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**Demographic mechanisms of disturbance and plant diversity promoting the establishment of invasive *Lupinus polyphyllus***

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## Abstract

***Aims*** Community characteristics, such as disturbances and interspecific competition that affect the availability of microsites and resources, contribute to the success or failure of the establishment of exotic plant species. In particular, these two community characteristics may have adverse effects on plant emergence and survival which are particularly important for population establishment and therefore, it may be necessary to consider both these vital rates simultaneously when assessing demographic mechanisms. Here, we investigated the impacts of disturbance and interspecific competition on the establishment of a perennial invasive herb, *Lupinus polyphyllus* Lindl.

***Methods*** Over the course of two years, we conducted an experiment in 10 populations of this species in Finland in which we manipulated the levels of soil disturbance. We recorded community characteristics (i.e., the number of vascular plant species, vegetation height, and the proportions of bare ground, litter, and moss), and observed the emergence and survival of *L. polyphyllus* individuals in study plots.

***Important Findings*** A mild disturbance (breaking the soil surface mechanically) slightly increased seedling emergence but did not affect plant survival. Instead, an intense disturbance (vegetation and litter removal) had no effect on seedling emergence, although it significantly increased the proportion of bare ground and, consequently, seedling survival. Survival was not affected by the height of the surrounding vegetation, but both seedling emergence and plant survival increased with an increasing number of plant species in the study plots. These findings demonstrate that single disturbance events may considerably promote the establishment of invasive herbs, although the overall effect and demographic mechanisms behind the increased establishment are likely to vary depending on disturbance type. Moreover, our results suggest that species diversity *per se* may not be a crucial mechanism for locally preventing the establishment of exotic plants.

***Keywords*** community invasibility, interspecific competition, invasive species, species richness, vital rates

## INTRODUCTION

Why some plant species are able to invade new areas is a key question in ecology, and requires understanding of community characteristics that ultimately determine the success or failure of the establishment of exotic plant species. In particular, plant emergence and survival are necessary for the initial establishment of plant invasions. Both these vital rates may be affected by community characteristics, such as the levels of disturbance and interspecific competition, which have the potential to alter the availability of microsites and resources. Disturbances (e.g., fire, trampling, and grazing) typically cause partial or total destruction of plant biomass (Grime 1977; Shea and Chesson 2002), and have often been suggested to promote plant invasions (Hobbs and Huenneke 1992; Burke and Grime 1996; Jauni *et al*. 2015). The removal of plant biomass due to disturbances creates patches of open ground, increases the availability of resources, and reduces competition with co-occurring native plant species, which may favour the establishment of invasive plants (e.g., Alpert *et al*. 2000; Davis *et al*. 2000; Shea and Chesson 2002). This increased establishment after disturbance may occur because invasive plant species are often more efficient resource users than native plant species are (Funk and Vitousek 2007). However, the effect of disturbance on plant invasions may vary depending on disturbance type and intensity (Hobbs and Huenneke 1992; Duggin and Gentle 1998; Lake and Leishman 2004; Jauni *et al*. 2015), with the invasion success of exotic plants tending to increase with intensifying disturbance (e.g., Duggin and Gentle 1998; Belote *et al*. 2008; Mayor *et al*. 2012). Not all studies, though, have observed that invasive plant species benefit considerably from disturbance (e.g., Moles *et al*. 2012; Fensham *et al*. 2013; Ramula *et al*. 2015).

Interspecific competition, in turn, often impedes the establishment of invasive plants. For example, high native plant species diversity may locally buffer communities against plant invaders (i.e. the biotic resistance hypothesis; Elton 1958; Levine *et al*. 2004) because fewer resources are available per individual plant. For the same reason, vegetation height, which implies competition for light, might suppress the establishment of invasive plants (e.g., Bullock 2009). Still, a number of studies have also reported the opposite result, that is, interspecific competition and species diversity are positively associated with plant invasions regardless of the spatial scale (e.g., Stohlgren *et al*. 2006; Bullock 2009; Souza *et al*. 2011; Jauni and Hyvönen 2012; Skálová *et al*. 2013). These mixed reports of the roles of disturbance and interspecific competition in plant invasions may be due to different intensities of these two variables, but may also arise from the single time points used to assess impacts. Such single time points tend to capture a limited number of vital rates that do not necessarily reflect the overall performance of a given species (e.g., Young *et al*. 2005). For example, the positive effect of a disturbance event early in life may be counteracted by reduced vital rates later in life due to high plant density at disturbed sites (Warren *et al*. 2012), resulting in no net benefit for the invader. Therefore, longer-term field studies that are based on multiple vital rates may be necessary to quantify the overall effects of disturbance and interspecific competition on the establishment of invasive plant species. The use of multiple vital rates also provides a link to population fitness, which will enable comparisons among populations and species, and will ease management recommendations.

