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Title: Invasive Asclepias syriaca can have facilitative effects on native grass establishment in a water-stressed ecosystem

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Abstract

Question: What is the effect of invasive common milkweed (*Asclepias syriaca* L.) on the germination and early establishment of native grass species during open sand grassland vegetation recovery in old-fields?

Location: Fülöpháza Sand Dune Area, Hungary

Methods: A small-scale experiment was carried out in a sandy old-field infested by *Asclepias*. We designated 36 2x2 m plots in patches of *Asclepias*. We seeded two native grass species *Festuca vaginata* and *Stipa borysthenica* in twelve plots each (third of the plots were left unseeded). We applied repeated mechanical removal of *Asclepias* shoots on half of the plots for two growing seasons. The number and aboveground cover of the two grass seedlings were evaluated for two growing seasons.

Results: The number and aboveground cover of *Festuca* and *Stipa* seedlings did not increase by applying *Asclepias* shoot removal during the two years of the study. We found lower seedling number and cover of *Festuca* in plots with *Asclepias* shoot removal in the second year, when a severe summer drought occurred at the study site. The number and cover of the *Stipa* seedlings did not differ between plots with *Asclepias* shoot removal and control plots throughout the experiment.

Conclusions: We did not find any negative effects of the presence of the invasive *Asclepias* during open sand grassland regeneration in terms of germination and early establishment of the dominant grass species. We even detected a nurse effect of *Asclepias* on *Festuca* where the shade of *Asclepias* may have mitigated the unfavourable abiotic conditions for *Festuca* caused by summer drought. This mitigation was not observed in the case of *Stipa*, which can better tolerate summer droughts. Our results suggest that *Asclepias* control is not required for a successful open sand grassland restoration in the early phase of vegetation recovery and restoration efforts should focus on the mitigation of propagule limitation of native grasses. However, further information is needed about the effects of *Asclepias* on other elements of the biota and in later phases of secondary succession.

Keywords: facilitation, ecological impact, germination, inland sand dune, neighbour effect, nurse plant, propagule limitation, reintroduction, restoration, seeding, tussock grass

Taxon nomenclature: Király (2009)

Introduction

Invasive species are considered to be among the main threats for biodiversity (Sala et al. 2000). Adverse impacts of invasion are well documented and accepted in the ecological literature (Davis 2011), although damaging effects are often only based on simple negative correlations between abundances of exotic and native species, which are inappropriate to draw causal conclusions (Didham, Tylianakis, Hutchinson, Ewers, and Gemmell 2005, Davis et al. 2011). In contrast, neutral and facilitative effects of invaders on native species are frequently overlooked and underrepresented (Rodriguez 2006), which is especially true for plant-plant interactions (Walker & Vitousek 1991, Becerra & Montenegro 2013).

Positive and negative effects of invasive species on native species are often co-occurring, and the net result of these interactions depends on many factors including abiotic stress level and ontogenetic stage of the interacting species (Callaway & Walker 1997, Hamilton, Holzapfel, and Mahall 1999). This way an invasive species may have completely different effect on the same native species under various environmental and successional settings. As only limited resources are available for the management of invasive species, we need information on the complex impact of invasive species in special abiotic and biotic contexts to appropriately prioritize invasion control activities (Alvarez & Cushmann 2002).

Facilitative relationships are particularly important in stressed environments where harsh conditions influence the outcome of numerous positive and negative interactions between species (Bertness and Callaway 1994). Increased environmental severity has been found to tip the balance from negative or neutral to neutral or positive relations (Brooker et al. 2008, He, Bertness, and Altieri 2013). In arid and semi-arid environments, the most important drivers are drought and solar radiation stress (Osmond et al. 1987, Holzapfel, Tielbörger, Parag, Kigel, and Sternberg 2006, McCluney et al. 2012). Plants that are able to mitigate these hostile microenvironmental conditions can act as nurse plants enhancing survival, growth, and reproduction of other species (Stinca et al. 2015). Germination and seedling emergence is a key process during the regeneration of degraded ecosystems, and the period of seedling stage is one of the most vulnerable stages in the life cycle of plants (Kitajima & Fenner 2000, John, Dullau, Baasch, and Tischew 2016). This way, nursing can have a particularly important role during regeneration, especially in highly stressed habitats (Padilla & Pugnaire 2006). In the absence of native nurse plants, non-indigenous species already present in the recovering habitats have already been considered as facilitators of native species establishment (Becerra & Montenegro 2013).

