Native seed addition as an effective tool for post-invasive restoration

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Invasive plant species reduce biodiversity, alter ecosystem processes and cause economic losses. Control of invasive plants is therefore in high demand by land managers and policymakers. However, invasive plant control frequently fails, partly because management often concentrates only on the eradication of the invasive plants, but not on revegetation with native species that would use the available resources and prevent re-invasion. In this study, we focused on a within-continental invader *Rumex alpinus* L. that was introduced by humans from the Alps to lower mountains in Central Europe, where it spreads to semi-natural meadows, suppresses local biodiversity and reduces the quality of the hay as fodder for cattle. The species is effectively removed by herbicide but leaves behind a persistent seeds bank. Without further treatment, the invader rapidly regenerates and re-invades the area. We supplemented the herbicide treatment by seed addition of native grasses. Native seed addition effectively suppressed regeneration of the invader from the seed bank, reduced its biomass and consequently, prevented massive re-invasion. While the invader removal was successful, the restored community remained species poor because the dense sward of native grasses blocked regeneration of native forbs from the seed bank. Nevertheless, the addition of native seed proved to be an effective tool to prevent re-invasion after eradication of the invasive plant species.

Keywords: alien species; control; herbicide; seed bank; revegetation; ecological restoration; invader; weed; Rumex alpinus; seed limitation

Introduction

Biological invasions cause ecological and economic impacts around the globe ranging from biodiversity losses (Hejda, Pyšek, & Jarošík, 2009; Vilà et al., 2011), over changes in ecosystem processes and services (Liao et al., 2008; Pejchar & Mooney, 2009), to economical costs (Pimentel, 2002). Biological invasions were recognized as one of the main drivers of habitat degradation, and the scientific community is calling for management actions (IPBES, 2018). Management of invasive species includes prevention and early detection of new invasions, as well as eradication or mitigation of already existing invasive species and subsequent restoration (Pyšek & Richardson, 2010).

If a habitat is degraded through an invasion of an exotic plant species, its restoration can be challenging (Meyerson & D'Antonio, 2002). Many invasive plants are long-lived, perennial plants with high ability of vegetative propagation (Liu et al., 2006; Lowe, Browne, Boudjelas, & De Porter, 2000), and after mechanical eradication, they are able to re-grow from small vegetative fragments of rhizomes, roots or stolon that have been left behind (e.g. Klimeš, Klimešová, & Osbornová, 1993; Kollmann, Brink-Jensen, Frandsen, & Hansen, 2011; Weber, 2011). Even when the removal of vegetative plants was successful, for example after herbicide treatment, many invasive plants leave behind a legacy that challenges restoration success, for example in the form of physical or chemical alteration of the habitat or a buried seed bank (Corbin & D'Antonio, 2012; Loydi, Donath, Eckstein, & Otte, 2015). As seeds of invasive plants generally survive longer time in the soil than seeds of native congeners, soil seed banks contain a high proportion of invasive species (Drake, 1998; Gioria, Pyšek, & Moravcová, 2012). Seeds buried in the soil thus can be the source of rapid re-invasion of the space freed by removal of the vegetative plants. Management of seed bank is usually not effective (Cohen et al., 2018), and thus, post-invasion restoration requires filling the space that was emptied by removal of the invader, optimally by active revegetation with native species (Bakker & Wilson, 2004; Kettenring & Adams, 2011).

In ecological restoration, native species are frequently introduced in the form of seed (Hölzel, Buisson, & Dutoit, 2012). Seed addition proved to be an effective tool in post-mining restoration (Ballesteros et al., 2012; Kirmer, Baasch, & Tischew, 2012), re-establishment of semi-natural grasslands at former cropland (Coiffait-Gombault, Buisson, & Dutoit, 2012; Mitchley, Jongepierová, & Fajmon, 2012) or as a supplement to planting in forest restoration (Ceccon, González, & Martorell, 2016). On the other hand, seed addition in post-invasive restoration has mixed success (Petrov & Marrs, 2000; Pyke, Wirth, & Beyers, 2013; Wilson & Pärtel, 2003), suggesting this is a critical area for research in order to promote native species establishment and prevent repeated invasions (Kettenring & Adams, 2011).

