

# Different germination success may explain lower species richness of herbaceous vegetation below non-native than native shrubs

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Mechanisms by which invasive species affect native communities have been intensively studied. Invasive plants may influence other species through competition, altered ecosystem processes, or other pathways. It has been suggested that allelochemical interference is the key mechanism explaining a lower species richness of herbaceous plants below non-native than native shrubs. We studied plant recruitment from seeds sown inside and outside patches formed by *Sorbaria sorbifolia*, a shrub non-native to Finland, and a native shrub *Rubus idaeus*. Recruitment of seedlings was lower below non-native than native shrubs, in contrast to recruitment outside the shrub patches. Biotic filtering of subdominant plants was a stepwise process affected by the difference between non-native and native shrubs. Our results suggest that allelochemicals released by non-native species may be responsible for this difference. They thus give support to the hypothesis emphasizing the importance of allelopathy in the invasion of non-native plants. The slow and stepwise action of biotic filtering cautions against defining plant community membership merely based on the presence of seedlings.

## Introduction

Invasion by non-native plant species is well known to exert significant pressure on plant diversity, community dynamics and ecosystem processes (Vilà *et al.* 2011, Simberloff 2011, Dullinger *et al.* 2017). Extensive research has been conducted to characterize and predict the effect of invasion on resident communities (reviewed by Eviner *et al.* 2012) and dedicated to understanding factors which shape the magnitude of the invasion (Gioria *et al.* 2012).

Plant invasion may greatly affect above-ground–below-ground feedbacks, especially when the physiological traits of the non-native species differ from the native flora (Wardle *et al.* 2004).

Non-native species have been shown to inhibit the growth and survival of the seedlings of early successional trees and crops by releasing high amounts of natural toxins soluble in water, known as allelochemicals (Orr *et al.* 2005, Kaur *et al.* 2012). These exudates impair germination and subsequent establishment of native species (Amatangelo *et al.* 2008, Hovstad & Ohlson

2009, Loydi *et al.* 2015). Allelochemicals are released by the root system directly to the soil, reinforcing the invasion success (Callaway & Ridenour 2004, Bongard 2012), or they accumulate after above-ground plant parts have died at the end of the season. This applies especially to productive and fast growing non-native species. These allelochemicals may persist in the soil for long periods, and thus greatly limit the establishment of target communities (Lind *et al.* 2010, Lorenzo *et al.* 2013). Employment of the allelochemicals that are co-evolutionarily novel to the native plants is regarded as a ‘novel weapon’ (Callaway & Ridenour 2004) changing the competitiveness of co-occurring species. Native plants then may differ in their responses to allelopathy (by a newly introduced non-native species), which can lead to a shift in species dominance and community composition.

Previous studies provided evidence for allelopathic effects of non-native plants (e.g. Callaway *et al.* 2008, Jarchow & Cook 2009, Murrell *et al.* 2011), however, this evidence mainly relies on bioassays and pot experiment studies carried out under controlled conditions. Only few studies explored the allelopathic effects in field conditions and did compare these effects to those of native congener species in order to explain the success of non-native species in novel environments (Bousquet-Mélou *et al.* 2005, Gomez-Aparicio & Canham 2008, Cipollini & Schradin 2011, Del Fabbro *et al.* 2014).

Persistence of plant species at a site depends on the successful recruitment of individuals (Burkart *et al.* 2010) that can be limited by availability of seeds (seed limitation) and by availability of suitable sites (microsite limitation) for seedling emergence and establishment (Turnbull *et al.* 2000, Frei *et al.* 2012). Seed limitation is associated with low fecundity, seed consumption by animals and restricted seed dispersal (Turnbull *et al.* 2000), while microsite limitation with failures in seedling emergence or establishment due to adverse environmental conditions (Baskin & Baskin 1998, Burkart *et al.* 2010, Barney *et al.* 2016). Seed addition experiments is a tool that provide a direct method for distinguishing between these two types of recruitment limitation. Successful recruitment following seed addition refers to seed limitation mechanisms, and

conversely, if seed addition increases recruitment only after the environment has been disturbed or manipulated in some way (including, for example, planting of a non-native species); this is considered evidence for microsite limitation (Münzbergová & Herben 2005).