Quantitative evaluation of the ecological impacts of most invader species is poorly documented (Barney, Tekiela, Dollete, and Tomasek 2013, Barney 2016), even in case of widespread and locally abundant species (Hulme et al. 2013, Estrada & Flory 2015). In many cases, the reported impacts are anecdotal and speculative rather than proven (Hulme et al. 2013), or the studies assessing invasion impact did not set an appropriate control. This is also the case for common milkweed (*Asclepias syriaca* L., referred to as *Asclepias* hereafter) an exotic species of North American origin (Kelemen et al. 2016), despite that it has established in 23 countries and is considered invasive with expanding area in 11 countries in Europe (Tokarska-Guzik & Pisarczyk 2015). Its further invasion is also predicted due to future climate change (Tokarska-Guzik & Pisarczyk 2015). *Asclepias* carries many characteristics ascribed to highly invasive species such as tall canopy, large leaf area, effective clonal spread and seed dispersal, drought tolerance, and allelopathic activity (Sárkány, Lehoczky, Tamás, and Nagy 2008, CABI 2010, Kelemen et al. 2016). The species is reported to be a 'transformer' invader sensu Richardson et al. (2000) changing the character, form, condition and nature of ecosystems in Hungary (Török et al. 2003). Despite that it is a transformer invasive species and has reached high abundance in the invaded regions, only few studies assessed milkweed impact on native species and arrived at different conclusions (Szitár et al. 2014, 2016, Gallé, Erdélyi, Szpisjak, Tölgyesi, and Maák 2015, Kelemen et al. 2016, Somogyi, Lőrinczi, Kovács, and Maák et al. 2017).

Kelemen et al. (2016) concluded that the long-term net effect of *Asclepias* was negative on the cover of native grassland species in late successional old-fields. However, their results come from a single time point observational study where the time of establishment of the study species were unknown, thus the direction of the negative relationship between *Asclepias* and native species could not be determined. In a similar observational study, Szitár et al. (2014) did not find any negative correlation between the cover of *Asclepias* and native grassland species five years after a wildfire in pine plantations. In the same study site, Szitár et al. (2016) conducted a grass seeding experiment where they did not find any difference in seeded grass cover between plots previously invaded and uninvaded by *Asclepias* six years after seed sowing. However, in the above studies, the abundance of *Asclepias* was not set experimentally, thus causal conclusions for its impact could not be drawn. The dominance of correlational studies and their contrasting results call for further research to elucidate the effects of *Asclepias* on the regeneration and persistence of native vegetation. This would also have great practical importance for the management of *Asclepias* because mowing and chemical control, the two widely used control methods, can have low efficacy and large non-target impact under some special abiotic and biotic circumstances (Szitár et al. 2014, 2016).

In this study, we experimentally manipulated the abundance of *Asclepias* to assess its impact on vegetation recovery in old-fields. We eliminated the aboveground cover of milkweed for two years with repeated mechanical shoot removal in a small-scale experiment carried out in an old-field previously invaded by *Asclepias*. In this experimental setting, we assessed whether

Asclepias affects the germination and establishment of two dominant grass species of Pannonian open sand grasslands during secondary succession.

Methods

Study area

Our study was conducted in the Kiskunság region (Pannonian biogeographical region) in central Hungary (46°53' N, 19°24' E). The study area is a lowland region with inland sand dunes (80-120 m a.s.l.; Biró et al. 2013). The climate is continental with a sub-Mediterranean influence (Csecserits et al. 2011). The mean annual precipitation is 550-600 mm and the mean annual temperature is 10-11 °C (Szitár et al. 2014). The dominant soil type is calcareous sand (Calcaric Arenosol) with sand content of over 90% and with extremely low (below 1%) humus content (Lellei-Kovács et al. 2011).

The natural vegetation of the sand dunes is forest steppe composed by a mosaic of edaphic communities. Open sand grasslands (*Festucetum vaginatae danubiale*) cover sand dune tops, while closed sand grasslands (*Salicetum rosmarinifoliae*) and poplar-juniper woodlands (*Junipero-Populetum albae*) dominate interdune depressions (Biró et al. 2013). Open sand grassland is an endemic community dominated by perennial tussock grasses *Festuca vaginata* and *Stipa borysthenica* (hereafter referred to as *Festuca* and *Stipa*, respectively). The aboveground vegetation is sparse with an average vascular plant cover of about 30-40%. Open surfaces among tussocks are occupied by cryptogams (mosses and lichens) and subordinate herb species.