Here, we investigated the impacts of community characteristics (i.e. disturbance, the number of co-occurring vascular plant species, and vegetation height) on the establishment of a short-lived, perennial herb, *Lupinus polyphyllus* Lindl that is invasive on several continents. Although the species often inhabits frequently disturbed habitats, such as road verges and wastelands (Fremstad 2010), seedling establishment has been previously reported to be insensitive to a mild mechanical soil disturbance (Ramula *et al*. 2015). However, it is not known how the establishment of this species depends on disturbance type, and how other community characteristics, such as species diversity and vegetation height, affect establishment. Over the course of two years, we conducted an experiment in

10 populations of the study species in which we disturbed the soil surface, recorded the number of plant species, vegetation height, the proportions of bare ground, litter, and moss, and observed the emergence and survival of *L. polyphyllus* individuals. We hypothesised that disturbance would increase the amount of bare ground and consequently create open microsites, which would then result in an increase in the emergence and survival of *L. polyphyllus*. We predicted that an intense disturbance with vegetation and litter removal prior to seed sowing would increase the vital rates more than a mild soil disturbance (breaking the soil surface with a spade). In addition, we hypothesised that plant species diversity and vegetation height would buffer against invasions by decreasing the performance of *L. polyphyllus* individuals.

## MATERIALS AND METHODS

### **Study species**

*Lupinus polyphyllus* Lindl. (Fabaceae) is a nitrogen-fixing, 50-100 cm high, perennial herb, with an estimated lifespan of a few years (Li S-L, unpublished). It is native to North America, but is considered an exotic invasive species in many European countries, southern Australia, and New Zealand (Fremstad 2010; Q-bank 2015). In the invaded range, *L. polyphyllus* can form dense stands, thus decreasing the richness of local vascular plant species (Valtonen *et al*. 2005; Ramula and Pihlaja 2012). An individual plant usually produces several hundred, ballistically dispersed seeds (Aniszewski *et al*. 2001) that germinate in spring, or that may remain viable in the soil seed bank for several years (Timmins and Mackenzie 1995). The species is also able to reproduce vegetatively via creeping underground rhizomes (Rapp 2009), although vegetative reproduction might be less common than sexual reproduction (Ramula 2014).

**Study system**

We examined the effects of mechanical soil disturbances, the number of co-occurring vascular plant species, and vegetation height (as a proxy for competition for light) on the establishment of *L. polyphyllus* in 10 populations of this species over two years. All populations were located in wastelands (including road verges and abandoned fields, n=7) or forest understoreys (n=3) in southwestern Finland, close to the town of Turku. The distance between populations varied from 3 to 35 km. In each population, we established five blocks in July 2012, with each block consisting of three plots of 0.5 × 0.5 m (i.e. 15 plots per population). This block-wise design was used to minimise differences in the vegetation and underlying abiotic conditions among plots. The plots were located, on average, 7.5 m (± 6.3 m, SD) from the closest *L. polyphyllus* individual, and 0.5 m from another plot. No seedlings of *L. polyphyllus* were observed in the plots when they were established. Although the seeds of *L. polyphyllus* disperse only up to a few metres, we cut the inflorescences of the closest flowering plants of that species to avoid its natural spread to the study plots. In each block, the three plots were randomly assigned to the following three treatments in September 2012: 1) no disturbance (control), 2) soil disturbance, in which we broke the soil surface with a spade, and 3) vegetation and litter removal, in which we removed all vegetation and litter to a depth of 5 cm from the surface. After conducting the treatments, we sowed 50 seeds of *L. polyphyllus* in each plot; all seeds for a given population had been collected from that population in the same summer. We used only fully developed seeds with a viability of 97% (± 2% SD based on a tetrazolium test, n=10 populations).