Lanta *et al.* (2013) showed that the biomass and species diversity of low-growing herbaceous vegetation differed between patches formed by non-native *vs.* native shrubs. After excluding the possibility that the availability of resources (light and nutrients) would be sufficient to explain this difference, they suggested allelopathy as the most probable explanation. Yet, they could not exclude the possibility that the difference could be caused by other factors, such as slower colonization of the patches of planted non-native shrubs. Here we designed a sowing experiment where the recruitment of ten plant species differing in their life strategies were monitored for two years (2012 and 2013). Sowing of the same amount of seeds into non-native and native shrubs allowed us to test the hypothesis that allelopathy rather than slow colonization (seed limitation) limited species richness below the non-native shrubs. We predicted that plant recruitment will be more inhibited under non-native than native shrubs, which may be due to allelopathy associated with the non-native species. We focused on the following questions: (1) Is plant recruitment associated with different origin (non-native *vs.* native) of the shrub species? (2) What role do life-span characteristics of sown species play in successful recruitment of the individuals?

We tested this in the system of Lanta *et al.* (2013), in patches formed by *Sorbaria sorbifolia*, a shrub non-native to Finland, and a native shrub *Rubus idaeus*. The patches were of comparable physiognomy, height (1.5–2 m), availability of resources (light and nutrients) and microclimate, growing in similar type of environments (Lanta *et al.* 2013, 2015).

## Material and methods

### Model system

The study was conducted in southwestern Finland (60°27′N–60°23′N, 22°16′E–23°07′E),

near the towns of Turku, Paimio (12 km east of Turku) and Salo (50 km east of Turku). The region consists of a mosaic of inhabited areas, forests and agricultural fields along the main road connecting Scandinavia with Russia (E18); biogeographically it belongs to the hemiboreal zone. The geomorphology of the study area is characterized by clay fields and forested bedrock areas covered with glacial till (e.g. Yli-Halla & Mokma 2001). The study patches were situated on previously disturbed soils (for soil characteristics see Lanta *et al.* 2013). Average temperature in the area in January is  $-4.4\text{ }^{\circ}\text{C}$  and in July  $17.5\text{ }^{\circ}\text{C}$ . The snow period with below-zero average temperatures lasts from December to March; average snow depth in mid-March is 24 cm. Growing season lasts from late April to October.

Our study system consisted of eight patches of the non-native shrub *Sorbaria sorbifolia* that had been planted for decorative purposes along roads and eight patches of a native shrub occurring in the same habitats, the raspberry *Rubus idaeus*. *Sorbaria sorbifolia* is able to spread locally by forming rhizomes and also by seeds, threatening the indigenous flora.

We monitored 10, 2 and 4 shrub patches in the Turku, Paimio and Salo areas, respectively. The distances between the patches were 0.7–10.7 km, 0.5 km, and 0.3–3.5 km, respectively. All patches (i.e., continuous stands formed by a single shrub species) represented a bush environment characterized by mature shrubs with dense canopy; available information on the history of the roads and study sites suggests that the patches were at least 15 years old. The average size of a patch was ca.  $140\text{ m}^2$ ; there were no differences in patch size or in their distance from the nearest roads (ANOVA:  $F = 1.01\text{--}3.05$ ,  $p > 0.103$ ). The between-species distances of *S. sorbifolia* and *R. idaeus* patches varied from 16.1 to 52.6 m.

### Sowing experiment

Based on vegetation relevés recorded during our previous investigation in the study region, we chose 10 species (eight polycarpic perennials and two biennials) greatly differing in their taxonomy and ecological traits. These included

grassland plants common in the study region (grass *Festuca rubra*, forbs *Achillea millefolium*, *Lathyrus pratensis*, *Leucanthemum vulgare*, *Melilotus alba*), two forest herbs (*Geum urbanum*, *Myosotis sylvatica*) and three perennial herbs taller than 1.0 m which occur but are not native to the study region (*Oenothera biennis*, *Rudbeckia laciniata*, *Telekia speciosa*). Plant nomenclature follows Tutin *et al.* (2010).

In autumn 2011, we established two  $0.5 \times 0.5\text{-m}$  permanent plots inside and outside (ca. at 1 m distance from the edge) each shrub patch. In each plot, a 10-species mixture was sown close to the centre of the plots, within an area of  $0.3 \times 0.3\text{ m}$ . In total, 1000 seeds were sown into every plot (i.e., 100 seeds per species). None of the sown species were present in the plots before. Seeds were not added in the following years. The numbers of recruited individuals of the sown species were counted in June and August of 2012, and in June and September of 2013. Numbers of recruited plants may have included some individuals originating from the seedbank, which would overestimate species recruitment. However, the number of seedlings of the species detected in the surroundings was negligible and both type of patches were subject to the same potential bias. Thus, the possible overestimation was most likely small and would not hamper comparisons between the native and non-native shrub patches.