We focus on a within-continental invader *Rumex alpinus* (Alpine dock), a species native to high European mountains like the Alps and Carpathians, but introduced by humans to lower Central European mountains like the Krkonoše Mts or Orlické Mts at the beginning of the 17th century, probably as a medicinal plant and vegetable. It typically grows on wet, nutrient-rich soils along mountain streams above tree line or at anthropogenic places around mountain chalets or cattle shelters (Šťastná, Klimeš, & Klimešová, 2010). Even in its native range, the species is considered a weed (Leuschner & Ellenberg, 2018), but it became especially troublesome in its introduced range, where it grows in lower altitudes and is more vigorous (Šťastná, Klimešová, & Doležal, 2012). In the Krkonoše Mts, the species invades semi-natural meadows under the tree line where it creates large stands. These meadows were created by humans centuries ago as grasslands traditionally used for hay production or grazing and as such, they depend on mowing or grazing in order to prevent natural succession towards forests. Such meadows are an inherent part of the cultural landscape in Europe, they typically host vast biodiversity and have high conservation value (Bengtsson et al., 2019). The current large stands of *R. alpinus* in the Krkonoše Mts. originated after WWII when many mountain meadows were abandoned due to societal changes (Šťastná, Klimeš, & Klimešová, 2010). Additionally, mountain chalets still lacked proper sewage treatment, their vicinity was rather wet, nutrient-rich and as such, it was optimal for the establishment of dense stands of *R. alpinus*. Although the nutrient input decreased several decades ago (Rehder, 1982), stands of *R. alpinus* persist and they strongly suppress native biodiversity (Delimat & Kiełtyk, 2019; Hejda, Pyšek, & Jarošík, 2009). As the species is avoided by cattle (Bohner, 2005), the stands are useless for mountain farmers who potentially wish to mow the mountain meadows for hay or as pasture. Consequently, there is a high demand for invasive plant control and restoring native vegetation. The target of such restoration is twofold: reduction of the invader and restoring native biodiversity. While suppressing the invader will make the meadows again suitable for haymaking or grazing, restoring community composition and native biodiversity will re-create the conservation value of these habitats.

Once *R. alpinus* has established a dense stand on a former grassland, restoration of the area is problematic. The first necessary step is the return of traditional management practices for semi-cultural mountain meadows because its cessation was among the main causes of the invasion. However, only returning to traditional management is not sufficient, because R. *alpinus* has large storage rhizomes that allow rapid regeneration after removal of aboveground biomass (Klimeš, Klimešová, & Osbornová, 1993). Topsoil removal, very frequent mowing, burning or chemical treatment suppresses the *R. alpinus* plants (Šilc & Gregori, 2016), but the species rapidly regenerates from a massive seed bank (Handlová & Münzbergová, 2006). Although seedlings of large docks are generally weak competitors and sensitive to mowing (Hujerová, Pavlů, Hejcman, Pavlů, & Gaisler, 2013; Zaller, 2004), seed banks contain only a limited number of native seeds which is not sufficient for rapid re-establishment of native vegetation (Handlová & Münzbergová, 2006). Thus, seed addition could be a possible tool for post-invasion restoration.

In this study, we tested whether the addition of native grass seed is a possible tool for restoring mountain meadows after eradication of an invasive species *Rumex alpinus*. We hypothesize that (1) seedlings of grasses will suppress *R. alpinus* seedlings, resulting in grass dominance at the restored plots, and thus, increase of biomass quality as fodder and that (2) suppressing *R. alpinus* via seed addition will increase native plant biodiversity.

