For Arthropod-Plant Interactions

The invasive herb *Lupinus polyphyllus* attracts bumblebees but reduces total arthropod abundance

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Abstract Invasive plant species generally reduce the abundance and diversity of local plant species, which may translate into alterations at higher tropic levels, such as arthropods. Due to the diverse functional roles of arthropods in the ecosystems, it is critical to understand how arthropod communities are affected by plant invasions. Here, we investigated the impact of the invasive ornamental herb *Lupinus polyphyllus* (Lindl.) on arthropod communities during its main flowering period in southwestern Finland over two years. The total number of arthropods was about 46% smaller at invaded sites than at uninvaded sites in both study years, and this difference was mainly due to a lower abundance of beetles, Diptera, Lepidoptera, and ants. However, the number of bumblebees (particularly *Bombus lucorum*) was about twice as high at invaded sites compared to uninvaded sites, even though bumblebee richness did not differ between sites. There was no statistically significant difference between invaded and uninvaded sites in the abundances of the other arthropod groups considered (Hymenoptera (excluding bumblebees and ants), Hemiptera, and Arachnida). In addition, *L. polyphyllus* affected the relative abundance of four arthropod groups, with the order Lepidoptera being less common at invaded sites than at uninvaded sites, while the opposite was true for bumblebees, Hemiptera, and Arachnida. Overall, these results demonstrate that the negative impact of *L. polyphyllus* on biodiversity goes beyond its own trophic level, suggesting that this species has the potential to alter the abundance of different arthropod groups and, consequently, the structure of arthropod communities at a large scale.

Keywords Arthropods, Insects, Invasive species, Species abundance, Species richness

Introduction

Invasive plant species often form dense populations and thereby reduce the abundance and diversity of local plant species (reviewed by Vilà et al. 2011) or alter plant community composition (e.g., Hejda et al. 2009). As a consequence, plant invaders may considerably modify the habitat directly by affecting food resources (DiTomaso 2000) as well as indirectly by increasing shadiness and/or structural complexity (McKinney and Goodell 2010; Dutra et al. 2011). Such changes may in turn translate into alterations at higher tropic levels with consequences that may affect species interactions (Pearson 2009; Schirmel et al. 2016). For example, arthropods that use plants for food or habitat may be more sensitive to changes in a plant community than higher trophic levels (e.g., mammals; Schirmel et al. 2016), making them potential indicators of local ecological conditions (Hodkinson and Jackson 2005). Moreover, given the ecological and economic importance of numerous ecosystem services provided by arthropods, such as pollination services and decomposition (Losey and Vaughan 2006), it is crucial to understand how plant invasions affect arthropod communities.

Although arthropod abundance tends to correlate positively with plant diversity or abundance (e.g., Haddad et al. 2001; Dinnage et al. 2012), not all arthropods are necessarily equally affected by invasive plants. Previous studies have reported that effects may vary from negative to neutral or positive depending on the arthropod group and its functional role in question (e.g., Litt et al. 2014; Elleriis et al. 2015; Fenesi et al. 2015), and different effects have been observed even within closely related arthropod groups (e.g., Kajzer-Bonk et al. 2016; Tiedeken et al. 2016). As an example, invasive plant species with showy inflorescences may attract flower visitors, resulting in an increased abundance and diversity in pollinator fauna (Lopezaraiza-Mikel et al. 2007; Russo et al. 2016), while other arthropod groups might show a reduced abundance in the presence of plant invaders (Litt et al. 2014). Furthermore, increased pollinator abundance at invaded sites does not always translate into higher pollinator diversity, particularly if the flower visitors predominantly belong to a single or a few species.

The widely spread invasive ornamental herb *Lupinus polyphyllus* Lindl. reduces the number of co-existing vascular plant species (Valtonen et al. 2006; Ramula and Pihlaja 2012) and the abundance of Lepidoptera fauna (Valtonen et al. 2006) in a part of its introduced range. However, Jakobsson and Padrón (2014) observed that the number of bumblebees (the main pollinator group of this species) increased at sites invaded by flowering *L. polyphyllus* compared to uninvaded sites, suggesting that at least some arthropod groups might benefit from this plant invader. To our knowledge, the impact of *L. polyphyllus* on different arthropod groups has not been systematically assessed, and we therefore asked the following two questions. How does *L. polyphyllus* affect the number of individuals in different arthropod groups (primarily flying and foliage arthropods) and the relative abundance of these groups in local arthropod communities? Due to a positive relationship between arthropod abundance plant species richness (Haddad et al. 2001), we predicted that the presence of *L. polyphyllus* would reduce plant diversity and thereby the total number of arthropods at invaded sites, and would modify the relative abundances of different arthropod groups. How does this plant invader affect the diversity of its main pollinator group, bumblebees (*Bombus* spp.)? Due to pollen resources provided by *L. polyphyllus*, we hypothesised that bumblebees would be more abundant and would show higher species richness at invaded sites than at uninvaded sites during the flowering period of the plant invader.