A vegetation survey conducted inside the study plots in June 2011 revealed a clear pattern demonstrating that patches formed by *S. sorbifolia* hosted significantly fewer herb species and accumulated more leaf litter than patches of *R. idaeus* (Lanta *et al.* 2013, 2015). Biomass production and allocation of growth to leaves was comparable between the shrub species, suggesting that the quantity of leaf litter produced annually would be comparable between the shrub patches. Species richness was similar in plots sampled outside the patches, but vegetation composition in the plots located in the plots inside the patches differed depending on whether the patch-forming shrub was native or non-native. Also, the amount of photosynthetically active radiation at ground level appeared to be comparable between *S. sorbifolia* and *R. idaeus* patches (Lanta *et al.* 2013). Supportive data on

the vegetation characteristics inside and outside the studied patches were from Lanta *et al.* (2013, 2015) (Table 1).

## Data analyses

Numbers of recruited individuals counted in the two seasons were analysed separately for inside and outside shrub environments using generalized linear mixed-effects model (GLMM) with a maximum likelihood method to estimate the model parameters on data with a Poisson distribution. The type of the shrub (non-native *S. sorbifolia* vs. native *R. idaeus*), time (year) and their interaction were explanatory variables. We were in particular interested in the ‘shrubs type × time’ interaction because the significant term would indicate different patterns between shrub types in time. To account for the variation among sown species, we fitted the model with species identities as a random effect. This model structure ensured that an appropriate number of degrees of freedom was used in parameter estimation. Linear mixed-effects model (LMM) with the restriction likelihood estimation method to estimate the model parameters was used to analyse differences in numbers of recruited individuals between inside and outside shrub environments. Type of the shrub, time and their interaction were explanatory variables and identity of sown species was the only random effect. All statistical analyses were performed in R ver. 3.2.1 (R Development Core Team 2015).

Differences between the number of individuals in the plots inside and outside the shrub patches were further characterized for each sown species (shade-sensitive *Melilotus alba* and *Rudbeckia laciniata* were excluded as they estab-

lished poorly below the shrubs) by calculating standardized difference,  $D_{st}$  as follows:

$$D_{st} = (N_{in} - N_{out}) / [(N_{in} + N_{out}) / 2]$$

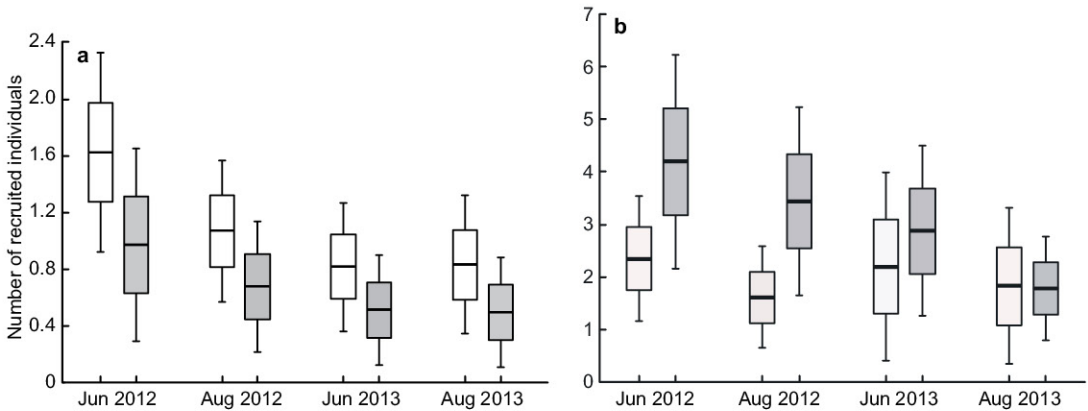
where  $N_{in}$  and  $N_{out}$  are the numbers of individuals in the plots inside and outside the shrub patches, respectively. The difference between the number of individuals in the plots inside and outside the shrub patches was divided by the average number of individuals because it could be expected that the magnitude of the difference is proportional to the total number of recruited individuals of every sown species. Negative values mean lower number of individuals in the plots inside the shrub patches.

