Sudden changes in environmental conditions do not increase invasion risk in grassland

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Abstract

After direct habitat transformation, biological invasions are considered to be the second most important threat to biodiversity. A better understanding of the factors affecting invasion success in new areas is crucial, and may provide insight into potential control actions. We hypothesized that invasion risk increases in habitats undergoing a sudden change in the disturbance regime or environmental conditions. For testing this assumption we initiated a seed sowing experiment while introducing two novel treatments, mowing twice and fertilizer application, in two grassland sites (one dryer and one mesic) in Romania. The seeds of two invasive species, Solidago canadensis and Rudbeckia laciniata, and two resident natives of similar seed sizes, life-forms and strategies were sowed in treated and control plots, and seed germination, seedling establishment and growth were followed during four months. Contrary to our expectations, there was no difference in the treatment effects on seed germination and seedling establishment between species, while there was on seedling vigour of the larger seeded species in the dryer grassland site, where the native had a higher performance especially in increased nutrient conditions. Indifferently from applied treatments, invasive species had greater cumulative germination in the mesic site, while natives were far more successful in seedling establishment in the drier site. At the same time, seed size was found to be a very important factor explaining germination and establishment success, with large seeded species outperforming small seeded species in any circumstances. Our results call the attention upon management interventions in mesic, productive grassland sites opening colonization windows for the recruitment of those invasive species of which ecological requirements correspond to local environmental conditions.

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1. Introduction

The introduction and spread of non-native species have become a global ecological and conservation crisis as alien invasive organisms are increasingly altering terrestrial and aquatic communities worldwide (Parker et al., 1999; Byers et al., 2002; Mack et al., 2000; Gurevitch and Padilla, 2004). Thus, biological invasions are stated to be a serious threat to biodiversity (Vitousek et al., 1997). In this context, assessing the effects of invasive nonindigenous species on native species and ecosystems has become one of the world’s most serious conservation issues (Byers et al., 2002).

Invasion success is known to be influenced by two main factors: the tendency of the new species to invade, i.e. invasiveness, and the susceptibility of the environment to invasion by new species, i.e. invasibility (e.g. Lonsdale, 1999; Sakai et al., 2001). The search for traits characteristics that promote invasiveness constitutes one of the most challenging tasks in invasion ecology, however, only a few traits have been proved to be generally associated with invasiveness (Pyšek and Richardson, 2007). Therefore, it is increasingly considered that the role of plant traits in the invasion process is to a very large extent context dependent (Mack et al., 2000; Pyšek and Richardson, 2007).

Concerning invasibility of plant communities, several factors have been identified to influence this process with topography, soil type, land use, land cover, disturbance, resource availability, biotic interactions and microclimate operating at smaller, e.g. local, spatial scales (sensu Milbau et al., 2009). For example, it has been shown that a high supply of nutrients (high productivity) and disturbances are particularly responsible for promoting invasion (Burke and Grime, 1996; Daehler, 2003; Gross et al., 2005). Even so, invasion success may not be a temporally stable property of
the invader/invaded system because of possible influences of ecosystem alteration over time (e.g. climate warming, land-use change or resource fluctuations such as eutrophication) (Davis et al., 2008; Weltzin et al., 2003).

The majority of plant invasions seem to occur in areas where environmental conditions such as the disturbance regime or resource availability have recently changed (e.g. Hobbs and Huenneke, 1992; Davis et al., 2000; Facon et al., 2006; Seastedt and Pysek, 2011). In accordance to this, the new conditions would be less suitable for the resident species, since these were adapted to the former conditions, but might represent new, empty niches to species coming from outside the system, e.g. invasive species ready to colonize. In case the propagules of an invasive species are present, of which the ecological attributes or demands match the altered environmental conditions, it will successfully colonize. This approach, which is combining two well known hypotheses formulated to explain the success of exotic species in their recipient communities: the ‘empty niche hypothesis’ and the ‘disturbance hypothesis’ (reviewed by Hierrro et al., 2005), was used by Moles et al. (2008) for predicting traits that are likely to confer invasion success. However, this approach can also present a useful methodology for predicting invasions that result from changes in environmental conditions.