We revisited the plots twice per growing season (late May and mid-July) in the next two years (2013 and 2014), and recorded the number of *L. polyphyllus* individuals. We calculated emergence in both 2013 and 2014 as the number of *L. polyphyllus* seedlings in May of each year divided by the total number of seeds sown in September 2012. At that time most plant species in the study plots had already emerged and sprouted. Background germination was estimated from three additional plots per population (the additional plots were located between the pre-existing *L. polyphyllus* stands and study blocks) and revealed no germinated seedlings. The survival of *L. polyphyllus* individuals in the study plots was calculated separately for each year (2013, 2014) as the number of plants in July of that year divided by the number of emerged seedlings in May 2013. Due to the low flowering probability of the emerged *L. polyphyllus* individuals (0.86%; 14 out of 1629), we were unable to consider fecundity. We also note that there were no signs of vegetative reproduction during the study. Moreover, in each plot we annually (in July 2012-2014) recorded the total number of vascular plant species, measured the mean vegetation height (cm) from the soil surface based on the height of the most abundant vascular plant species, and estimated the proportions of bare ground, litter, and moss (0-100%, the proportions of bare ground and moss were mutually exclusive categories, while the proportion of litter was estimated separately).

## Statistical analyses

*Models for community characteristics*

Since the disturbance treatments were conducted just once in the beginning of the experiment (Sept 2012), the study plots may have recovered from disturbances before they were visited again in the following spring. To quantify the impacts of our disturbance treatments on community characteristics (the number of vascular plant species, vegetation height, and the proportions of bare ground, litter, and moss), we constructed linear mixed models with treatment (control, soil disturbance, vegetation and litter removal), year (July 2013 and 2014), and their interaction as fixed explanatory variables for each response variable. Block nested within population was considered a random effect to account for the spatial relatedness of the plots, and plot was added to the models as a random factor to account for the repeated measures of the environmental factors assessed in two consecutive years. For each response variable, its level prior to treatment (i.e. a given variable measured in July 2012) was used as a covariate to account for differences in the initial environmental conditions among plots. For the total number of vascular plant species, we used a generalised linear mixed model with a negative binomial distribution to correct for overdispersion. For vegetation height and the proportions of bare ground, litter, and moss, we used linear mixed models with a normal distribution. The proportions of bare ground, litter, and moss were logit-transformed (log (p / (1-p)), and a small positive constant (equal to the smallest non-zero observation) was added to the numerator and denominator in the logit-transformation to handle plots with zero cover (Warton and Hui 2011). For the models based on the normal distribution, the assumptions of normality and homogeneity of variances were confirmed by visual examination of the residuals. As we performed identical tests for multiple community characteristics measured from the same study plots, we adjusted *P*-values with a sequential Bonferroni correction (e.g., Holm 1979) to minimise the probability of type I errors. All analyses were conducted in R 3.1.2 using the *lmer* and *glmer* functions in the lme4 package (R Development Core Team 2013).

*Models for emergence and survival*

To examine the impacts of disturbance and other community characteristics on the establishment of *L. polyphyllus*, we constructed generalised linear mixed models for the emergence and survival of *L. polyphyllus* individuals using a binomial distribution (*glmer* in the lme4 package). Due to low seedling emergence in the second year of the study (2.2% in 2014) compared to that of the first year (21.5% in 2013), the analysis used emergence data from the first year only. For the emergence model, disturbance treatment (three levels) was used as a fixed explanatory variable, and block nested within population was considered a random effect. Moreover, as disturbance treatments had no effect on plant diversity in the following summer (Table 1), the number of vascular plant species and a two-way interaction between the number of plant species and treatment were included as explanatory variables in the model. To explore whether species diversity affects emergence nonlinearly (i.e. whether there is s threshold), a quadratic term of the number of vascular plant species was also included as a fixed explanatory variable. Other community characteristics (the proportions of bare ground, litter, and moss) were not included in the model because they correlated with treatment and/or with the proportion of bare ground