The main land cover types of the region are agricultural fields, forest plantations, semi-natural habitats, and ex-arable lands (Csecserits et al. 2016). Land abandonment has been occurring in agricultural fields with the lowest productivity due to socio-economic changes and a decrease of the regional groundwater table level since the 1960's (Csecserits & Rédei 2001, Biró, Révész, Molnár, Horváth, and Czúcz 2008). Ex-arable fields provide possible areas for restoring semi-natural vegetation (Török et al. 2014), but are also increasingly invaded by exotic species such as *Asclepias syriaca*, *Robinia pseudoacacia*, and *Ailanthus altissima* that may hamper vegetation recovery (Albert et al. 2014).

Study site

The study was conducted in an abandoned field located in the strictly protected Fülöpháza Sand Dune Area in the Kiskunság National Park near Fülöpháza village (Fig. 1, 46°52.92'N, 19°23.94' E). The 22 hectares site was covered by open sand grasslands with probable sheep grazing until the 1950's. It was used as a vineyard between the 1960's and 1980's according to aerial photographs. The area was transformed to grey poplar (*Populus* x *canescens*) plantation in 1989 but poplar trees failed to establish due to wood theft on the largest part of the site. Subsequent spontaneous regeneration resulted in a vegetation similar to old-fields in the surroundings with large treeless grassland patches interspersed with some grey poplar tree groups. According to aerial photographs, the site has been invaded by *Ascepias* since 2000. Since then common milkweed clones have formed dispersed patches throughout the old-field.

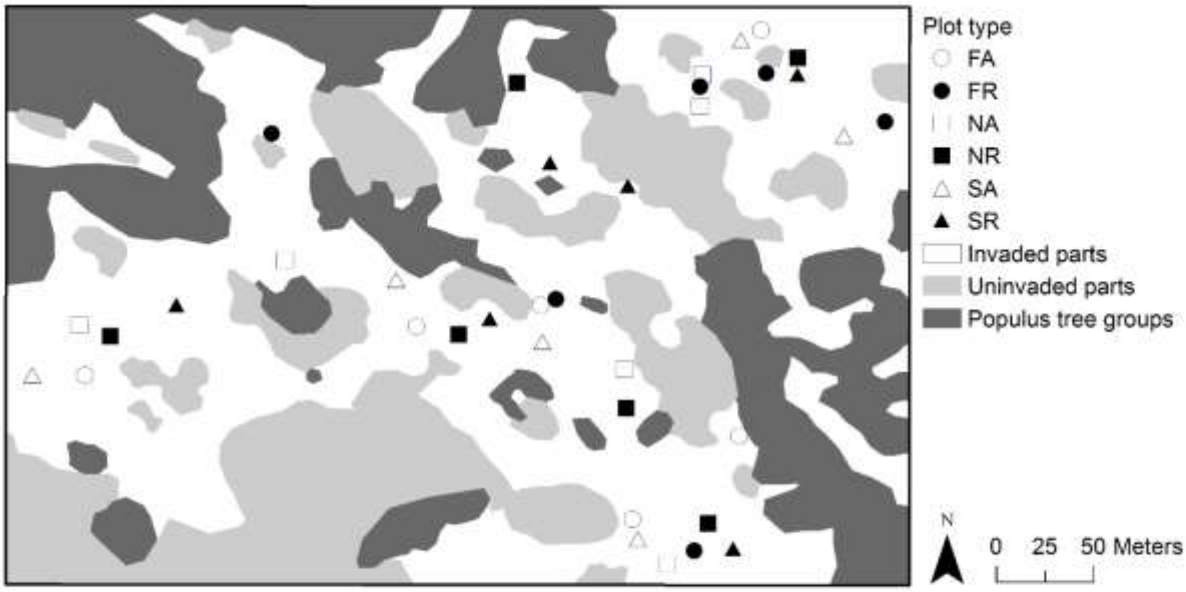

Fig. 1. Map of the study site showing the parts of the old-field uninvaded and invaded by *Asclepias*, the patches of *Populus x canescens* tree groups (based on the interpretation of an aerial photograph made in 2009), and the localities of the experimental plots. Abbreviations for plot types: FA: *Festuca* seeding-*Asclepias* control, FR: *Festuca* seeding-*Asclepias* removal, NA: non-seeded-*Asclepias* control, NR: non-seeded-*Asclepias* removal, SA: *Stipa* seeding-*Asclepias* control, SR: *Stipa* seeding-*Asclepias* removal.

