cutting of stems or reproductive parts, or even chemical control (Tyler et al. 2006; Nielsen et al. 2007; Ramula 2020; and see also Kettenring & Adams 2011). Thereafter, target communities may be promoted by sowing, turf or green hay transfer or soil seed bank activation (Kiehl et al. 2010; Klaus et al. 2018; Wagner et al. 2021). Many plant species build up persistent soil seed banks to overcome unfavorable times (Thompson et al. 1997). Hence, depending on the number of target species lost from the vegetation, their respective densities, and, to a lesser extent, overall seed density, species richness, and evenness in the soil seed banks, mechanical sward disturbance for soil seed bank activation may be a simple and inexpensive restoration tool. However, grassland communities are considered rather stable and therefore grassland species do not typically produce long-term persistent or many seeds (Bossuyt & Honnay 2008; Klaus et al. 2018). Accordingly, the soil seed banks of grassland sites targeted for restoration have to be investigated, to determine their suitability for restoration (Bossuyt & Honnay 2008). The restoration potential of the soil seed banks of the three most characteristic vegetation types in the Rhön Biosphere Reserve has been studied by Ludewig et al. (2021). Since the seed banks were specific to the vegetation types in question and contained the respective target species, they were deemed suitable for restoration. Moreover, the authors could not find any effects of the invasive *L. polyphyllus* on seed density and species richness of the seed bank. However, they recommended to actively introduce species not present in the soil seed bank, for instance by the application of green hay, that is, seed containing plant material transferred directly after cutting (Ludewig et al. 2021).

Restoration of degraded ecosystems is costly and hence projects must be planned carefully (D'Antonio & Meyerson 2002; Nielsen et al. 2007). To ensure that resources are used with maximum efficiency, the effects of restoration measures have to be tested and evaluated. In the case of invaded ecosystems, it is crucial to test restoration techniques that simultaneously control invasive species and promote the recovery of native species. Moreover, studies focusing on concrete management actions are urgently needed (Habel et al. 2013; Catalano et al. 2019). While many studies applied the abovementioned restoration measures on floodplain meadows (e.g. Donath et al. 2007; Klimkowska et al. 2007; Harnisch et al. 2014), only few studies used them to restore mountain meadows (but see Scotton 2019; Sullivan et al. 2020). To our knowledge, there have been no studies simultaneously exploring the effects of these restoration measures and of invasive plant removal across a range of mountain meadow communities. The present study focuses on restoring three different types of mountain meadows invaded by the legume *Lupinus polyphyllus* Lindl. in the UNESCO Rhön Biosphere Reserve. We applied a combination of different grassland restoration methods to restore plant species composition of three characteristic vegetation types in the Rhön region (namely *Nardus* grassland, mesic and wet mountain hay meadows). We used seed bank activation combined with application of green hay from uninvaded donor sites to overcome possible seed bank depletion. We investigated the vegetation development before (2017) and in 3 years after the treatments (2018, 2019, and 2021). We could not sample in 2020 due to the Covid pandemic.

We address the following research questions:

(1) Is seed bank activation an effective method for restoring different invaded mountain meadow vegetation types, that is, for reducing *L. polyphyllus* cover and/or promoting typical mountain meadow species?
(2) Is the additional application of green hay necessary for restoring the different mountain meadow vegetation types, that is, to reduce *L. polyphyllus* cover and/or promote typical mountain meadow species?
(3) Is manual removal of *L. polyphyllus* needed in order to reduce *L. polyphyllus* cover and hence to promote native species effectively?

Methods

Study Area

The study area is located in the UNESCO Rhön Biosphere Reserve in Central Germany, which was founded in 1991 and comprises an area of 2,400 km^2. The Rhön region is characterized by extended grassland areas used as hay meadows or for pastoral sheep herding. Low fertilizer input over centuries and the low-intensity land use resulted in species-rich semi-natural grasslands. The most frequent vegetation types that developed here are *Nardus* grasslands, mesic and wet mountain hay meadows (Otte & Maul 2005). As these vegetation types form habitats for many rare and endangered species they are of high conservation value and thus protected by the European Habitats Directive (92/43/EEC, habitat type 6,520: mountain hay meadows and 6,230: species rich *Nardus* grasslands). The dominant bedrock types in the Rhön region are Tertiary basalt rock, Triassic sandstones, and shell limestone (Klausing 1988). Although soils that developed on basaltic parent material are usually well supplied with cations, high precipitation and a traditional land use have resulted in low nutrient availability and low pH values in the area (Puffe & Zerr 1988). The precipitation on the highest peak in the region (Mt. Wasserkuppe with 950 m above sea level) amounts to 1,135 mm (mean of 1981–2010; DWD 2019) and the mean annual temperature is 5.5°C (mean of 1981–2010; DWD 2019).