Methods

The experiment was carried out at two sites in the Krkonoše Mts, that is Černá Voda (N 50°44'04"N, 94 15°48'40"E) at 950 m a.s.l. and Klínovky (50°42'32"N, 15°39'18"E) at 1200m a.s.l (Czech Republic). At each site, we selected vegetation with near 100% cover of *R. alpinus*. In early May 2000, we set up four pairs of experimental plots per site. As a run-off from the neighboring slope damaged two pairs of plots at the site Černá Voda, we established additional four pairs in 2001. In total, the experiment comprised of ten pairs of plots. Each pair consisted of two 1.5 x 1.5 m plots next to each other with 1 m spacing. In June 2000 (2001 for the replacement plots), the stands of *R. alpinus* were treated with glyphosate-based herbicide (Roundup, Monsanto, concentration 5%), which completely destroyed the vegetation on the plots. Three weeks after the herbicide treatment, we added grass seed to one random plot from each pair, while the other one remained without seed addition as a control. The seeds were collected the previous year in the neighborhood of the plots. Specifically, we used a mixture of *Alopecurus pratensis*, *Festuca rubra* and *Agrostis capillaris* in the densities of 500, 560 and 6500 viable seed per m2, respectively. We selected these species because they are common at the sites and have easy-to-collect seeds, and the different densities were determined by seed availability. The total seeding density approximately corresponds to high seed density recommended for restoration in difficult conditions (https://www.rieger-hofmann.de).

We monitored the vegetation for three consecutive years (two for plots established in 2001), always in June. We used the core 1x1 m of each plot to avoid edge effects and divided it into to 3x3 subplots. For each subplot, we recorded all species of vascular plants and estimated their cover using the Braun-Blanquet scale. For the data analysis, we use the mean percentage cover of each unit ("r,+" –

0.5%; "1" – 3%; "2" – 15%; "3" – 37.5%; "4" – 67.5%; "5" – 87.5%). At three randomly selected subplots, we clipped the biomass 3 cm above ground, separated it to grass, forbs and *R. alpinus*, dried it for 48 hours at 70 °C and weighed it. We collected the biomass at the same subplots in all three years of monitoring (two for plots established in 2001). The rest of the plot and surrounding vegetation was mown, as mowing is the traditional management necessary to maintain the target community in semi-natural mountain meadows.

Data analysis

In the first step, we evaluated the effect of seed addition on vegetation cover and biomass composition of the restored grasslands. We related (1) the proportion of biomass and (2) the cover of *R. alpinus* per subplot to the seed addition treatment, the year since plot establishment and their interaction in a linear mixed model. To account for non-independency of the samples, we fitted site, year of establishment, plot pair and plot identity as nested random factors. As the variances within the factors "seed addition" and "years since establishment" was not homogeneous (Levene test), we estimated variance separately for each level of the respective factor using the function varComb of the R package nlme (Pinheiro, Bates, DebRoy, & Sarkar, 2018). We did not test specifically for the differences between the sites because we did not have enough independent replicates for such analysis. Instead, we kept the sit as a random factor and focused on the main effect of the seed addition. We ran the same model also for grass biomass (cover) and forb biomass (cover) as response variables.

In the second step, we evaluated the effect of seed addition on plant biodiversity, represented as the richness of native species. We related the number of native species per plot to seed addition, years since establishment and their interaction in a model with the same structure as above. To illustrate to what degree the diversity difference was driven by sowing species, we also ran the same model for native species excluding the sown grasses.

Results

Seed addition had a profound impact on the vegetation of the plots. Without sowing, *R. alpinus* massively regenerated from the seed bank and constituted the majority of the biomass. In the first year, the unsown plots were rather variable, dominated by native forbs and *R. alpinus*, but forb biomass decreased over time. After three years, *R. alpinus* comprised 60-90% of the biomass (Fig. 1, Table 1). At the plots with seed addition, the sown grasses effectively suppressed *R. alpinus* and other forbs, and grasses constituted more than 90% of the total biomass in all three years (Fig. 1, Table 1). Although the biomass proportion of *R. alpinus* increased over time in the sown plots, it rarely reached more than 5-10% of the total plot biomass. Interestingly, the proportion of grasses increased in plots without seed addition as well (Fig 1). Results based on vegetation cover largely confirmed the pattern observed for biomass (Fig. S1, Table S1).