In the present study we hypothesize that invasion risk increases with a sudden change in the disturbance regime and resource availability. In addition, since the relative performance of invasive species compared to natives is known to be different depending on the specific combination of water, nutrient and light availability (see for e.g. Daehler, 2003), invasion success of the same species is expected to depend strongly on site abiotic conditions. To this end, we followed and compared early establishment after sowing of native and invasive plant species in two experimental grassland sites, one dryer and one mesic. Based on our hypothesis we were interested in whether, by introducing repeated mowing and fertilizer application to simulate intensified land-use, suddenly altered environmental conditions negatively influence recruitment success of resident species adapted to the former conditions, and will promote establishment of the invasive species. Our experiment refers to the very early stages of plant establishment, germination and seedling recruitment (the initial colonization phase of the invasion process sensu Jongejans et al., 2007). The success of these processes is known to be primarily influenced by environmental factors but also by the interplay between environmental factors and the quantity of seed reserves (Moles and Westoby, 2004, 2006; Eckstein and Donath, 2005; Ruprecht et al., 2010b). Thus, seed size is expected to shape considerably the establishment success of species under different scenarios (with or without mowing and fertilizer application, higher or lower water availability).

Field experiments conducted in semi-natural habitats are indispensable in order to assess the real contamination risk of high nature value habitats and the real conservation threats posed by the spreading of invasive species. Thus, we selected hardly disturbed semi-natural sites having different abiotic conditions, induced sudden changes in environmental conditions by experimental manipulations to the resident communities and tested the initial colonization phase of two invasive species that were absent from the sites compared to resident natives. The manipulations were chosen in a way as to imitate realistic land use interventions. Being aware of the risks of this study, we applied all measures assuring the ecological value of the grassland sites during and after the experiment. In addition, in order to find out the ecological requirements of the invasive species involved and to unravel potential mechanisms responsible for invasion success under different manipulations and site conditions, we complemented our field study with a controlled pot experiment involving the germination of the two invasive species under different levels of three environmental factors (light, nutrient and water availability). With our field experiment, we tested in a broader context whether invasive species are recruited more successfully when the environmental conditions are altered experimentally, as opposed to natives being more successful in unchanged environments.

2. Material and methods

2.1. Field experimental design and data collection

A factorial field experiment was performed in two meadow sites in Romania (Corneşti and Sic), which had not been managed (mowed or grazed) for a longer time. One of the sites (Corneşti) was dryer (average depth of ground water table during March–May 2011 was 43 cm) than the other (Sic, 20 cm), they had slightly different soil properties, especially in terms of pH (soil samples analysed by the Belgian Soil Service: Corneşti 522 mg total N, 3 mg P, 23 mg K in 100 g soil, pHKCl = 4.6; Sic 384 mg total N, 3 mg P, 18 mg K in 100 g soil, pHKCl = 7.3), and harboured different plant communities. The experimental site at Corneşti was a meso-xeric grassland dominated by Festuca pratensis and Festuca rubra which was very rich in dicotyledonous species, while that at Sic was a mesic grassland dominated by Carex hirta and Agrostis stolonifera with a high representation of Ranunculus acris, Lysimachia nummularia and Cirsium canum.

Four resident native (two in both sites) and two invasive species were selected for the seed sowing experiment. The two invasive forbs, Solidago canadensis and Rudbeckia laciniata, were both introduced in Central-Eastern Europe from North-America. These species are widespread in Romania, but not occurring in the experimental grassland sites or their surroundings. Lack of the two invasive species in the study sites and their surroundings can be explained rather by dispersal limitation and not by unsuitable environmental conditions, since they occur in other regions of the country with similar climate, and have small, isolated populations in the study region (Cluj county) as well (especially S. canadensis). The resident natives were abundant in the grassland plant communities, sharing similar seed sizes, life-forms and strategies with the invasive species. Seeds of the resident natives were collected in the experimental grassland sites (Table 1), while that of the invasives from one population each near Cluj-Napoca (S. canadensis) and Praid (R. laciniata), Romania, during August and September 2010. For all six species used in the experiments, seed collection included at least 12 different individuals per species. Seeds (in fact seeds or fruits) cleaned from appendages were subsequently dry-stored in darkness at room temperature (c. 20 °C) until sowing.