The investigated vegetation types (i.e. *Nardus* grassland, mesic mountain hay meadow and wet mountain hay meadow) are located in the nature conservation area “Lange Rhön” that has been designated as such in 1982. All grasslands within the nature reserve are mown between 15 June and 1 August, with mowing dates varying between individual grasslands. Mowing may not be carried out before 15 June due to the protection of ground-nesting birds. Aftermath grazing by migratory sheep flocks is carried out after 15 August (Klinger et al. 2021). In the High Rhön, mountain hay meadows deliver annual yields between 2.5 and 4 tons dry matter/ha (Volz 2003). *Nardus* grasslands and mountain hay meadows developed on formerly forested sites after cutting and forest pasturing. *Nardus* grasslands can be found on shallow soils with low nutrient supply, whereas mesic and wet hay meadows occur on more base-rich soils with a good water and nutrient supply. The vegetation types are characterized by the regular occurrence of the following plant species: *Nardus* grasslands—*Nardus stricta*, *Potentilla erecta*, and *Galium saxatile*; mesic mountain meadows—*Geranium sylvaticum*, *Trisetum flavescens*, and *Alchemilla monticola*; wet mountain meadows—*Bistorta officinalis*, *Trollius europaeus*, and *Deschampsia cespitosa* (Peppler-Lisbach & Petersen 2001). The seed density of the soil seed bank (of all species and the target species) varies between the vegetation types with wet mountain hay meadows having higher seed densities than mesic mountain hay meadows and *Nardus* grasslands having the lowest density (Ludewig et al. 2021). This might influence restoration success via seed bank activation. Differences between these grassland types were also mentioned by Hansen et al. (2020), who showed that they responded differently to *L. polyphyllus* invasion.

Experimental Design

We set up experimental blocks in each of the investigated vegetation types. For each vegetation type, we selected two heavily invaded meadows and thus, restoration treatments were applied in six experimental blocks. In each restoration block we implemented two parallel strips separated by a guard row of 10 m. Each of the strips contained six 5 × 5–m permanent subplots (arranged in line) with a buffer of 5 m between the subplots, respectively. In each strip, two subplots each were assigned at random to each of three disturbance treatments, including: (1) soil seed bank activation—the soil seed bank of the upper 10 cm was activated with a cultivator, increasing the amount of bare soil and thus creating gaps in the vegetation; (2) seed bank activation plus *L. polyphyllus* removal—we manually removed all *L. polyphyllus* plants prior to the seed bank activation. *L. polyphyllus* plants were removed with weeding forks carrying two prongs of 27 cm, enabling us to uproot the whole plants and (3) control plots without any treatment. Finally, one of each pair of strips was covered with green hay from donor sites (Fig. 1). Thus, four repetitions for every treatment were set up. For each

(A)

(B)

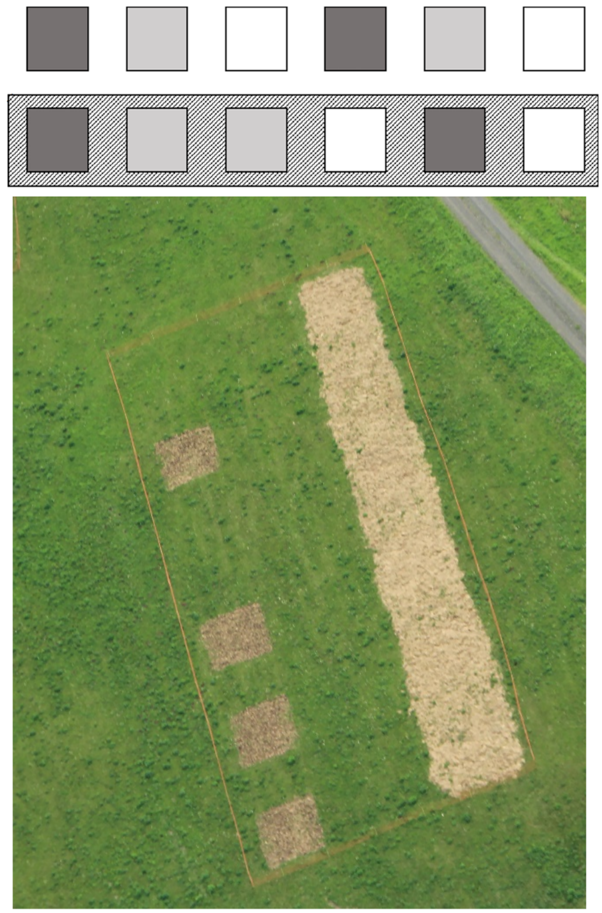

Figure 1. (A) Experimental design: with dark gray: *L. polyphyllus* removal; light gray: seed bank activation; white: control; dashed lines: green hay application. (B) The restoration experiment conducted on *Nardus* grassland; each treatment square is 5 × 5 m. Image: Torsten Kirchner.

vegetation type, the two restoration sites were located no more than 5 km from their corresponding donor site (Fig. 2). The donor sites were *L. polyphyllus*-free, species-rich, and belonged to the three investigated vegetation types, thus each restoration block received green hay from the corresponding vegetation type. The green hay of 5,000 m^2 was freshly cut and transferred to the restoration sites on the same day. The chosen amount enabled spreading of green hay from one donor site onto two recipient sites. The green hay was loosely spread, and the resulting hay layer was between 10 and 20 cm thick, with some variability due to the texture of the material, as well as target vegetation type. The restoration measures (seed bank activation and green hay application) for each vegetation type were carried out at the same day between July and the end of August (*Nardus* grassland: 8 July 2017; mesic hay meadows: 8 August 2017; wet hay meadows: 30 August 2017). This was the first cut of these sites in that year.