We did not detect any effect of the seed addition on the number of native species per plot. However, seed addition affected how the species richness developed in time. While the number of species did not change with the time in the unsown plots, it decreased in the plots with seed addition (Fig. 2. Table 1). Moreover, the majority of the native species in plots with seed addition were the sown grasses that suppressed almost all naturally regenerating native species (Fig S2, Table S2).

Discussion

Invasive plant control often fails, partly because the removal of the invader is not followed by active revegetation with native plants (Kettenring & Adams, 2011). Here we show that an addition of native grass seeds after herbicide application can effectively suppress invader regeneration and restore the target community. While without the seed addition, the invader regenerated from the seed bank and formed 60-90% of biomass after three years, seed addition reduced this number to less than 10%. This method is definitely the most effective control of *R. alpinus* (Šilc & Gregori, 2016). Moreover, such success exceeds the average success reported in other studies on plant invasion control (Kettenring & Adams, 2011). On the other hand, the restored community was species poor because sown grasses created so dense sward that they suppressed other native species.

Invader suppression

There are three possible reasons why the control of the invasive plant species was so effective in this study. First, we focused on a biological invasion with a known underlying change in abiotic conditions, in this case, cessation of traditional management. It was relatively straightforward to re-introduce mowing and re-establish abiotic conditions as the pre-requisite of any successful restoration (McDonald, Gann, Jonson, & Dixon, 2016). Second, we combined two suppression methods, i.e. herbicide treatment, and seed addition. While this combination is relatively common in invasive control, such a success as in the present study is rare (e.g. Mahmood et al., 2018; Sheley, Mangold, & Anderson, 2006). Generally, a combination of methods is usually more successful than a single method (e.g. Averill, DiTommaso, & Morris, 2008; Baer & Groninger, 2004; Dodson & Fiedler, 2006; Kilbride & Paveglio, 1999). Third, detailed knowledge of the biology of both the invader and the target community allowed us to design a restoration strategy that takes advantage of the weaknesses of the invasive and the strengths of the native species. While adult *R. alpinus* plants are competitively strong, seedlings are weak and sensitive to mowing (Hujerová et al., 2013; Zaller, 2004). In contrast, European grasses, as dominants of semi cultural meadows, faced extensive mowing or grazing for centuries and they are adapted to it. When clipped or mown, they often produce more tillers, spread clonally and form a dense ground cover that is competitively strong (Alexander & Thompson, 1982; Pecháčková, Hadincová, Münzbergová, Herben, & Krahulec, 2010). This mechanism allowed the sown grassed to suppress seedlings of *R. alpinus* that regenerated from the seed bank.

Although seed addition significantly contributed to the suppression of *R. alpinus*, some plants did regenerate, yet stayed rather small. In fact, the proportion of *R. alpinus* increased over time on plots with added seeds. The obvious question remains whether the few established dock plants will eventually suppress the grasses and form dense stands. We believe such a scenario is unlikely as long as the meadows are mown. The seedlings may still die due to competition from grasses, as mortality of dock seedlings in a mown grassland is highest among plants that are three to four years old (Hongo, 1989). Even if the dock plants survive, they are unlikely to spread. Historically, *R. alpinus* grew for two centuries in small, isolated stands in the Krkonoše Mts, and was relatively harmless as long as the meadows were managed (Šťastná, Klimeš, & Klimešová, 2010), while it started spreading after the management stopped. Such a scenario may repeat, and cessation of mowing of the restored grassland may trigger re-invasion from the persistent seed bank (Handlová & Münzbergová, 2006). This indeed happened to the plots presented in this study, because the management terminated together with the end of the experiment in 2003. After few years without mowing, the restored 1.5 x 1.5 m grasslands were taken over by a dense stand of *R. alpinus* (personal observation).