## Results

More recruited individuals were found in the plots inside the native *R. idaeus* than non-native *S. sorbifolia* patches (Table 2) but the seedlings started dying out at the same rate (Table 2; non-significant interaction term) below both shrubs (Fig. 1a). At the end of the experiment (in the second year), out of the 16 000 seeds sown into the plots there were 60 individuals of sown species in the plots inside the *R. idaeus* patches while only 36 in the *S. sorbifolia*; i.e., 0.75% of the sown seeds recruited below *R. idaeus* and 0.45% below *S. sorbifolia*. At the same time, in the plots outside the shrub patches there were twice as many individuals than in the plots inside the *R. idaeus* patches (131 at *R. idaeus* stands and 128 at *S. sorbifolia* stands; i.e., 1.6% of the seeds sown recruited in both types of outside plots). Only six plant species survived until the end of the experiment, with *F. rubra* and *A. millefolium*

**Table 1.** Vegetation characteristics (mean ± SE) of 16 shrub stands studied. Outside and inside refer to paired sample plots outside vs. inside the shrub patches.  $n = 8$  for both species.

Species	Position	Number of species	Litter (%)	Bare ground (%)	Mosses (%)	Vegetation (%)
<i>Sorbaria sorbifolia</i>	outside	6.6 ± 0.5	24.4 ± 6.7	24.7 ± 6.7	1.1 ± 0.3	71.2 ± 7.5
	inside	1.8 ± 0.2	55.8 ± 10.2	35.9 ± 10.0	0.0 ± 0.0	12.6 ± 2.0
<i>Rubus idaeus</i>	outside	7.3 ± 0.8	34.2 ± 4.8	6.4 ± 0.6	4.5 ± 0.6	84.3 ± 2.6
	inside	4.3 ± 0.3	20.8 ± 1.1	36.7 ± 1.7	7.3 ± 0.6	47.8 ± 1.9



**Fig. 1.** Numbers of recruited individuals (all sown species pooled) (a) inside and (b) outside native *Rubus idaeus* (white boxes) and non-native *Sorbaria sorbifolia* (grey boxes) shrub patches. Bars inside boxes are means, boxes are standard errors, and whiskers are 95% confidence intervals.

being the most successful (Table 3). At the beginning, the number of recruited individuals was much higher in the plots outside the *S. sorbifolia* patches than in the plots outside the *R. idaeus* patches (Table 4), but the number of surviving individuals decreased more in the plots situated next to the *S. sorbifolia* patches (Table 2 and Fig. 2) so that, after two years, there were similar numbers of surviving individuals in the plots outside the patches of both shrub species (Fig. 1b).

Two groups of species could be distinguished based on the calculation of the standardized difference index (Fig. 3). The first group included grassland species that require gaps in vegetation to germinate (Grime 2001) and, hence,

**Table 2.** Effects of shrub environment, time and their interaction on the number of individuals recruited in the plots inside and outside the shrub patches. Sorb = *Sorbaria sorbifolia*, Rub = *Rubus idaeus*.

	Estimate	SE	z	p
<b>Inside plots</b>				
Intercept	-0.16	0.40	-0.42	0.68
Sorb vs. Rub	-0.41	0.21	-2.42	0.015
Time	-0.25	0.05	-4.76	< 0.0001
Sorb vs. Rub × time	0.00	0.08	0.05	0.96
<b>Outside plots</b>				
Intercept	-0.46	0.52	-0.90	0.37
Sorb vs. Rub	0.91	0.13	7.31	< 0.0001
Time	-0.05	0.04	-1.35	0.18
Sorb vs. Rub × time	-0.21	0.05	-4.32	< 0.0001

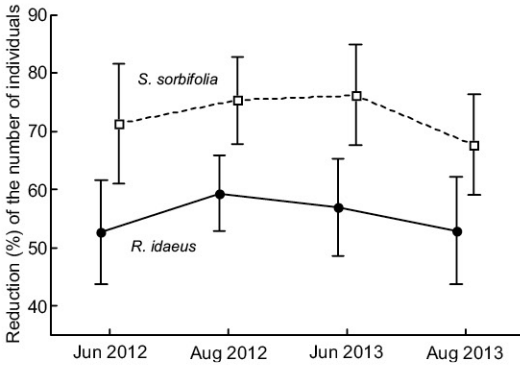
did not perform well in the plots inside the shrub patches. The second group included species recruiting similarly in both environments, or even better below the shrubs such as tall-stature *T. speciosa* and *O. biennis*.