Vegetation surveys on the 5 × 5–m subplots were carried out in 2017 prior to the restoration experiment and repeated at the end of May in 2018, 2019, and 2021, resulting in 72 vegetation relevés per year. On each donor site the vegetation was surveyed on three 5 × 5–m plots in 2017 in those areas where the green hay was cut, resulting in nine donor site plots. Plant composition and cover were estimated using the modified Braun-Blanquet scale (Braun-Blanquet 1964). Taxonomy was based on Wisskirchen and Haeupler (1998).

Green Hay Sampling

In order to analyze the seed content of the transferred green hay, for each vegetation type, a composite sample of 160 L of plant material was taken after transfer. Germinable seed content of these samples was determined using the emergence method (Ter Heerdt et al. 1996). The green hay samples were threshed, and the fine material was spread in layers of approximately 10 mm on a sterile potting compost (Fruhstorfer Pikiererde LD80 Archut, Hawita Group)–sand mixture (2:1 relation) in styrofoam trays (18 × 28 cm). For the samples of each vegetation type, we prepared 30 trays in this way. To control for windborne seeds, additionally six trays only with sterile potting compost were randomly placed among the others; species that germinated in these trays were excluded from further analysis. In total, 96 styrofoam trays were exposed to optimized controlled greenhouse conditions for temperature (T_{day}: 18–24°C, T_{night}: 12–18°C), light (>10,000 lx from 06:00 to 22:00 hours) and humidity (<70%) and watered every third day. Emergence took place from

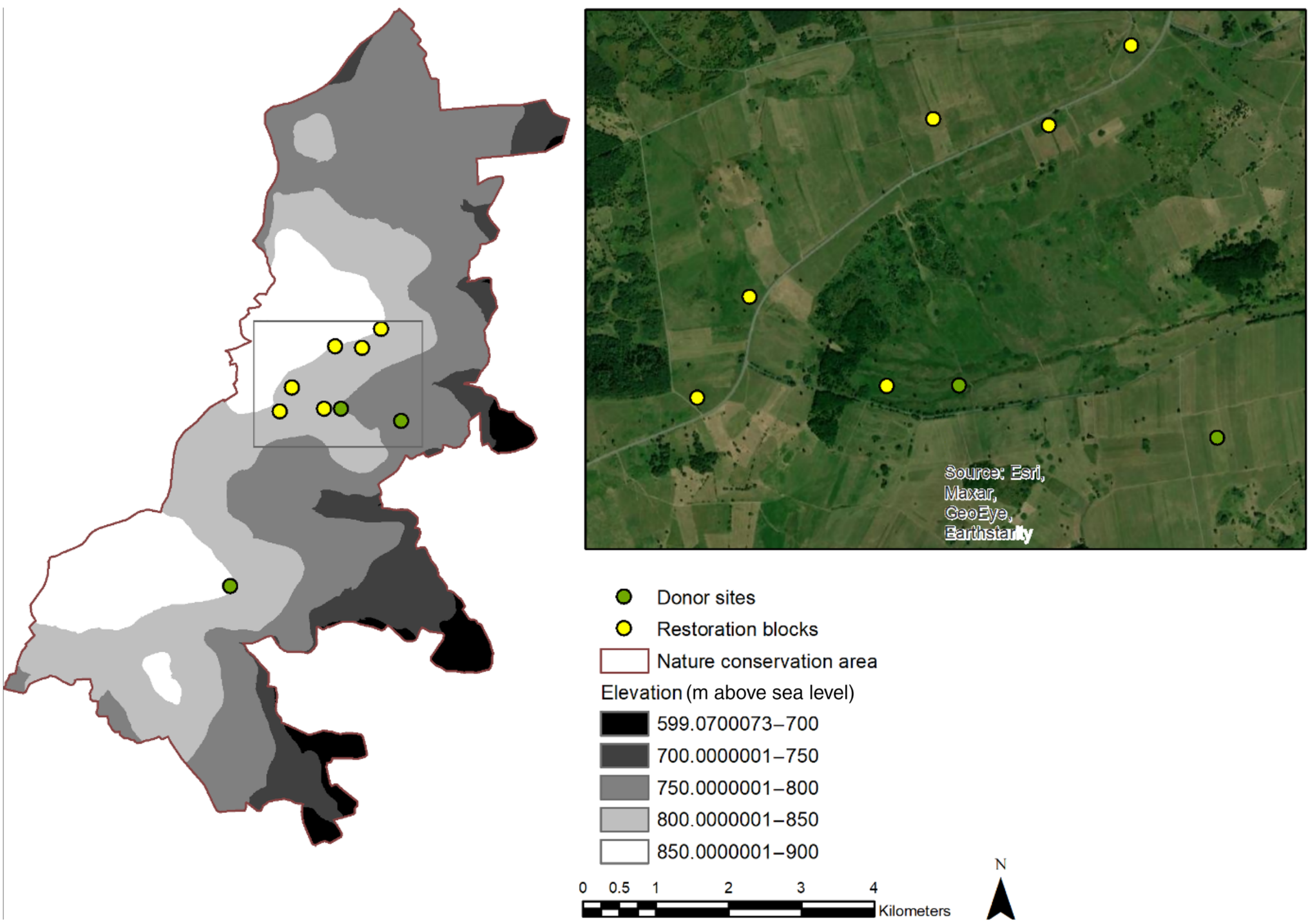

Figure 2. Location of the restoration blocks and donor sites in the nature conservation area and a zoom-in insert map.