Two experimental treatments were applied in 3 m × 3 m main plots in both sites. We selected management interventions that plant communities in the two grassland sites had not experienced for a long time, which were (i) mowing twice and (ii) mowing twice combined with fertilizer application. These treatments simulate a potential management of the grasslands as intensive hayfields. As well, we had main plots with biomass left intact and without fertilizer application as a control. In treated plots, mowing was performed at the beginning of the experiment, in November 2010, and in mid June 2011. Mowing comprised removal of clippings, and at first mowing litter was also removed by raking. Nutrient addition amounted to 10 g m⁻² year⁻¹ N-fertilizer, which was delivered in two items to decrease leaching losses and to avoid scorching. Half of the total fertilizer quantity was added in March, before the beginning of the vegetation period, and half at the end of May 2011. Within the main plots 25 cm × 25 cm subplots (seed sowing plots) were set out. Fifty seeds of the two invasives and two
resistant natives (Table 1) were sowed separately in the experimental subplots. In addition, we designated subplots without seed sowing to estimate the natural seed rain and spontaneous germination of the natives involved in the experiment.

The experimental design was a blocked split-plot (Gomez and Gomez, 1984), with three blocks designated at both sites. Within each block, we established three main plots, each main plot randomly receiving one of the three treatments (mowing twice, mowing twice combined with fertilizer application and control). Within each main plot we had two seed sowing plots per species or without seed sowing, thus there were 10 subplots in total per main plots.

Emerging seedlings were counted, marked and followed between April and August, and height of survived seedlings was measured at the end of the experiment. We paid special attention to effectively eradicate all the established individuals of the invasive species at the end of the experiment and also to remove the soil cores where the seeds had been sown to prevent contamination.

In both experimental sites we measured light availability (photosynthetic active photon flux density; PPFD) on the soil surface and above the vegetation in mowed and control plots at peak germination in May using a quantum sensor. Averages of 12 measuring points were used as estimates of PPFD transmission (%) reaching the soil surface. Productivity of the experimental sites was quantified by harvesting aboveground biomass from five randomly selected 1 m × 1 m plots outside of the main plots in July 2011. Collected samples were dried at 65 °C for 48 h and then weighed.

### 2.2. Controlled pot experiment

To find out the ecological requirements of the invasive species involved and to facilitate the interpretation of the field experimental results, we carried out a germination experiment under controlled conditions. In this supplementary experiment, seeds of the two invasive species were sowed in pots filled with 2:1 mixture by weight of commercial potting soil and sand in December 2010. The pots were placed outside in the University Botanical Garden at Cluj-Napoca, Romania, and subjected to three different levels of water (15, 28 and 51 vol%; the two field sites differed in soil moisture), light (3, 14 and 100% PPFD of incident) and nitrogen availability (0, 5 and 10 g m⁻² N added). To each pot 0.025 g of nutrient mixture (20% P₂O₅, 44% K₂O, 0.05% Fe, 0.025% Mn, 0.008% Zn, 0.006% Cu, 0.02% B, 0.0035% Mo) was added in order to have no shortage (except for N) in any of the necessary nutrients. In each series, other environmental factors than the one manipulated were kept on an adequate level (e.g. full light and medium N content if water availability was manipulated). We used 50 seeds per pot in six replicates for each treatment type. From March until the end of July the germinating seeds and appearing seedlings were counted and removed, and cumulative germination was calculated.

### 2.3. Data analysis

For the field experiment, the number of seedlings appearing during the experimental period (cumulative number of seedlings) as well as the percentage of seedlings that survived until the end of the experiment (establishment success) in the two subplots (seed sowing types) within each main plot (treatment plot) was averaged. Since in one of the sites (Sic) we experienced spontaneous germination of the two native species in the additional plots without seeds sowed, we corrected the cumulative germination of sowed plots for this within each main plot.

To test for differences in treatments and species effects on the germination and establishment success of sowed species, an analysis of variance for a split-plot design was applied separately for the two sites, where treatment and species were used as fixed factors and block as a random factor. The effects of treatments were tested against the interaction with block, while the species effects as well as their interaction with treatments were tested against the residual variance among the subplots. Cumulative germination was arcsin square root transformed prior to the analysis.