(Table 1). Note that habitat type and vegetation height were not considered because the former was associated with the number of plant species and the latter varied little among study plots in late May. For the survival model, we included treatment (three levels), year (2013 and 2014), the number of vascular species per plot of a given year (as both linear and quadratic terms), vegetation height (linear and quadratic terms), and two-way interactions between treatment and year, between treatment and vegetation height, and between treatment and the number of plant species as fixed explanatory variables. Block nested within population was again included as a random effect to account for the spatial relatedness of the plots, and plot was added to the models as a random effect to account for the repeated measures over time. For the emergence model, we were unable to correct slight overdispersion (dispersion parameter = 3.0), whereas for the survival model overdispersion was not a major problem (dispersion parameter = 1.19). For all statistical models, we examined the significance of the fixed variables using a likelihood-ratio test (LR) fit with maximum likelihood (Pinheiro and Bates 2000). In other words, we simplified the models starting from non-significant interaction terms ($P$ >0.05). The random effects were not tested because they were not our primary interest.

## RESULTS

### The effect of disturbance on community characteristics

The proportion of bare ground in the study plots differed among treatments (Table 1); plots with the vegetation and litter removal treatment had the greatest proportion of bare ground in the summer following the treatments, while the proportion of bare ground did not differ between the soil disturbance and control treatments (Fig. 1a). The two disturbance types considered here had no effect on other community characteristics in the summers following the treatments (the number of vascular plant species, vegetation height, the proportions of litter or moss) either on their own or through an interaction with year (Table 1; Figure S1). The number of vascular plant species and the proportion of bare ground declined over time in the study plots (Table 1; Fig. 1b,c).

**The effects of disturbance and community characteristics on invasion establishment**

A fifth (21.5 ± 14.7%) of the sown *L. polyphyllus* seeds emerged in the first spring (May 2013) after sowing. Emergence differed among treatments (Table 2), being significantly higher in the soil disturbance treatment than in the vegetation and litter removal or control treatments (Fig. 2a). Moreover, seedling emergence tended to increase with the increasing numbers of vascular plant species in the study plots (Table 2, Fig. 3a).

There was a significant treatment × year interaction for the survival of the emerged *L. polyphyllus* individuals (Table 3). In the first summer (July 2013), seedling survival was higher in the vegetation and litter removal treatment than in other treatments, whereas in the second summer (July 2014) survival did not differ among treatments (Fig. 2b). The survival of *L. polyphyllus* increased linearly with the number of vascular plant species in the study plots (Fig. 3b), but was not associated with vegetation height (Table 3, note that a marginally significant treatment × vegetation height interaction revealed no clear pattern).

DISCUSSION

Many exotic plant species are ruderals whose colonisation success at least partially depends on the availability of suitable microsites (e.g., Radosevich *et al*. 1997). Therefore, we might expect disturbances that create open microsites to increase the colonisation success of invasive plant species. We observed that disturbance indeed promoted the establishment of the invasive herb *Lupinus polyphyllus*, although its exact impact depended on the type of the disturbance treatment in question. Interestingly, the two disturbance types considered here (a mild mechanical soil disturbance and an intense disturbance with vegetation and litter removal) had differing demographic effects early in life. The mild soil disturbance increased the emergence of *L. polyphyllus* by about 5% compared to control, whereas the intense disturbance had no effect on emergence (Fig. 2a). This finding is somewhat surprising because the mild soil disturbance did not significantly affect the community characteristics (the number of vascular plant species, vegetation height, or the proportions of bare ground, litter, and moss), indicating that it did not increase the availability of microsites in the study plots. However, it is possible that the soil disturbance treatment promoted seedling emergence by altering other soil characteristics (e.g., the level of nutrients, soil moisture) that were not measured here. The result also contrasts to our previous finding for the same species, where a mild mechanical soil disturbance had no statistically significant effect on seedling establishment (Ramula *et al*. 2015). These contrasting findings might be partially because of different study designs, years, and populations used. Moreover, although the intense disturbance treatment (vegetation and litter removal) increased the proportion of bare ground in the study plots and, consequently, microsite availability, this increase did not result in considerable changes in the emergence of *L. polyphyllus*. The negligible effect of the intense disturbance on the emergence of *L.*

*polyphyllus* might be because this disturbance type may have created a drier microclimate and therefore, unfavourable conditions for seed germination. In this, our results are similar to those of Rauschert and Shea (2012), who observed that the emergence of the invasive thistle *Carduus nutans* was lower at heavily disturbed sites than at moderately disturbed sites.