November to the end of December 2017, subsequently the green hay samples were cold-wet stratified under outdoor conditions. After stratification, the experiment continued until no more seedlings emerged in August 2018. Emerged seedlings were identified using the key of Muller (1978). Seedlings that could not be identified were planted into pots and grown until identification was possible with Jäger et al. (2017).

Statistical Analyses

Phytosociological character species of the investigated vegetation types serve as target species in this study and were identified using appropriate literature (Oberdorfer 1977; Peppler-Lisbach & Petersen 2001; see Tables S2–S4). The vegetation cover data were transformed into percentage values ($r = 0.01\%$, $+ = 0.5\%$, $1 = 3.0\%$, $2 = 15\%$, $3 = 38\%$, $4 = 62.5\%$, $5 = 87.5\%$) for statistical analyses.

In order to investigate the effects of the different treatments on *L. polyphyllus* and target mountain meadow species, we ran four mixed effect models. *L. polyphyllus* cover and cumulative wet mountain hay meadow target species cover were log+1-transformed and the models calculated with the lmer function of the lme4 package (version 1.1.27.1; Bates et al. 2015). The cumulative cover of *Nardus* grassland species and the cumulative cover of mesic mountain hay meadow target species were analyzed with beta distribution (Damgaard & Irvine 2019), logit-link generalized linear mixed effect models using the glmmTMB function of the glmmTMB package (version 1.1.2; Brooks et al. 2017). The model structure was the same in all four models: we entered *L. polyphyllus* cover and the cover of the three groups of target species as response variable, vegetation type (three levels: *Nardus* grassland, mesic hay meadow, and wet hay meadow), disturbance treatments (three levels: i.e. *L. polyphyllus* removal, seed bank activation, and control), the transfer of green hay (two levels: yes and no), and year of the vegetation surveys (four levels: 2017, 2018, 2019, and 2021) with interactions served as explanatory variables. Hay strip ID (12 levels) nested in Block ID (six restoration sites) formed the random structure of the models. By this we accounted for the similarity in environmental conditions due to the spatial proximity between the strips within one restoration site. The significance of the fixed variables was tested with Wald chi-square test using the analysis of variance function of the car package (Fox & Weisberg 2019). Vegetation-type-specific treatment effects were obtained by calculating contrasts to the respective treatment group in 2017 within the vegetation types using the emmeans package (version 1.6.3; Lenth et al. 2021).

We computed nonmetric multidimensional scaling (NMDS) ordinations for each type separately with 20 random starts and three dimensions based on a Bray–Curtis dissimilarity matrix and including *L. polyphyllus* to identify main floristic gradients and changes within the vegetation types over time using the vegan package (version 2.5.6; Oksanen et al. 2019). We had one NMDS ordination calculated with the donor sites included to see if the restoration plots would shift in this direction over time, that is, donor and restoration sites become more similar regarding their vegetation composition (Fig. S1a) and one NMDS without the donor sites to enhance visibility of the single restoration relevés (Fig. S1b).

Species composition of restoration sites was compared to species composition of donor sites in order to assess performance of the different restoration measures. To this end, we calculated the mean Bray–Curtis similarity index (1 − Bray–Curtis dissimilarity) between the vegetation relevés of the restoration areas and the relevés surveyed on the donor sites (see Fig. S2).

All data analyses were carried out in the R statistical environment (version 4.0.3; R Core Team 2020).

Results

In total, we found 120, 137, 131, and 147 plant species in 2017, 2018, 2019, and 2021 in the aboveground vegetation, respectively. Numbers of species found in the three vegetation types and years are listed in Table S1. The total numbers of species increased slightly, whereas the numbers of target species in all three vegetation types stayed roughly the same during the investigation period.

A total of 25,769 seedlings belonging to 57 species germinated from the green hay samples. In total 29 species, 8 of which were target species, germinated from *Nardus* grassland samples; 37 species including 8 target species germinated from the mesic; and 42 species including 11 target species germinated from the wet hay meadows green hay samples. The highest number of individuals of target species germinated from the wet hay meadow samples, the lowest in the *Nardus* grassland samples (Table S2).

Species that were not present on the restoration sites in 2017 and only appeared in subsequent years are *Phyteuma orbiculare* in mesic hay meadows, *Agrostis canina*, *Galium palustre*, *Pedicularis sylvatica*, *Poa palustris*, and *Stellaria alsine* in wet hay meadows (Table S3). In turn, *Juncus effusus* was very abundant on wet hay meadows in 2017 but vanished completely in 2019 and 2021 (Table S4) just like *Cynosurus cristatus* in mesic hay meadows (Table S3).