In a next analysis, still on the field data, we tested whether the applied treatments had an effect on the vigour of established seedlings. To this end we averaged the height of seedlings established and surviving until the end of the experiment within each subplot. Since our dataset was highly unbalanced, i.e. when no seedlings established we coded missing height, we reduced the model to a two factorial ANOVA. The two factors were treatment and species. Because of the very low seedling survival, thus missing values, experienced in case of the smaller seeded Hypericum perforatum (native) and S. canadensis (invasive) in the dryer site, we could perform this analysis only for Pastinaca sativa and R. laciniata (the two larger seeded species, one native and one invasive) for this site. In order to make our results comparable between the two sites, separate analyses were performed for Epilobium tetragonum and S. canadensis (small seeded species) and C. canum and R. laciniata (larger seeded species) for the mesic site. Data was Box–Cox transformed prior to the analysis.

We analysed the effect of controlled environmental conditions (soil moisture, light availability and nitrogen content) on the cumulative germination of the two invasive species obtained from the pot experiment by a factorial ANOVA. Data was arcsin square root transformed prior to the analysis.

### 3. Results

The dryer grassland site had a lower productivity (192 g m⁻²) than the mesic site (254 g m⁻²), which caused the light availability on the soil surface to be higher in case of both the mowed (18.3% incident PPFD) and control main plots (8.7%) compared to the mesic site (mowed = 13.1%, control = 3%). The treatments had a significant positive effect on seed germination and establishment success.
of germinated seedlings only in the mesic grassland site, and this effect was induced by mowing, since nitrogen addition caused no further difference between the treatments (cumulative germination: control = 9.25 ± 4.17% (SE), mowing = 27.42 ± 5.84%; mowing + N application = 26.50 ± 6.93%; seedling establishment: 25.57 ± 7.62%, 58.23 ± 6.81%, 51.16 ± 7.98%; Table 2). In the mesic site, the treatments influenced seed germination and establishment success of all the four species in a similar way (no significant interaction between treatments and species identity). However, in both sites, there was a significant species effect, which means that germination and establishment success differed between species (Table 2). Invasive vs. native status influenced cumulative germination of species only in the mesic site, with invasive species performing better (Table 2, Fig. 2a), and seedling establishment in the dryer site, where native seedlings had a superior establishment success compared to invasives (Table 2, Fig. 1b). In turn, it seems that species rather behaved based on their seed size, with larger seeded species (P. sativa, C. canum and R. laciniata; Table 1) being more successful in germination and seedling establishment compared to small seeded species (H. perforatum, E. tetragonum and S. canadensis; Table 1) under any circumstances (Figs. 1 and 2).

In the dryer site, again, treatments had no effect on seedling growth, but there was a significant interaction between treatments and species, showing that treatments affected differently the height of seedlings in the native P. sativa and the invasive R. laciniata. While mowing reduced seedling height compared to the control in case of the native, mowing + N addition reduced seedling height compared to mowing and to the control in case of the invasive (Table 3, Fig. 3a). On the other hand, in the mesic site, treatments had a significant effect on seedling size (Table 3). Similar to germination and establishment success, mowing and mowing + N addition promoted seedling growth in case of the native E. tetragonum and the invasive S. canadensis (both small seeded) compared to the control, with no difference between the two treatments comprising mowing, while only mowing alone increased seedling vigour compared to the control and to mowing applied together with N addition in case of the native C. canum and the invasive R. laciniata (both larger seeded) (Table 3, Fig. 3b and c). Native and invasive species responded similarly to the treatments (no significant interaction between treatments and species identity) (Table 3).

In the controlled pot experiment on the two invasive species soon under different environmental conditions, germination was influenced by soil moisture (results of the factorial ANOVA: soil moisture MS = 0.88, df = 2, p < 0.0001, species MS = 0.11, df = 1, p = 0.027, soil moisture × species MS = 0.07, df = 2, p = 0.040) but not by the nitrogen content of the soil (nitrogen content MS = 0.05, df = 2, p = 0.061, species MS = 0.04, df = 1, p = 0.143, nitrogen content × species MS = 0.03, df = 2, p = 0.143), with the lowest water content applied diminishing seed germination in both species (Fig. 4a and c). Further, cumulative germination of one of the species, the small seeded S. canadensis, depended highly on light availability (light availability MS = 0.35, df = 2, p < 0.0001, species = 2.30, df = 1, p < 0.0001, light availability × species MS = 0.68, df = 2, p < 0.0001; Fig. 4b).