**Table 3.** Numbers of recruited individuals at the end of the experiment in seed addition plots inside and outside (in parentheses) the shrub patches.

Sown species	Total	<i>R. idaeus</i>	<i>S. sorbifolia</i>
<i>Festuca rubra</i>	271	42 (117)	31 (81)
<i>Achillea millefolium</i>	58	1 (7)	5 (45)
<i>Geum urbanum</i>	8	2 (6)	0 (0)
<i>Leucanthemum vulgare</i>	8	7 (1)	0 (0)
<i>Lathyrus pratensis</i>	7	5 (0)	0 (2)
<i>Myosotis sylvatica</i>	3	3 (0)	0 (0)
<i>Melilotus alba</i>	0	0 (0)	0 (0)
<i>Oenothera biennis</i>	0	0 (0)	0 (0)
<i>Rudbeckia laciniata</i>	0	0 (0)	0 (0)
<i>Telekia speciosa</i>	0	0 (0)	0 (0)

**Table 4.** Effects of shrub environment, time and their interaction on the difference between the numbers recruited in the plots inside and outside the shrub patches. Sorb = *Sorbaria sorbifolia*, Rub = *Rubus idaeus*.

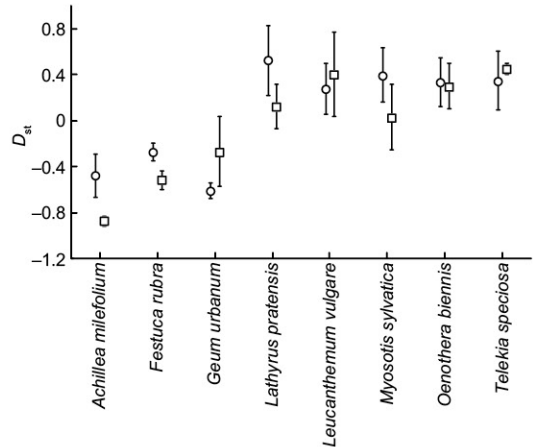
	Estimate	SE	z	p
Intercept	-0.65	1.42	-0.46	0.647
Sorb vs. Rub	-3.63	1.10	-3.30	0.001
Time	-0.16	0.28	-0.55	0.580
Sorb vs. Rub × time	0.81	0.40	2.01	0.045



**Fig. 2.** Reduction in numbers of individuals (%) in the seed addition plots (pooled data), as based on the comparison between the plots inside and outside the shrub patches. Reduction was significantly higher in *Sorbaria sorbifolia* than in *Rubus idaeus* shrub patches (ANOVA:  $F_{1,56} = 8.04$ ,  $p = 0.006$ ).

## Discussion

The results of our experiment suggest that the difference in seedling recruitments between patches formed either by the non-native or native shrubs was not due to seed limitation. In our previous study (Lanta *et al.* 2013), we showed that species compositions of low-growing herbaceous vegetation differed between patches formed by non-native and native shrubs. Differences in the availability of resources (light and nutrients) could be excluded as a sufficient explanation for the pattern, and we suggested allelopathy as the most probable reason for that. The lower number of individuals below *S. sorbifolia* than *R. idaeus* might be explained by two biotic interactions: (1) lack of shelter for plant recruitment (facilitation) due to a paucity of other plants below non-native shrubs, and (2) the presence of toxic chemicals that directly or indirectly (via microbial soil fauna) inhibit germination and reduce survival of the newly emerged seedlings (allelopathy). Toxic chemicals may be released by roots and/or decaying litter (Lind *et al.* 2010, Lorenzo *et al.* 2013, Wu *et al.* 2015, Parepa & Bossdorf 2016). Leaves of *S. sorbifolia* contain high levels of toxic hydrogen cyanide (Kim & Zee 2000) that contributed to the lower decomposition rate of the leaves of this species in the study system (Lanta *et al.* 2015). Contrary to that, faster leaf decomposition was recorded in the plots inside the *R. idaeus* patches, probably because the