The effect on native biodiversity

While seed addition suppressed *R. alpinus*, it did not have any positive effect on native biodiversity. On the contrary, sown grasses were competitively strong, and thus prevented the establishment of other species from the seed bank or seed rain. This is a common problem when grasses are seeded in high densities (Dickson & Busby, 2009). A possible solution would be a more diverse seed mixture. In this study, we collected seed manually, and we restricted ourselves to the most common grasses with easy-to-collect seeds. The more suitable alternative could be species-rich seed mixtures produced by threshing of local hay or commercial regional mixtures that are increasingly available throughout Europe and other areas of the world (e.g. (Breed et al., 2018; Bucharova et al., 2019; Kiehl, Kirmer, Shaw, & Tischew, 2014; Mitchley, Jongepierová, & Fajmon, 2012). Another reason for the strong grass dominance may be a high content of available nutrients in the soil. As *R. alpinus* produces a lot of biomass that accumulates in the topsoil, the substrate is rich in humus and thus, available nitrogen (Bohner, 2005). Together with a possible legacy of increased phosphorus due to historical sewage pollution, the nutrient content in the soil could have allowed the grasses to be more productive and outcompete forbs (Hájek et al., 2017). With the regular mowing and removal of biomass, the nutrient content will decrease over time (Oelmann et al., 2009). However, even in this case, the addition of a species-rich seed mixture may be necessary to restore a diversity comparable to the reference habitat, a species-rich mountain meadow (Stampfli & Zeiter, 1999).

Conclusion

We have shown that addition of native seeds is a powerful tool for post-invasive habitat restoration, as native vegetation established from seeds prevents re-invasion from the seed bank, restores native vegetation cover and ecosystem services in the form of biomass suitability as fodder for cattle. The success was determined by detailed knowledge of the biology of both invasive and native species, which allowed us to design a method that uses the weaknesses of the invader and the strengths of the local species. This highlights the importance of research on invasive plants because lack of information on species biology resulting in suboptimal management can be among the reasons why invasive plant control and subsequent restorative efforts often fail (Kettenring & Adams, 2011).

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Figure 1: The effect of seed addition on the proportion of biomass of *Rumex alpinus*, grasses and forbs, and its development over time since establishment of the plots. Plots on the left visualize results without seed addition and on the right after seed addition. Biomass data values are represented as colored dots in the graph. Significant effects are shown in Table 1.