Experimental design

In a 10 ha treeless area of the abandoned field, we selected altogether 36 2x2 m plots invaded by *Asclepias* with a minimum distance of 10 m from each other. We designated the plots where *Festuca* and *Stipa* did not occur, and the total cover of perennial plant species did not exceed 10%. The mean shoot number of *Asclepias* was 45.8 +/- 11.5 (SD) per plot (corresponding to a mean aboveground cover of 47.1%). *Tortula ruralis,* a moss species dominant in abandoned fields, covered the plots with an average cover of 95%. Therefore, as a pre-treatment, we removed the moss layer with a rake from each plot to help seed germination. We intended to assess the effect of *Asclepias* shoot removal therefore, half of the plots were cleared from *Asclepias* shoots by regular hand pulling (six times per year from April till September between September 2010 and September 2012). *Asclepias* shoots were removed in the plots with a 50 cm wide buffer zone around the plots.

We seeded two native grass species *Festuca vaginata* and *Stipa borysthenica* that are characteristic of open sand grasslands. In *Festuca* seeded plots, *Festuca* seeds were broadcast seeded by hand on the soil surface at a density of 0.8 g m^{-2} (approx. 1200 seeds m^{-2}). In *Stipa* seeded plots, *Stipa* seeds were pushed into the soil one-by-one by hand at a density of 1.3 g m^{-2} (100 seeds m^{-2}). Seeding was performed in September 2010. Seeded plots did not get any further treatment. Third of the plots were left unseeded to quantify spontaneous establishment of the species. This way we had six plot types each with six repetitions: *Festuca* seeding-*Asclepias* removal, *Stipa* seeding-*Asclepias* removal, non-seeded-*Asclepias* removal, *Festuca* seeding-*Asclepias* control, *Stipa* seeding-*Asclepias* control, non-seeded-*Asclepias* control.

The number of *Asclepias* shoots and *Stipa* and *Festuca* seedlings were recorded in May, June and September 2011 and in May and September 2012. Percentage cover of *Stipa* and *Festuca* seedlings were estimated at the same dates starting from June 2011.

Data analysis

The effects of *Asclepias* on *Festuca* and *Stipa* seeding were analysed separately. The impact of *Asclepias* removal and time was assessed on the seedling number and cover of *Festuca* and *Stipa* as response variables.

Statistical analyses were performed using R version 2.15.2 (R Core Team 2013). Linear mixed effects models (LME) and generalized linear mixed effects models (GLMM) were applied to investigate the differences in response variables among the treatments by using lme4 (Bates et al. 2014) and nlme packages (Pinheiro, Bates, DebRoy, and Sarkar 2012). The presence of *Asclepias* shoots, seeding and time were treated as fixed categorical explanatory variables, while plots were treated as random effects in the models. The effects of seeding on the seedling number and the cover of *Festuca* were clear, as unseeded plots did not harbour any specimens of the species throughout the experiment. Therefore, in order to meet test assumptions, unseeded plots were excluded from the statistical analyses. Cover data were square root transformed to meet assumptions of normality and homoscedasticity. Seedling numbers were analysed with Poisson error distribution and log link function. The significance of fixed factors was based on Type II Wald chi-square tests.

In case of significant interactions between fixed factors, we used Tukey HSD tests to detect pairwise differences across the treatments (Hothorn, Bretz, and Westfall 2008). Means and standard errors reported in figures and in the text are based on untransformed data.

Results

Hand-pulling decreased *Asclepias* shoot number significantly in non-seeded *Asclepias* removal plots from 10.4 +/- 2.3 (mean +/- SE) per sqm in September 2010 to 4.6 (+/- 2.2) in September 2011 and 2.0 (+/- 1.4) in September 2012 compared to non-seeded *Asclepias* control plots (13.2

+/- 5.3 in September 2010, 22.3 +/-11.4 in September 2011 and 18.6 +/- 3.2 in September 2012; Table 1).