Fig. 1. Cumulative germination (a) and establishment success of germinated seeds (b) of two native (H. perforatum and P. sativa) and two invasive (S. canadensis and R. laciniata) species in the dryer grassland site. Values are means and SE.

<table>
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<th>Source of variation</th>
<th>df</th>
<th>Dryer site Cumulative germination</th>
<th>Mesic site Cumulative germination</th>
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<th>Mesic site Establishment success</th>
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<td></td>
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<td>P</td>
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<td>P</td>
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<tr>
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<td>&lt;0.0001</td>
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Table 2 Effects of treatments (C = control, M = mowed, M + N = mowed + N addition) and species identity on cumulative germination and establishment success. df = degrees of freedom, MS = mean sum of squares. Significant differences are in bold.
4. Discussion

Our experiment studied three very early phases of plant life, namely seed germination, seedling establishment and seedling growth. The observed plant performance during these three phases provides good insight into the establishment possibilities of invasive vs. native species under different scenarios. A better understanding of the factors affecting colonization success of newly establishing populations is essential for developing potential control actions in the critical early stage of plant invasion. Our field study carried out in semi-natural plant communities, gives a realistic basis for predicting invasibility (Morrison and Mauck, 2007).

4.1. Germination and seedling establishment

Mowing, which caused a sudden change in the environmental conditions (increased light availability on the soil surface), enhanced recruitment of all four species (invasives and natives) involved in the seed sowing experiment, but only in the mesic grassland site. Biomass removal, by decreasing competitive pressure from established vegetation and by creating microsites for recruitment, is known to increase establishment possibilities in grasslands (Kotorová and Lepš, 1999; Ruprecht et al., 2010a). The fact that the mesic site was more productive, suggests that the effect of biomass removal on recruitment may highly depend on grassland productivity. In agreement with this, Huston (2004) stresses that plant establishment is more successful in communities with lower productivity, even if disturbances are absent, while under higher productivity establishment is promoted only in the presence of disturbances. Further, increased nitrogen availability had no additional effect on seedling recruitment in any of the sites. Nitrate concentrations have been shown to regulate the onset of germination in several plant species, but this germination cue seems to be more relevant for agricultural weeds with light sensitive seeds (Baskin and Baskin, 2001).

The plant species used in the present experiment differed in their germination and seedling establishment success, but the treatments had no differential effect on these processes. Invasive vs. native status influenced seedling fate in the dryer site, where the native species had been far more successful in seedling establishment than the invaders. Probably, native seedlings were better adapted to the less favourable local environmental conditions (e.g. lower soil moisture or slightly acidic soil) compared to invasive species coming from outside of the system. In a review of many experimental studies comparing the performance of native and invasive species, Daehler (2003) concluded that natives are favoured over invasives in environments with low resource availability (e.g. water, light, or nutrients). Further, ecological requirements of the two invasive species involved in the present study were different than environmental conditions occurring in the dryer grassland site, since these species prefer higher soil moisture during seed germination as demonstrated by our supplementary pot experiment (Fig. 4a). In-line with this, the two invasive species had higher cumulative germination in the mesic site compared to the dryer site (Figs. 1a and 2a).

Furthermore, seed size was found to be a very important factor explaining germination and establishment, with large seeded...
species outperforming small seeded species in any circumstances (in both grassland sites and across all treatments). It has been shown that larger seeds are better able to establish as seedlings under particular hazards, such as competition from dense vegetation, drought and shading, than smaller seeds (reviewed by Moles and Westoby, 2004, 2006, but see also Westoby et al., 1992; Burke and Grime, 1996). In both grassland sites, small seeded species had very poor seedling recruitment. *S. canadensis*, the small

**Fig. 3.** Height of seedlings in the dryer grassland site (a) and in the mesic grassland site (b and c) under different treatments (control: grey bars, mowed: white bars, mowed + N addition: hatched bars) at the end of the experiment. Values are means and SE. Different letters denote significant differences at $p < 0.05$ as obtained by the Fisher post-hoc test.