In contrast, the two disturbance treatments reversed roles in their effects on seedling survival. Intense disturbance (vegetation and litter removal) increased the seedling survival of *L. polyphyllus* in the first summer following the treatment by about 15%, but not in the second, while the mild soil disturbance had no statistically significant effect on plant survival during the experiment. The increase in seedling survival in the summer following vegetation and litter removal probably resulted from a reduction in interspecific competition for resources. This view is also supported by the fact that the proportion of bare ground decreased during the experiment in all plots (Table 1), indicating that environmental conditions (e.g., availability of microsites and resources) may have been less favourable in the second than in the first year of the experiment. However, we cannot rule out the possibility that weather conditions may have also contributed to our findings. While there was no major difference in mean summer temperature between 2013 and 2014 (about 16.3°C and 16.6°C, respectively), summer 2013 was drier than summer 2014 (total precipitation about 183 mm and 262 mm, respectively; data accessed from the Finnish Meteorological Institute, http://en.ilmatieteenlaitos.fi). Harsher growing conditions due to dryness during the first summer of the experiment might have enhanced the positive effects of the disturbance treatments on emergence and seedling survival. Overall, our findings demonstrate that single disturbance events of different types may promote the establishment of *L. polyphyllus*. However, it should be noted that, as we did not observe the entire life-cycle of the study species, we may have missed possible reductions in survival or fecundity occurring later in life due to the high density of *L. polyphyllus* individuals in the disturbed plots. Such joint reductions in survival and fecundity may be critical to the population growth of short-lived plant invaders (Ramula *et al*. 2008). Therefore, the present study may have overestimated the longer-term performance of the study species at disturbed sites.

Competition with native plant species is assumed to be an important mechanism that defines the biotic resistance of plant communities against plant invasions (e.g., Burke and Grime 1999; Lonsdale 1999; Gioria and Osborne 2014). At the local scale, species-rich plant communities are generally expected to be more resistant to plant invasions than species-poor plant communities (Shea and Chesson 2002). In contrast to this biotic resistance hypothesis, we observed that the number of vascular plant species in the study plots was positively associated with both the emergence and survival of *L. polyphyllus*, indicating that species-rich plant communities were particularly suitable for this herbaceous plant invader. Thus, we found no evidence that increased diversity of native plant species would locally act as a barrier for the establishment of *L. polyphyllus*. Instead, increased species diversity seemed to promote the establishment of this invasive species, specifically, it improved emergence and survival. Several other studies have also reported that species-rich plant communities contain a larger number of exotic plant species than species-poorer plant communities (e.g., Stohlgren *et al*. 2006; Long *et al*. 2009; Souza *et al*. 2011). In fact, these studies, together with the present study, are in line with the hypothesis that plant communities may accommodate the establishment and coexistence of exotic plant species despite the presence and diversity of native plant species (Gilbert and Lechowicz 2005; Stohlgren *et al*. 2006). This hypothesis is also supported by the fact that vegetation height, which was used as a proxy for the intensity of competition for light in the present study, had no statistically significant effect on the survival of *L. polyphyllus*. Still, in addition to the number of plant species, their relative abundance in the community may also be important for the establishment of other species (e.g., Brandt and Seabloom 2012), but this factor was not considered here.

To conclude, single soil disturbance events generally enhanced the emergence and seedling survival of *L. polyphyllus*, although the exact effect depended on disturbance type. In other words, the two soil disturbance types considered here both promoted the establishment of *L. polyphyllus*, but through different demographic mechanisms early in life. This finding demonstrates the necessity of considering multiple vital rates of a given invader when exploring mechanisms for population establishment after disturbance events. For example, if we had considered seedling emergence only, we would have underestimated the demographic effects of the disturbance treatments on the early life stages of the study species. Moreover, the use of multiple vital rates will enable more targeted and, consequently, more efficient management recommendations to be made, which may be critical to invasion and restoration studies. In addition to disturbance, the number of vascular plant species in the study plots was positively associated with the emergence and survival of *L. polyphyllus*, suggesting that species diversity *per se* may not be a crucial mechanism for preventing the establishment of our study species.