**Fig. 3.** Standardized differences between numbers of recruited individuals in the plots inside and outside the shrub patches. Mean values and standard errors were calculated for each species sown at *Rubus idaeus* (circles) and *Sorbaria sorbifolia* (squares) patches. Negative values mean fewer individuals inside shrub patches.

leaves contain relatively little lignin and a high proportion of water-soluble substances which facilitate decomposition by soil fauna (Staaf 1980). In addition, *R. idaeus* leaves contain high levels of potassium which may improve seed germination during periods of soil water deficit (Shim *et al.* 2008). Shrub stands providing a sheltered and shady environment may facilitate colonization by shade-tolerant plants by reducing competition with herbaceous vegetation (Holmgren *et al.* 2012). However, it is a less likely explanation for the patterns since facilitation was not strong enough to compensate for the general decline in the species richness, cover and biomass of herbaceous vegetation within the shrub patches (Lanta *et al.* 2013, 2015). The findings presented here give support to the hypothesis that allelochemical negative interference is the reason for the lower plant biomass and species richness below non-native and native shrub species (Lanta *et al.* 2013). The importance of allelochemicals for the success of recruiting plants has been documented in other kind of systems (Bertin *et al.* 2003, Wu *et al.* 2015), which gives credibility to our conclusions.

The responses of seeded plant species to allelopathic inhibition differed. This may have important consequences for the assembly of

plant communities and, thereby, plant succession (Orr *et al.* 2005). The species-level differences in recruiting observed in this study are in line with the previous findings that the invasion of shading shrubs may facilitate colonization by shade-tolerant plants (Callaway 1995, Holmgren *et al.* 2012) by reducing competition with herbaceous vegetation, providing a moist microclimate or by protecting seedlings from disturbances. A vegetation survey conducted in the same study system (Lanta *et al.* 2013) showed that the cover of shade-tolerant species (grass *Milium effusum*, herbs *Geum urbanum*, *Galeopsis tetrahit*, *Anthriscus sylvestris*, and *Urtica dioica*) was higher inside than outside the shrub patches.

Only a very small proportion of sown seeds produced reproductive individuals. Seedling success is always a probabilistic event (Turnbull *et al.* 2000) but our results suggest that some species were more likely to establish in the plots than the others. *Achillea millefolium* and *F. rubra* survived the best and, in the plots outside the shrub patches, some individuals reached the reproductive stage. Similarly, several individuals of the forest herb *M. sylvatica* were flowering in the second year even below the shrubs. These species likely produced seeds during the experiment although the seeds produced *in situ* probably germinated after our experiment ended. However, low-stature species such as *A. millefolium* and *F. rubra* require more light than shade-tolerant species and, thus, are not likely to persist for long below shading shrubs.

Higher numbers of seedlings were observed in the plots outside the *S. sorbifolia* than *R. idaeus* patches. Based on our observations, a possible explanation for this pattern may have been frequent grass cutting around *S. sorbifolia* plots, which may have increased the proportion of bare ground (Table 1). Disturbance by frequent grass cutting produced a similar effect in previous studies: even though conditions for germination were favourable, greater plant mortality was observed later (Morgan 1997, Vítová & Lepš 2011, Song *et al.* 2013). Frequent disturbance is also a likely explanation for the lower coverage of mosses and litter in the plots outside the *S. sorbifolia* patches as compared with coverage in the plots outside *R. idaeus* patches (Table 1). The lower cover of mosses and litter

may have contributed to the pattern observed; the positive effect of moss and litter removal on plant recruitment was earlier demonstrated by Špačková and Lepš (2004).

Although it was not our primary aim, we also found that plant community development is a stepwise process, from differing probabilities to germinate to survival through the first years. Factors limiting germination success (the first phase of recruitment) and survival through the following year appeared to differ but jointly led to the filtering of the species that were capable to persist in the community. This observation cautions against defining community membership merely based on the presence of seedlings. Seedlings may be viewed as ‘candidates’ flowing from the local species pool and subject to a relatively slow and stepwise abiotic and biotic filtering process that selects the species that form the resident community. However, the slow speed of the filtering process makes it possible for even poorly adapted species to be continuously present, through repeated arrival of new seeds (mass effect; Leibold *et al.* 2004).

To conclude, our study provides experimental support to the hypothesis that allelopathy, rather than seed limitation, explains low biomass and species diversity of subdominant vegetation in the stands of non-native shrubs. Allelochemicals released by non-native species most probably caused the difference between the non-native and native shrubs.

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