Festuca seeding had evident effect on seedling number as the species did not establish in non-seeded plots spontaneously in the study period except for a single specimen in a non-seeded *Asclepias* control plot in May 2011. The number of *Festuca* seedlings decreased in both Festuca seeded plot types through time, however, *Asclepias* removal resulted in lower seedling number throughout the study period with significant differences in May and September 2012 (Fig. 2a).

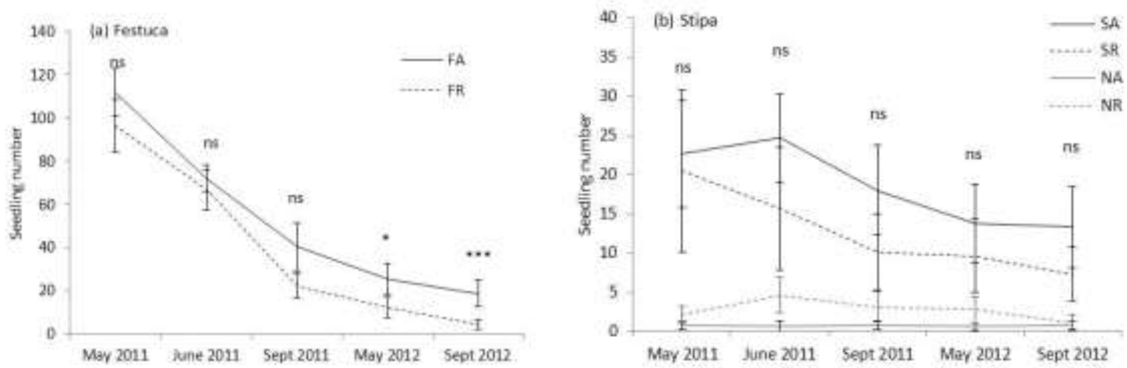

Fig. 2. Mean number of (a) *Festuca* and (b) *Stipa* seedlings in *Asclepias* removal and control plots in the course of the experiment. Non-seeded plots are not shown for *Festuca* as they did not harbour any specimen except for a single one in an *Asclepias* present plot in May 2011. For abbreviations see Fig. 1. Error bars denote standard errors. Significant differences between *Asclepias* shoot present and *Asclepias* removal plots within each date in seeded plots are indicated by asterisks.

Stipa seeding led to a significant increase in *Stipa* germination (Fig. 2b). The number of *Stipa* seedlings was 18 times higher in May 2011 in seeded than in non-seeded plots. *Stipa* seedling number did not differ significantly in *Asclepias* removal and control plots at any sampling dates.

The total cover of both seeded grasses increased in the course of the experiment despite the decrease in seedling number. The cover of *Festuca* seedlings was significantly higher in *Asclepias* control than in plots with *Asclepias* removal in September 2012 (Fig. 3a). The cover of the *Stipa* seedlings was not higher in *Asclepias* removal than in control plots (Fig. 3b).

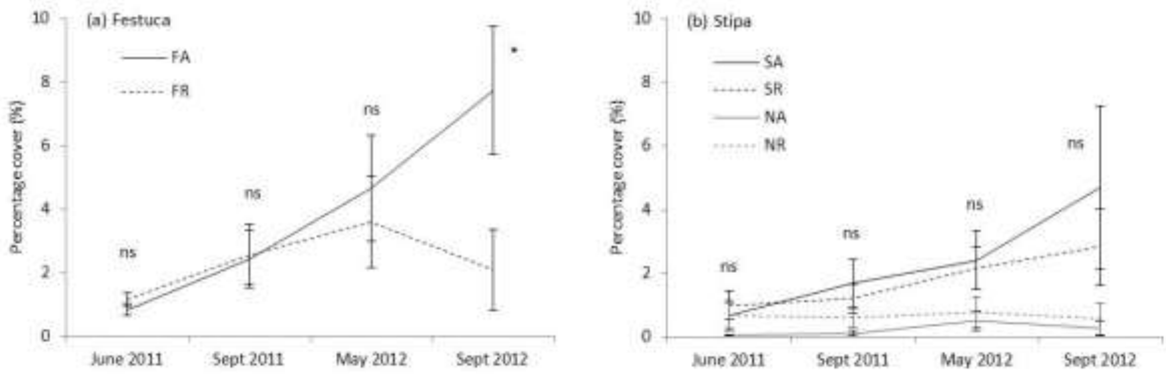

Fig. 3. Mean cover of (a) *Festuca* and (b) *Stipa* seedlings in *Asclepias* removal and control plots in the course of the experiment. Non-seeded plots are not shown for *Festuca* as they did not harbour any specimen except for a single one in an *Asclepias* present plot in May 2011. Abbreviations as in Fig. 1. Significant differences between *Asclepias* shoot present and *Asclepias* removal plots within each date in seeded plots are indicated by asterisks.