SUPPLEMENTARY MATERIAL

**Figure S1:** Variation in the community characteristics studied in the paper.

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**Table 1:** results from linear mixed models used to examine the effects of disturbance treatments (control, soil disturbance, vegetation and litter removal) and year on the community characteristics studied here (number of vascular plant species, vegetation height, proportions of bare ground, litter, and moss) in 10 populations of *Lupinus polyphyllus*. Block nested within population was included as a random effect in the models. The likelihood-ratio test (LR) was used to assess significance of the fixed explanatory variables ($P <$ 0.05 in bold after a sequential Bonferroni correction). For each community characteristic, the value of that variable prior to treatment was used as a covariate in the model

| | Number of plant species | | Vegetation height (cm) | | Bare ground (%) | | Litter (%) | | Moss (%) | |
|---|---|---|---|---|---|---|---|---|---|---|
| Explanatory variables | $LR_{df}$ | $P$ | $LR_{df}$ | $P$ | $LR_{df}$ | $P$ | $LR_{df}$ | $P$ | $LR_{df}$ | $P$ |
| Treatment (3 levels) | $0.46_{2,9}$ | 0.795 | $2.13_{2,9}$ | 1 | $86.38_{2,9}$ | **<0.001** | $1.94_{2,9}$ | 1 | $8.7_{2,9}$ | 0.1285 |
| Year (2013, 2014) | $12.92_{1,9}$ | **<0.001** | $0.09_{1,9}$ | 1 | $15.83_{1,9}$ | **<0.001** | $0.06_{1,9}$ | 1 | $1.89_{1,9}$ | 1 |
| Treatment × Year | $0.122_{2,9}$ | 0.941 | $2.13_{2,11}$ | 1 | $4.43_{2,11}$ | 0.981 | $0.22_{2,11}$ | 1 | $0.46_{2,11}$ | 1 |
| Covariate | $16.39_{1,9}$ | **<0.001** | $32.00_{1,9}$ | **<0.001** | $26.43_{1,9}$ | **<0.001** | $33.67_{1,9}$ | **<0.001** | $54.79_{1,9}$ | **<0.001** |

**Table 2:** results from a generalised linear mixed model used to examine the effect of disturbance treatments (control, soil disturbance, vegetation and litter removal) and the number of vascular plant species on the emergence of *Lupinus polyphyllus* (n = 10 populations). Block nested within population was included as a random effect in the models. The likelihood-ratio test (LR) was used to assess significance of the fixed explanatory variables ($P < 0.05$ in bold)

| | Emergence | |
|---|---|---|
| Explanatory variables | $LR_{df}$ | $P$ |
| Treatment (3 levels) | $31.69_{2,6}$ | **< 0.001** |
| No. plant species | $4.22_{1,6}$ | **0.040** |
| Quadratic no. plant species | $1.30_{1,7}$ | 0.254 |
| Treatment × No. plant species | $1.11_{2,9}$ | 0.574 |

**Table 3:** results from a generalised linear mixed model used to examine the effect of disturbance treatments (control, soil disturbance, vegetation and litter removal), number of vascular plant species, and mean vegetation height on the survival of *Lupinus polyphyllus* (n = 10 populations) over two years. Block nested within population was included as a random effect and plot was included as a repeated factor in the models. The likelihood-ratio test (LR) was used to assess significance of the fixed explanatory variables ($P < 0.05$ in bold); not all main factors were tested because of significant interactions