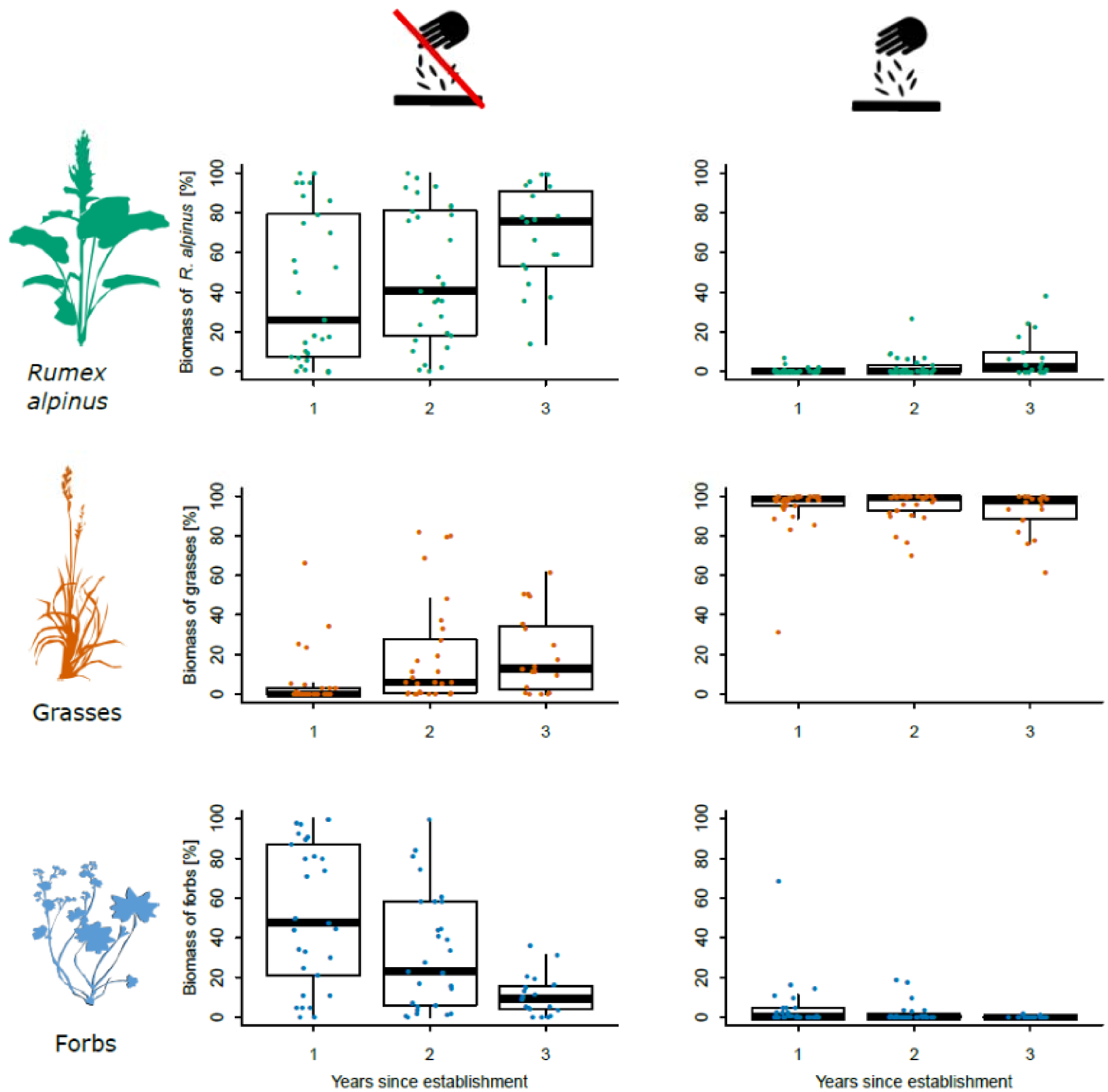

Figure 2: The effect of seed addition on native plant species richness, and the development of species richness over time since establishment of the plots. Plots on the left visualize results without seed addition and on the right after seed addition. Species number values are represented as dots in the graph. Significant effects are shown in Table 1.

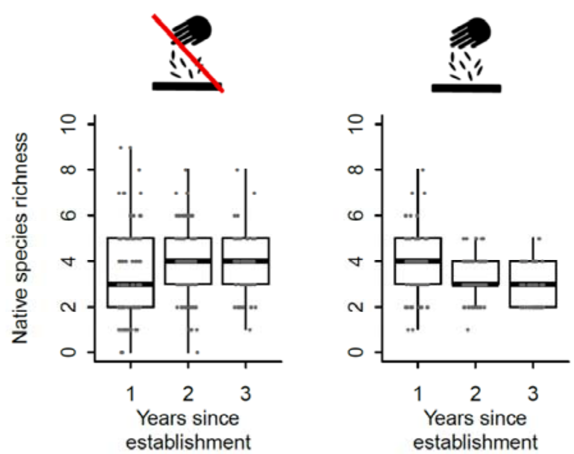

Table 1: The effect of seed addition and the time since plot establishment on the proportion of biomass of *Rumex alpinus*, grasses and forbs, and the richness of native species. Results of ANOVA of linear mixed models, terms fitted sequentially, significant values (P<0.05) are in bold.