Discussion

We found that the presence of invasive *Asclepias syriaca* did not limit open sand grassland regeneration in terms of germination and early establishment of the dominant grass species *Festuca vaginata* and *Stipa borysthenica*. Similarly, Szitár et al. (2014) did not find any correlations between *Asclepias* cover and species richness and cover of natural grassland species during the first five years of spontaneous secondary succession in burnt pine plantations. In the same burnt pine plantations, in an experimental setup, Szitár et al. (2016) did not find any persistent detrimental impact of *Asclepias* on the establishment of the same dominant grasses seven years after grass seeding in *Asclepias* invaded plots.

We did not find any effects of *Asclepias* on the number and cover of *Festuca* seedlings in 2011. Nevertheless, this neutral effect turned into positive in 2012, when both the number and cover of *Festuca* seedlings became significantly lower in plots where *Asclepias* shoots were removed. The annual precipitation was lower in both 2011 and 2012 (410 mm and 385 mm, respectively) than the long-term average of 550 mm (Szitár et al. 2014). In 2011, there was a four-month dry period between August and November with a precipitation of only 68 mm (compared to the long-term average of 200 mm for this period). In 2012, severe summer drought with only 73 mm precipitation (compared to the long-term mean of 190 mm) occurred between June and August in the study area. As the aboveground *Asclepias* biomass and cover usually peaks between May and July, and grass species in open sand grasslands are most sensitive to water deficiency early in the summer when grass biomass production is also the highest (Simon & Batanouny 1971), the impact of *Asclepias* shoots are probably the highest in the same period. This may explain why we did find differential effects of *Asclepias* shoots on *Festuca* seedlings in 2011 and 2012. Shade provided by the foliage and litter of *Asclepias* seemed to mitigate unfavourable abiotic conditions for *Festuca* caused by summer drought as suggested by Szitár et al. (2016).

We did not observe any impact of *Asclepias* shoots in case of *Stipa* in either year. The differential effect of *Asclepias* for the two seeded grasses may be the result of their differential drought tolerances (Szitár et al. 2016). *Stipa* individuals are able to exploit larger soil volume than *Festuca* by growing longer lateral roots and have roots that penetrate deeper in the soil and can reach moister soil layers during drought (Simon & Batanouny 1971).

The lack of spontaneous colonization of *Festuca* and the minor spontaneous establishment of *Stipa* in the course of our study showed that these species experienced propagule limitation in an old-field abandoned approximately 30 years ago despite the close proximity of natural open sand grasslands (50-200 m). This suggests that assisted reintroduction may be necessary especially in case of *Festuca* to accelerate grass establishment to restore open sand grasslands. Furthermore, in Hungary, summer precipitation is predicted to become lower by 10-33% and maximum temperature is expected to increase with 4-5.3°C in summer according to regional climate change scenarios projected for the period 2071-2100 (Bartholy, Pongrácz, and Gelybó 2007). Thus, the frequency and strength of droughts may increase in the future, and this may constrain the recolonization of degraded areas by native species (Hau & Corlett 2003, Suding, Gross, and Houseman 2004).

The presence of *Asclepias* can help the establishment of dominant grasses thus assisting vegetation recovery if grass propagule availability is not limited. Many studies point out that the potential nursing effects of exotic species on native plant species could be exploited if there is no native facilitator available during regeneration (D'Antonio & Meyerson 2002, Dewine & Cooper 2008, Fischer, Von Der Lippe, and Kowarik 2009, Becerra & Montenegro 2013). However, the advocated subsequent removal of the exotic species (Becerra & Montenegro 2013) is not always feasible without damaging the already established native populations (D'Antonio & Meyerson 2002). Nursing provided by exotic species can also help other exotic species colonize the invaded areas thus causing invasion meltdown as in the study by Stinca et al. (2015).