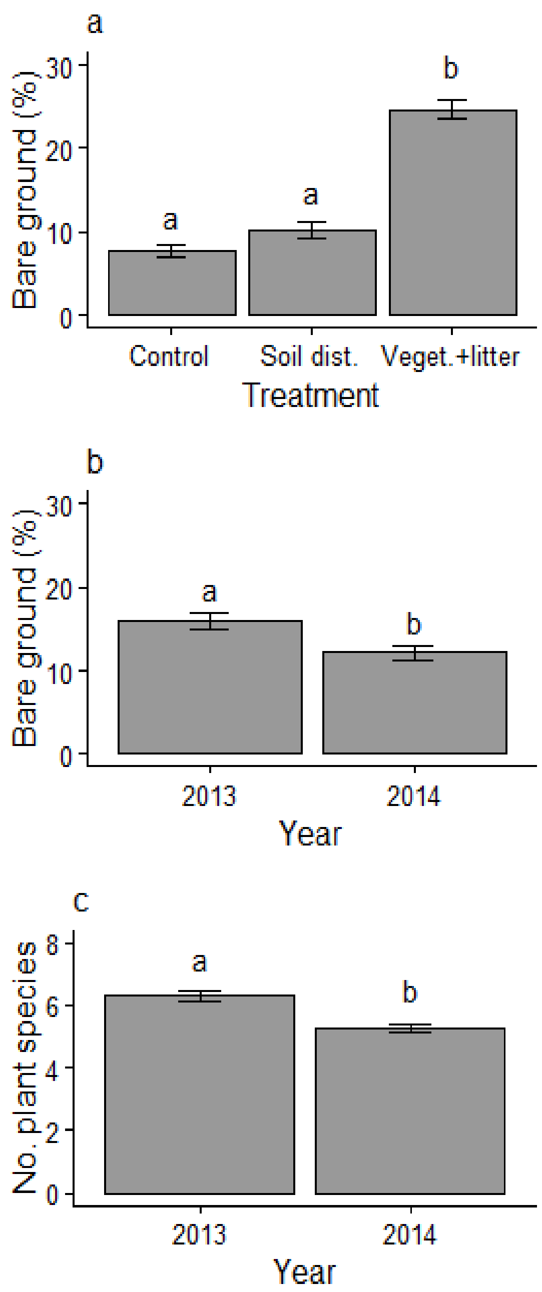
| | Survival | |
|---|---|---|
| Explanatory variables | $LR_{df}$ | $P$ |
| Treatment (3 levels) | Not tested | |
| Year (2013, 2014) | Not tested | |
| No. plant species | $3.91_{1,9}$ | **0.048** |
| Vegetation height | $1.63_{1,10}$ | 0.201 |
| Quadratic no. plant species | $1.32_{,1,12}$ | 0.251 |
| Quadratic vegetation height | $2.68_{1,11}$ | 0.101 |
| Treatment × Year | $14.78_{2,8}$ | **<0.001** |
| Treatment × No. plant species | $2.66_{2,15}$ | 0.264 |
| Treatment × Vegetation height | $5.791_{2,13}$ | 0.055 |

Figure legends

**Figure 1:** the proportion of bare ground in (**a**) different disturbance treatments (control, soil disturbance, vegetation and litter removal) and (**b**) each study year, and **c** the number of vascular plant species in the study plots over time. Shown are means ± SE (n = 10 populations). Different letters indicate statistically significant differences ($P < 0.05$, Tukey's or likelihood-ratio test).

**Figure 2:** (**a**) the emergence of *Lupinus polyphyllus* in different disturbance treatments and (**b**) the survival of the emerged individuals over time in 10 populations (mean ± SE). Different letters indicate statistically significant differences ($P < 0.05$, Tukey's test).

**Figure 3:** relationships between the number of vascular plant species in the study plots and (**a**) emergence and (**b**) survival of *Lupinus polyphyllus* individuals (mean ± SE, n = 10 populations).