Effects of the Restoration Measures on the Target Species Cover

The cover of *Nardus* grassland target species was significantly affected by the vegetation type (which could be expected), green hay application, and the interaction between year and green hay application. Year, green hay application, the interaction between year and green hay application, as well as the interaction between disturbance treatment and green hay application had a significant effect on the cover of characteristic mesic mountain hay meadow species. The cover of wet mountain hay meadow target species was significantly affected by the vegetation type, disturbance treatment, and the interaction between year and disturbance treatment (Table S5).

Generally, the data showed large variation, but some patterns could be revealed by comparisons to the plots surveyed in 2017 that serve as control plots. On *Nardus* grassland, the cover of target species was significantly lowered by the application of green hay material on control plots and on *L. polyphyllus* removal plots during all monitoring years, on seed bank activation plots target species cover was lower in 2018 and 2019 compared to the control plots in 2017. On plots where green hay was not applied, target species cover was lower on control and *L. polyphyllus* removal plots in 2021 (Fig. 3A). On mesic hay meadows the target species cover was significantly increased with the application of green hay on control and seed bank activation plots in 2019 compared to 2017. This effect disappeared again in 2021. On *L. polyphyllus* removal plots target species

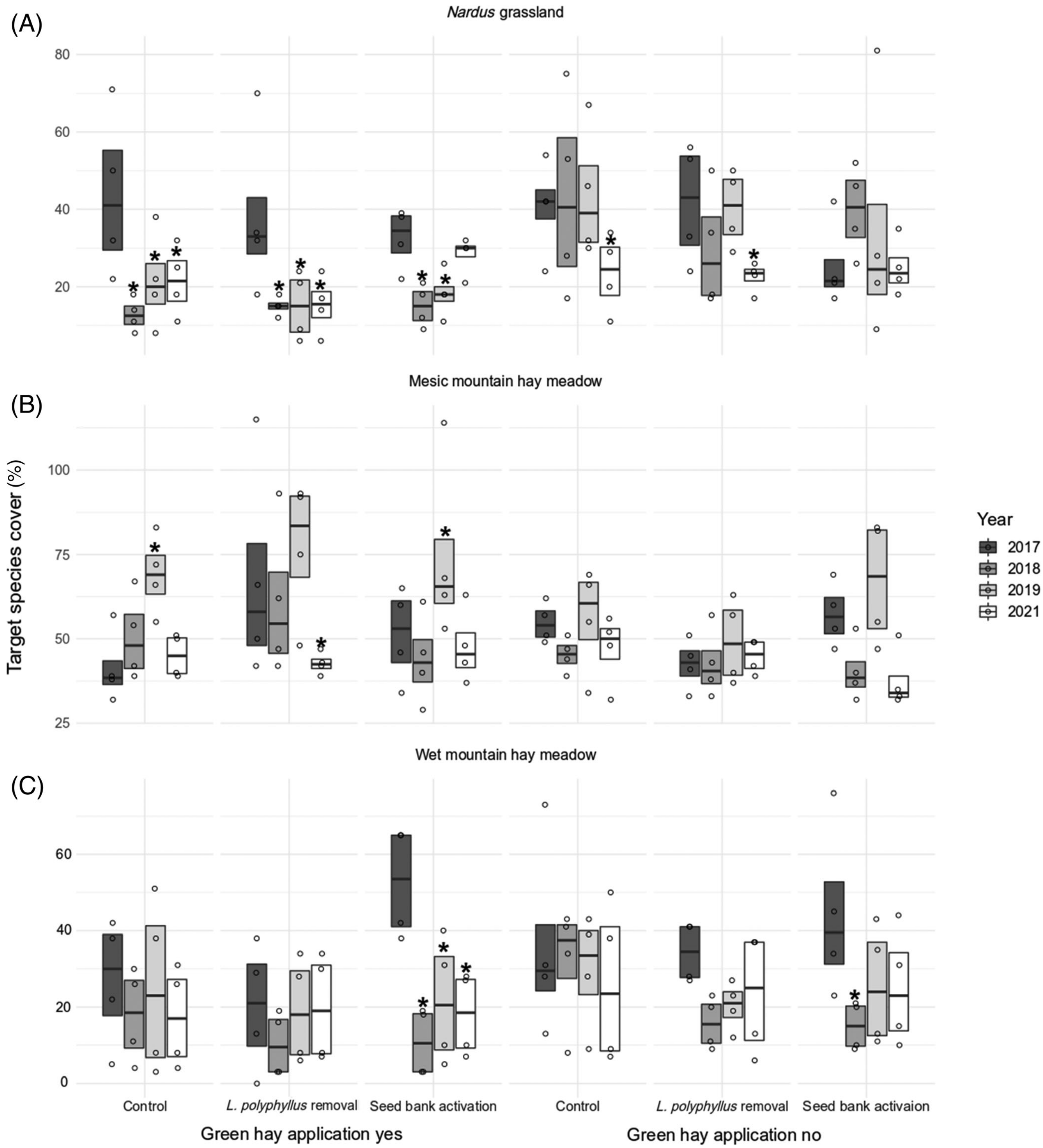

Figure 3. Box and scatter plots of the target species cover of (A) *Nardus* grassland, (B) mesic hay meadows, and (C) wet hay meadows during the study period. The boxes represent the upper and lower quartiles and the line the median. Asterisks indicate significant differences of pairwise comparisons within the vegetation type to the respective plots of 2017 ($p < 0.05$, contrasts to the respective treatment of 2017).