We are aware of the limitations of our study that tested the effect of removing the aboveground parts of *Asclepias* while leaving rhizomes intact underground. This way we may have underestimated the negative effects of *Asclepias* as the rhizomes in *Asclepias* shoot free plots still carried on functioning. However, we think that root competition was not strong between *Asclepias* and grass seedlings and thus probably had little effect on the results. In the first years of the grass ontogenetic cycle, competition between *Asclepias* and grass species for soil resources may be limited as milkweed roots dominate deeper (10-40 cm) in the soil (Bagi 2008) and exploit resources that young grass seedlings cannot reach. However, root competition may superimpose the beneficial impact of canopy shading later as grass roots also get deeper in the soil.

Although our results showed only neutral and positive effects of the presence of *Asclepias*, the impact of invasive species may change in the long term (Strayer, Eviner, Jeschke, and Pace 2006). The cumulative impact of long term *Asclepias* presence can be detrimental to the native vegetation as found by Kelemen et al. (2016). They assessed the effect of *Asclepias* on the vegetation composition during secondary succession and found a negative correlation with the total cover of native grassland species in late successional old-fields (abandoned more than 22 years ago). Negative effects of *Asclepias* on native species may also dominate in more productive, less stressful habitats as in the case of *Phalaris arundinacea* invasion into wetland ecosystems, where nutrient enrichment results in a shift of competitive dominance between native species and *P. arundinacea* favouring the invader species (Perry, Galatowitsch, and Rosen 2004). *Asclepias* invasion may also have adverse effects on other elements of the biota. For example, Somogyi et al. (2017) showed that in young (10-26 years old) poplar plantations with high *Asclepias* cover, many ant species – also those species characteristic for later successional stages – used *Asclepias* shoots as nesting habitats thus causing homogenization of different aged poplar stands. Gallé et al. (2015) found negative as well as positive effects of *Asclepias* on ground-dwelling arthropods in poplar forests and concluded that *Asclepias* threatened their diversity.

Our *Asclepias* shoot removal treatment mimicked mowing, which is a frequently used control method against *Asclepias*. With our study design, we could show that mechanical shoot removal did not eliminate *Asclepias* from the study site despite its repeated application for two growing seasons and it is an ineffective way of *Asclepias* eradication. Chemical control of *Asclepias* using herbicides is also a widely applied method in areas of high conservation value, as well (Szitár et al. 2008). The eradication of *Asclepias* in sandy habitats is controversial with high financial costs, low long-term efficacy, serious non-target effects (Szitár, Török, and Szabó 2008), and possible soil disturbance that help *Asclepias* re-establishment from its abundant soil seed bank (Bagi 2008). Therefore, the evaluation of ecological and economic costs and benefits of *Asclepias* control should be carefully implemented so that the present and potential future impacts of invasion exceed the cost of eradication (Myers, Simberloff, Kuris, and Carey 2000).

Based on our results we suggest that Asclepias removal is not essential in the early phase of recovery of open sand grassland and restoration efforts should be focused to mitigate the propagule limitation of native grasses. However, further information is needed about the effects of Asclepias in later phases of secondary succession and on other elements of the biota.

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Table 1. Results of the statistical tests of fixed effects from linear mixed effects models (LME) and generalized linear mixed effects models (GLMM). Significant results ($P < 0.05$) are shown in bold.

Variables and effects	df	F or Chisq	P
Asclepias shoot number in unseeded plots			
Removal	1	15.83	**0.003**
Time	4	8.57	**<0.001**
Removal × Time	4	13.22	**<0.001**
Festuca seedling number in seeded plots			
Removal	1	2.11	0.146
Time	4	1142.57	**<0.001**
Removal × Time	4	60.38	**<0.001**
Stipa seedling number			
Removal	1	0.30	0.584
Seeding	1	26.19	**<0.001**
Time	4	77.93	**<0.001**
Removal x Seeding	1	3.90	**0.048**
Removal × Time	4	7.99	0.092
Seeding × Time	4	8.41	0.078
Removal x Seeding x Time	4	4.75	0.313
Cover of *Festuca* seedlings in seeded plots			
Removal	1	0.92	0.360
Time	3	5.98	**0.002**
Removal × Time	3	5.14	**0.005**
Cover of *Stipa* seedlings			
Removal	1	0.26	0.618
Seeding	1	10.06	**0.004**
Time	3	2.55	0.064
Removal x Seeding	1	0.48	0.497
Removal × Time	3	0.48	0.700
Seeding × Time	3	2.40	0.076
Removal x Seeding x Time	3	0.10	0.962