520

521 Figure 1

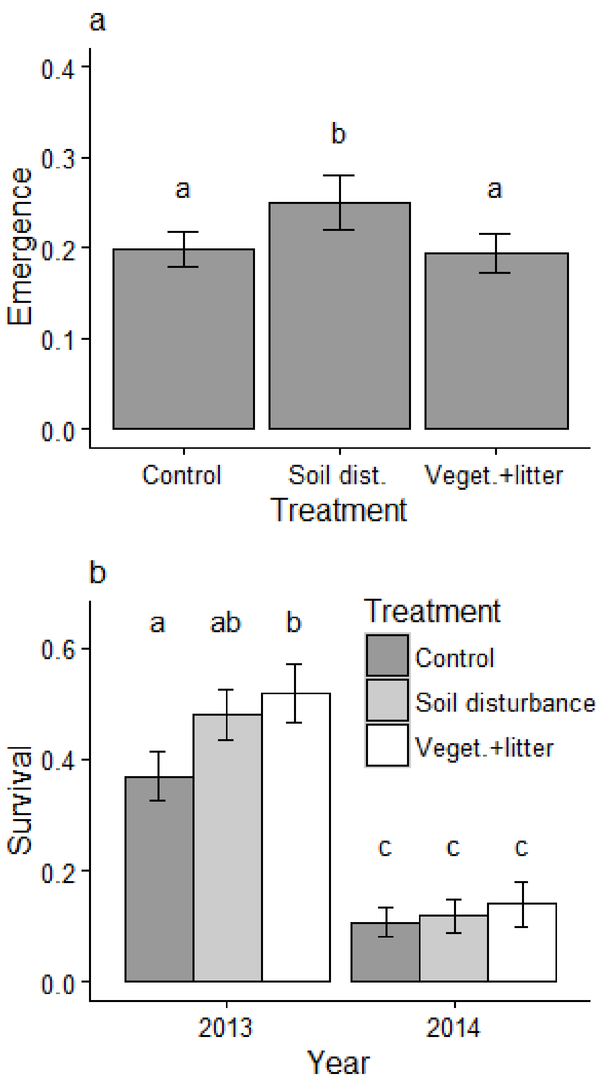

a
Emergence
0.4
0.3
0.2
0.1
0.0
b
a
a
Control
Soil dist.
Veget.+litter
Treatment
b
Survival
0.6
0.4
0.2
0.0
a
ab
b
c
c
c
Treatment
Control
Soil disturbance
Veget.+litter
2013
2014
Year

Figure 2

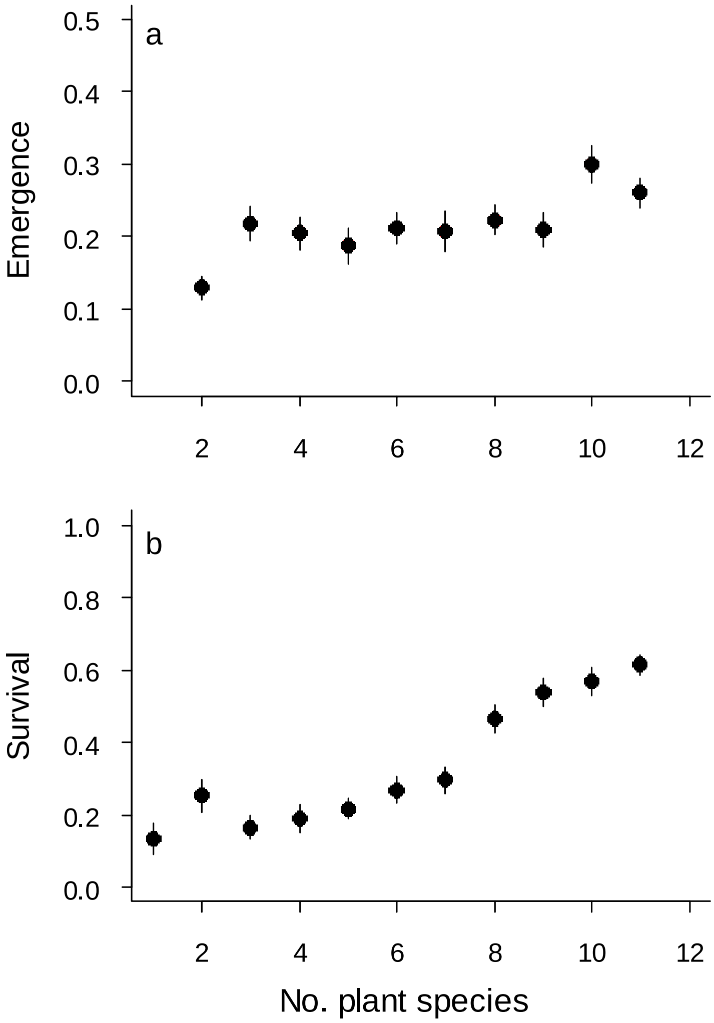

a
Emergence
0.5
0.4
0.3
0.2
0.1
0.0
2
4
6
8
10
12
b
Survival
1.0
0.8
0.6
0.4
0.2
0.0
2
4
6
8
10
12
No. plant species

Figure 3