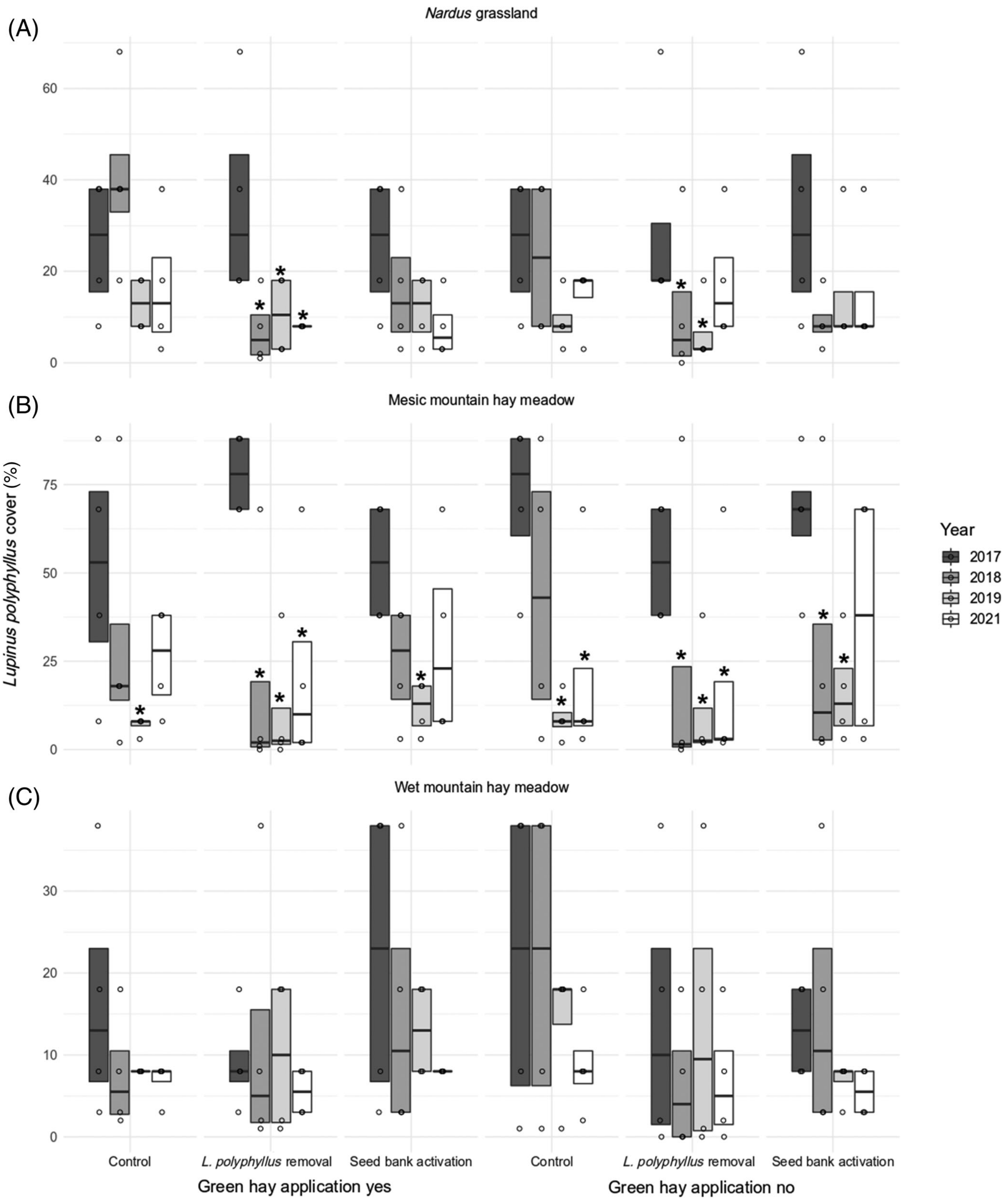

Figure 4. Box and scatter plots of the *Lupinus polyphyllus* cover of (A) *Nardus* grassland, (B) mesic mountain hay meadows, and (C) wet mountain hay meadows during the study period. The boxes represent the upper and lower quartiles and the line the median. Asterisks indicate significant differences to the respective plots of 2017 ($p < 0.05$, pairwise contrasts to the respective treatment of 2017).

cover was significantly lowered in 2021 (Fig. 3B). Seed bank activation with and without green hay application as well as *L. polyphyllus* removal without green hay application resulted in a significantly lower target species cover compared to the respective treatment in 2017 on wet hay meadows (Fig. 3C).