	Proportion of biomass								Native species richness			
			R. alpinus		Grasses		Forbs					
	Num DF	Den DF	F value	*P* value	F value	*P* value	F value	*P* value	Num DF	Den DF	F value	*P* value
Intercept	1	91	4.874	**0.030**	256.8	**<0.001**	12.32	**<0.001**	1	281	25.10	**<0.001**
Seed addition	1	9	47.09	**<0.001**	676.7	**<0.001**	66.00	**<0.001**	1	9	4.133	0:073
Years since establishment	2	91	6.501	**0.002**	0.844	0.433	7.500	**<0.001**	2	281	1.092	0.337
Seed addition × Years	2	91	0.566	0.570	5.352	**0.006**	11.298	**<0.001**	2	281	31.99	**<0.001**

FigureS1: The effect of seed addition on the cover of *Rumex alpinus*, grasses and forbs, and its development over time since establishment of the plots. Plots on the left visualize results without seed addition and on the right after seed addition. Cover data values are represented as colored dots in the graph. Significant effects are shown in Table S1.

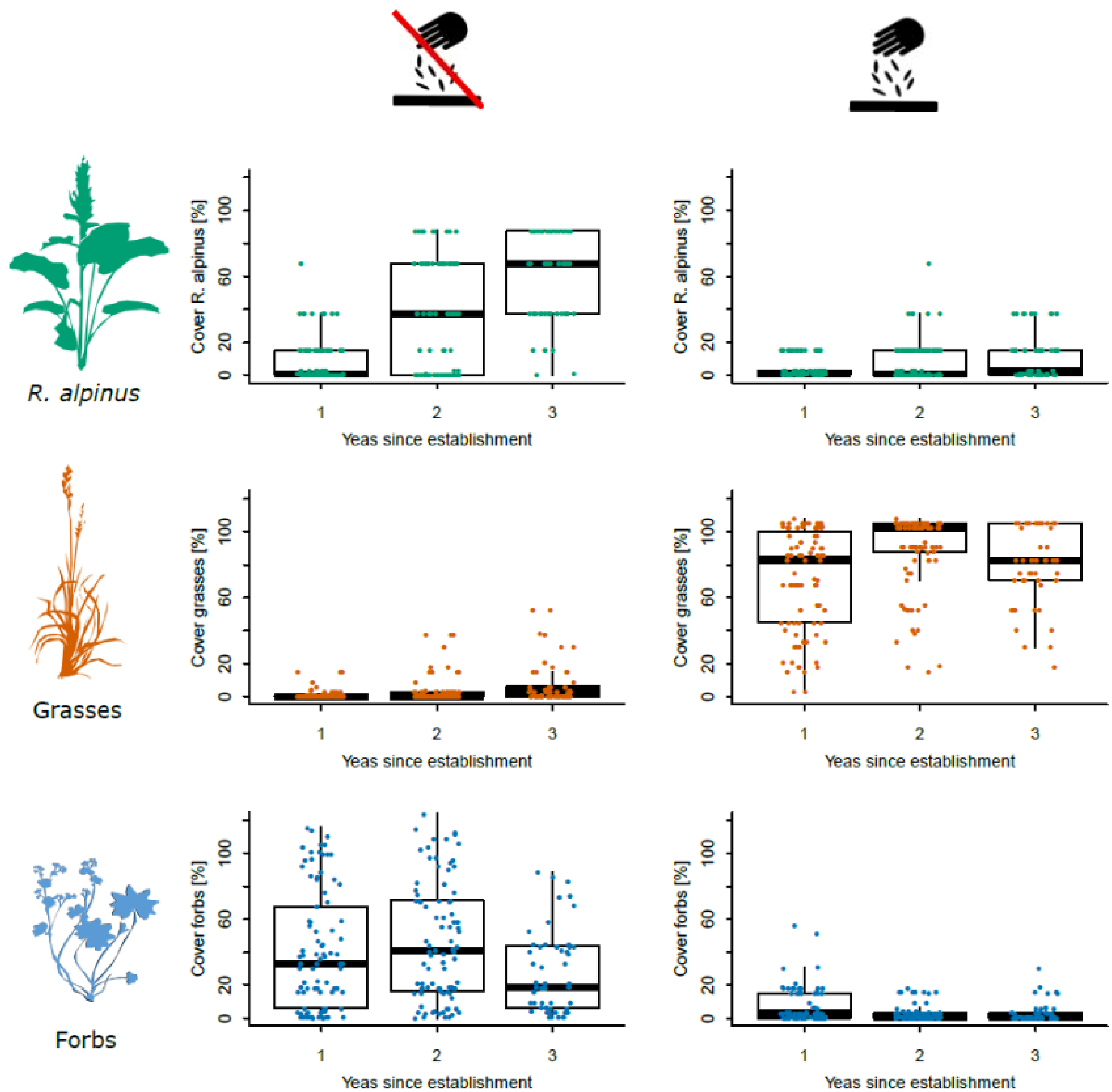

Figure S2: The effect of seed addition on the species richness of native plants regenerating from the seed bank, and the development of species richness over time since establishment