**Fig. 4.** Cumulative germination of the two invasive species (*S. canadensis*: white boxes, *R. laciniata*: black boxes) under controlled environmental conditions in the pot experiment: (a) three levels of soil water content, (b) three levels of light availability (PPFD = photosynthetic active photon flux density), (c) three levels of nitrogen availability. Values are means, SE and SD.
seeded invasive species, was proved to have a light demanding germination (Fig. 4b), which is a general phenomenon reported for small seeded species (Hodkinson et al., 1998; Milberg et al., 2000; Jensen and Gutekunst, 2003). It is interesting to mention that increased light availability on the soil surface through biomass removal was not enough to spectacularly increase germination in small seeded species. Possibly, mowing was too moderate a manipulation to create proper microsites for the recruitment of small seeded species in the dense vegetation of these grasslands (see also Kotorová and Lepš, 1999; Hofmann and Isselstein, 2004). At peak germination in early May light availability on the soil surface in treated plots was 18.3% of incident PPFD in the dryer site and 13.1% in the mesic site, which was probably still not enough for the massive germination of small seeded species (see also Fig. 4b).

### 4.2. Seedling vigour

While in the mesic site both treatments had the same positive effect on seedling growth of all the species as on seed germination and seedling establishment, they had no general effect on seedling vigour in the dryer site. However, in this dryer site the treatments affected differently the seedling size of the two larger seeded species. The native *P. sativa* was superior in its performance compared to the invasive *R. laciniata* in the control, unaltered situation and when mowing was applied together with nutrient addition, while the invasive was very much suppressed in the mowed and fertilized situation compared to its performance in the unaltered or mowed plots. Thus we can assume that the native species was more successful in nitrogen acquisition than the invasive, which resulted in higher seedling vigour after four months of seedling development. A lower ability of utilizing the nutrient surplus of the environment in the invasive *R. laciniata* seedlings can be observed in the mesic grassland site as well (Fig. 3c). This confirms the results of Meisner et al. (2011) that seedlings of invasive species do not possess by all means greater capacity for nutrient acquisition than those of natives.

### 4.3. Species origin and ecological requirements as determinants of invasion success in grassland

On the whole, our results on seedling establishment of invasive and native species in semi-natural experimental grassland sites do not support our hypothesis that invasion risk increases in habitats undergoing a sudden environmental change. Based on this hypothesis, by applying two novel treatments (mowing two times per year and mowing combined with fertilizer application) in grassland sites which had not been managed for a long time, we expected establishment success of two invasive species introduced by seed to be higher than that of the two natives assigned as a comparison. However, we found no interaction between the applied treatments and species identity in their effect on seed germination and seedling establishment success in any of the two grassland sites, apart from one on seedling vigour in the dryer site. Seed germination and seedling establishment, the very early and most vulnerable phases of plant life, are governed by specific cues (Baskin and Baskin, 2001), which often do not overlap with factors controlling plant development in the later life stages. We conclude that our hypothesis may apply better to vegetative performance (biomass accumulation, growth rate, competitive ability) of already established invasive species compared to indigenous natives in a particular site undergoing an unexpected change in the disturbance regime or environmental conditions. Full-grown invasive species are known to outperform natives under elevated nutrient conditions generally by their more successful nutrient acquisition (Maillet and Lopez-Garcia, 2000; Burns, 2004; Leishman and Thomson, 2005), but this has been shown not to be applicable for seedlings (Meisner et al., 2011).

Further, severity of changes in the disturbance regime and environmental factors may also influence invasibility of a habitat. In most cases, the treatments we applied were perhaps not strong enough to influence differentially early establishment of invasive and native species. Burke and Grime (1996) also showed that disturbance intensity and nutrient levels are very important in determining the success of invasive species in a new site. Following their results, only highly disturbed and highly fertilized conditions would notably promote invasion success in grassland.

In addition, our results support that early establishment success of invasive species in new sites is highly increased if their ecological requirements concur with site environmental conditions. Since the recruitment of the two invasive species involved in our experiment, *S. canadensis* and *R. laciniata*, was strongly limited by soil moisture (see Fig. 4a), their establishment success was higher in the mesic grassland site. At the same time, since highly productive communities are expected to be recruitment-limited, in such systems establishment of exotic species is dependent on the occurrence of disturbances (Huston, 2004). In such sites biomass removal is creating microsites for recruitment, for example through decreased competitive pressure from established vegetation and through increased light availability on the soil surface, as we found increased germination and seedling establishment as a result of our treatments in both invasive species. Based on these considerations, in more mesic grassland sites management interventions might particularly increase invasion probability by opening colonization windows.

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