Effects of the Restoration Measures on the *L. polyphyllus* Cover

Year, disturbance treatment, and the interaction between vegetation type and year significantly affected *L. polyphyllus* cover (Table S5). *L. polyphyllus* cover was significantly lower in plots where the plant had been removed and green hay was applied in all monitoring years on *Nardus* grasslands and mesic hay meadows. Furthermore, *L. polyphyllus* cover was also lower on control plots and plots where the seed bank was activated, and green hay was applied in 2019 on mesic hay meadows. On sites where green hay was not applied *L. polyphyllus* cover was lower on plots where the plants had been removed on *Nardus* grasslands in 2018 and 2019 and on mesic hay meadows in all monitoring years. Apart from that mesic hay meadow control and seed bank activation plots had significantly lower *L. polyphyllus* cover in 2018 and 2019 (Fig. 4A & 4B). Removal of *L. polyphyllus* had no significant effects on its cover in subsequent years on wet hay meadows (Fig. 4C).

Effects of the Restoration Measures on the Species Composition

The restoration relevés were situated very close together in the NMDS ordination plot, as opposed to the donor site relevés of *Nardus* grassland and mesic hay meadows that were rather scattered and furthermore far apart from the restoration sites. In all vegetation types a strong influence of time (i.e. the year of sampling) can be seen in the restoration relevés. Clear patterns of the restoration treatments are, however, absent. The vegetation relevés of the restoration sites shifted during the study period, but they did not move in the direction of the donor site relevés (Fig. S1a). The influence of year of sampling can also clearly be seen in Figure S1b where the samples of the year 2019 are outside of the range of the samples of the three remaining years.

The Bray–Curtis similarity between vegetation of donor and that of the restoration treatment sites was generally very low across all three vegetation types. There was no influence of the restoration treatments that would be indicated by an increase in similarity between restoration and donor sites during the study period (Fig. S2).

Discussion

Effects of the Restoration Measures on the Target Species Cover

The applied restoration measures did not increase target species cover in the three vegetation types. While some species that had been absent from the vegetation of the restoration plots prior to the experiment did establish during the study period, we could not determine if this was due to the restoration measures. Other species in turn disappeared completely. Accordingly, seed bank activation lowered the cumulative cover of target species in wet hay meadows. This contradicts results that had shown the suitability of seed banks, although slightly depleted in species, for restoration (Ludewig et al. 2021). However, the transferability of the results of seed bank analyses may be limited due to known limitations of soil seed bank sampling methods to adequately affect actual species composition due to small-scale variation in the soil seed bank and usually limited sample volume (Bossuyt & Honnay 2008). Thus, the soil samples may only weakly reflect the actual species composition of the soil seed bank. Moreover, germination conditions in the field differ from those in the greenhouse and despite the fact that they are optimized for germination, they might not be suitable for all species (Wagner et al. 2021). Large open gaps as we created in the framework of our study may be susceptible to year-specific effects such as drought, which may have lasting effects on restoration success (Groves et al. 2020). Moreover, gaps are less shaded in the center which could inhibit germination, especially during summer drought. Thus, the atypically hot and dry weather conditions in 2018 (DWD 2018) might have especially impeded target wet meadow species from germination and establishment. This would be in line with other studies that identified drought as a main source of germination failure (Lawesson 2000; Hölzel & Otte 2004) and high seedling mortality (Silvertown & Dickie 1981; Ryser 1993). In all, the results presented here suggest that seed bank activation via large gaps does not guarantee success in promoting the establishment of target species in mountain meadows.

Ludewig et al. (2021) suggested that species missing from the soil bank could be actively introduced. Species diversity in grasslands can often be enhanced by additional introduction of seeds (Müller et al. 2014) and green hay transfer is a very efficient method with regard to the high number of seeds that can be introduced (Scotton & Ševčíková 2017). Many of the target species still occurred on the restoration sites prior to the experiment, although at low cover. Thus, the aim of the green hay transfer was to boost the native plant communities, increase propagule pressure of native species, and increase competitive effects on *L. polyphyllus* plants. Contrary to this aim, in *Nardus* grasslands the cumulative cover of target species was lower in plots where green hay was applied. Since many of the target *Nardus* grasslands species are of low stature (Otte & Maul 2005; Peppler-Lisbach & Könitz 2017) and slow growing, they might struggle growing through the green hay layer (Schmiede et al. 2013). In fact, restoration of *Nardus* grassland is generally difficult (Finck et al. 2017) and restoration efforts had no beneficial effects in experiments in the Netherlands even after a period of 25 years (Bakker et al. 2009).

The application of green hay has been carried out successfully in numerous restoration studies in flood meadows (e.g. Donath et al. 2007; Kiehl et al. 2010; Schmiede et al. 2013). In contrast to these findings, and although in our study, the hay samples from the wet hay meadows had the highest numbers of target species seedlings, green hay application did not produce any benefits in terms of target species cover at wet and mesic meadow restoration sites. Klimkowska et al. (2007) compared restoration techniques across a range of wet meadow restoration studies and found that the overall restoration success was rather limited. However, they also stated that many of these were short-term studies, as was the case in our study. Other studies have shown that a number of species establish in the second or third year after green hay transfer due to initial dormancy of their seeds at the time of green hay transfer and an accompanying delayed germination (e.g. Wagner et al. 2021). Although we could not observe these effects 4 years after green hay transfer, larger effects of the restoration measures may be visible in the future. Similarity of restored vegetation to donor site vegetation remained low for all grassland types. These findings are similar to those of Sullivan et al. (2020) who could not find an increased similarity between most of their investigated donor and restoration meadows even after a period of 11 years. However, a strong effect of year is visible in the cover data of target species, which is most likely a strong influence of the weather conditions during the study period, which included years characterized by atypical weather.