of the plots. Plots on the left visualize results without seed addition and on the right after seed addition. Species number values are represented as dots in the graph. Significant effects are shown in Table 1.

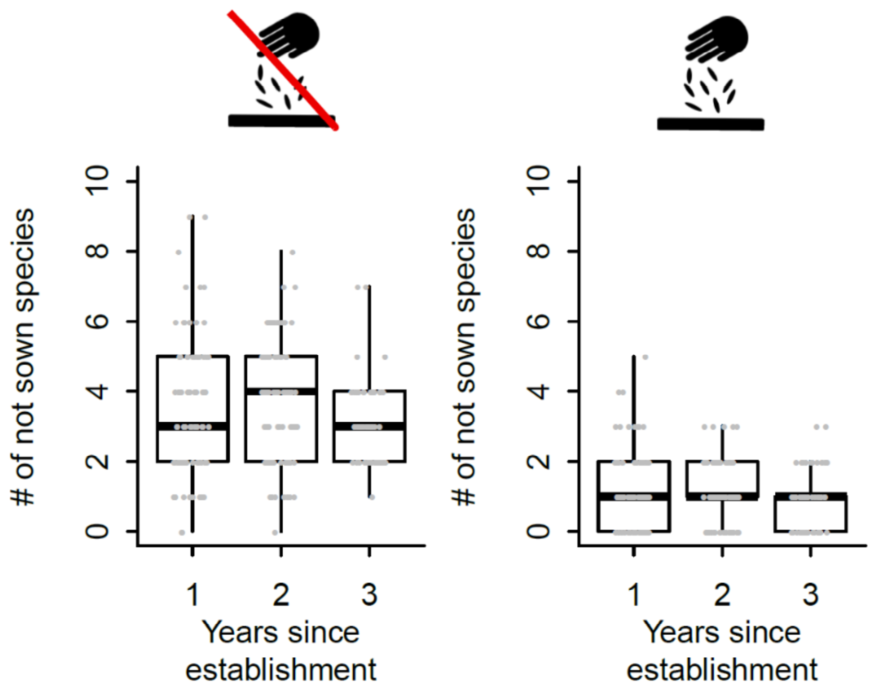

Table S1: : The effect of seed addition and the time since plot establishment on the cover of *Rumex alpinus*, grasses and forbs, and the richness of native species regenerating from the seed bank. Results of ANOVA of linear mixed models, terms fitted sequentially, significant values (P<0.05) are in bold.

	Cover								Native species richness (sown species excluded)			
			R. alpinus		Grasses		Forbs					
	Num DF	Den DF	F value	*P* value	F value	*P* value	F value	*P* value	Num DF	Den DF	F value	*P* value
Intercept	1	281	5.021	**0.026**	18.56	**<0.001**	2.915	0.089	1	281	9.886	**0.002**
Seed addition	1	9	15.40	**0.003**	237.0	**<0.001**	24.17	**<0.001**	1	9	51.71	**<0.001**
Years since establishment	2	281	52.61	**<0.001**	25.54	**<0.001**	3.518	**0.031**	2	281	0.040	0.961
Seed addition × Years	2	281	64.57	**<0.001**	16.86	**0.006**	8.823	**<0.001**	2	281	0.776	**<0.001**