Effects of the Restoration Measures on the *L. polyphyllus* Cover

Manual removal of *L. polyphyllus* was well suited to reduce *L. polyphyllus* cover in *Nardus* grasslands and mesic hay meadows. Soil disturbance via seed bank activation reduced *L. polpyhyllus* cover significantly in mesic hay meadows. Other studies have shown that manual removal of invasive species can be a successful measure for their reduction (e.g. Pysek et al. 2007). However, as *L. polyphyllus* cover was not affected by any of the applied restoration techniques on the investigated wet hay meadows, these measures partly failed in the course of our restoration project. But given the low number of replications in the experiment, any observed reduction might simply have been too small to be statistically detectable. Also, favorable site conditions may have led to rapid recovery of *L. polyphyllus* plants, as in dry vegetation periods the soil conditions might tend to be more in the mesic range. Finally, initial *L. polyphyllus* cover at restoration sites at the start of the experiment differed between target vegetation types, and tended to be lower for wet hay meadows, probably since its competitive ability and vitality might be reduced under wet conditions (Klinger et al. 2019). However, repeated *L. polyphyllus* removal may be necessary to generally guarantee lasting reduction, as in our study, in 2021, *L. polyphyllus* cover had again increased at several sites. This could be problematic as manual removal of *L. polyphyllus* is time consuming and thus, costly. Furthermore, it should be done very thoroughly, as the species is able to sprout from even small rhizome parts of 2 cm (unpublished data), and single plants left unattended have the potential to spread rapidly (Klinger et al. 2019). Moreover, as *L. polyphyllus* has been an established species in the area for many years, reinvasion processes following control measures might occur in the long term. Given reduced levels of competition in depleted plant communities (Banks et al. 2018), the high number of *L. polyphyllus* plants on nearby grasslands, road verges, or other linear structures (e.g. clearance cairns and creek sides) may lead to high propagule pressure of the invader. Furthermore, as the grasslands used in our experiment were heavily invaded (with over 100 *L. polyphyllus* shoots removed on some 5 × 5–m experimental subplots), some plants may have survived experimental removal of shoots. Accordingly, the management regime has to be adapted to avoid that *L. polyphyllus* outcompetes newly established target species. If possible, this should include an early mowing of *L. polyphyllus* plants during full bloom, to prevent production of viable seeds. On sites where this is not possible due to the protection of ground-nesting birds, other measures could be used, e.g. removal with weeding forks or mowing with hand scythe for small *L. polyphyllus* stands or single plants. Larger stands that need to be mown with mowing machinery can also be mown after full bloom of *L. polyphyllus* as long as the seeds are green and soft. What should be avoided in any case is the dispersal of ripe *L. polyphyllus* seeds (characterized by brown to black color and hardseededness; Klinger et al. 2020) by mowing machinery or zoochory. Although another study found that mowing once annually reduced vital rates and biomass of *L. polyphyllus* (Ramula 2020), this could not be confirmed for the present study area (Klinger et al. 2019). Consequently, at heavily invaded sites, mowing more than once per year may be required. However, since preventing initial establishment is often more cost-effective than postestablishment control (Banks et al. 2018), small stands of *L. polyphyllus* or single plants should have the highest priority for control measures. Our results also revealed that *L. polyphyllus* cover was also significantly lower on control plots in the monitoring years. *L. polyphyllus* prefers sites with rather humid soil conditions, as reflected by its Ellenberg indicator value for moisture of five (Ellenberg et al. 1992) and thus the dry weather conditions might have resulted in lower *L. polyphyllus* cover.

Overall, our results provide mixed evidence for the effectiveness of the applied restoration measures. Interestingly, none of the applied measures seemed to be suitable to restore the investigated vegetation types, at least not over the limited duration of this study. On the contrary, the measures have rather led to the opposite effect, as green hay application on *Nardus* grassland and seed bank activation on wet hay meadows led to a decline in target species cover. Another surprising result is that *L. polyphyllus* management was not sufficient to foster the recovery of target species 3 years after the restoration efforts in all the investigated vegetation types. However, our study indicates several caveats that can hamper the success of restoration measures carried out in invaded meadows. These are, e.g. dry weather conditions or the potential of reinvasion in heavily invaded areas. Furthermore, our results underline the fact that different grassland types react differently to restoration techniques, which is why restoration measures should be carried out adaptively.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. NMDS ordination graphic of the main floristic gradients in the three vegetation types.
Figure S2. Bray–Curtis similarity between vegetation relevés of the restoration sites and the donor site relevés of the three vegetation types.
Table S1. Total number of species and the number of target species in the vegetation relevés.
Table S2. Target species of *Nardus* grasslands and the average cover values (%).
Table S3. Target species of mesic hay meadows and the average cover values (%).
Table S4. Target species of wet hay meadows and the average cover values (%).
Table S5. Results from the linear mixed effects models and generalized linear mixed models.

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