Materials and methods

Invasive species

Lupinus polyphyllus (Fabaceae) is a perennial herb, 50-100 cm tall, that in the study area flowers in early summer. It is native to North America and has been widely used for ornamental purposes and landscaping in different continents (Fremstad 2010). The species is currently invasive in many European countries (including Finland, where it was introduced in the 1800s), New Zealand, Chile, and the southern parts of Australia (Fremstad 2010; Meier et al. 2013). Showy inflorescences whose colour ranges from blue to white or pink are nectarless but produce pollen, and are mainly pollinated by bumblebees (Haynes and Mesler 1984; Pohtio and Teräs 1995; Jakobsson and Padrón 2014). Seeds mature in hairy pods and are dispersed ballistically up to a few metres from the parent plant in August.

Arthropod sampling

We chose five paired study sites (five invaded by *L. polyphyllus*, five uninvaded) that were located in wastelands (i.e. uncultivated areas including local green space) in the Turku region, southwestern Finland. The invaded sites were 1.9-14.3 km from each other, with each uninvaded site being 200-800 m from the closest invaded site. No other *Lupinus* species were present at the study sites. The extent of *L. polyphyllus* invasions varied between 120-2400 m^2, with the average cover of *L. polyphyllus* being 58-82% per m^2 (mean ± SD = 73.1% ± 9.4) at the invaded sites. All study sites were dominated by herbaceous vegetation, with some bushes and trees growing in the vicinity. At each study site, we sampled the arthropod fauna with three window traps, which were designed to passively sample primarily flying and foliage arthropods over the main flowering period of *L. polyphyllus* in two summers (12-27 June in 2013 and 6-27 June in 2014). Note that due to a cold early summer in 2013, the flowering of *L. polyphyllus* started later that year than in 2014. Each window trap consisted of two crossed plexiglass panels (26 × 18 cm at a 90˚ angle) that were tied to a plastic pot (vol = 3 liter, diam = 19 cm), which hung from a green metal frame at the height of the surrounding herbaceous vegetation. The pot contained concentrated salt water (about 3 dl) with some drops of transparent unscented dishwashing soap. The traps were emptied once a week and the arthropods were stored in 50-ml centrifuge tubes filled with 70% ethanol for further identification. They were either identified to easily recognisable taxonomic levels (bumblebees, ants, beetles), orders (Diptera, Hymenoptera (excluding bumblebees and ants), Hemiptera, Lepidoptera), or a class (Arachnida). Overall, these levels roughly represented different functional groups: pollinators (bumblebees), herbivores (Hemiptera, Lepidoptera, beetles), predators (Hymenoptera, Arachnida) and detritivores (Diptera). An exception was ants that have diverse functional roles in communities (Folgarait 1998; Litt et al. 2014) and therefore, they were analysed as a separate group. Bumblebees were further identified to the species level. Due to handling damage, 1.14-6.76% of the individuals per trap (mean ± SD = 4.24% ± 1.60) were unidentifiable and were omitted from the final analyses, resulting in a total of 5729 and 3180 individuals in years 2013 and 2014, respectively.

Data analyses

To explore the effect of *L. polyphyllus* on arthropods, we constructed generalised linear mixed-effects models (function 'glmer' in the *lme4* package in R 3.2.2, R Core Team, 2016) for the total number of arthropods collected, the number of individuals per arthropod group (bumblebees, ants, Hymenoptera (excluding bumblebees and ants), beetles, Diptera, Hemiptera, Lepidoptera, Arachnida), the relative abundances of these groups, and bumblebee richness. As we were interested in a total effect rather than in variation among sampling seasons, we summed data from different sampling dates per trap within each study year. In all models, site status (invaded, uninvaded), year (2013, 2014), and their interaction were used as fixed explanatory variables, and site-pair was included as a random factor to account for measurements from the two repeated years per site. The Poisson distribution with log link was used for the models of the number of individuals and bumblebee richness, while the binomial distribution with logit link was used for the models of the relative abundances of different arthropod groups. Overdispersion in the models (dispersion factor > 3.5) was corrected by including a random term of trap in the analyses when necessary. The goodness of fit was confirmed by visual examination of the residual plots for each model. The significance of the fixed explanatory variables was examined using the likelihood ratio test fit with maximum likelihood by testing the model with a given variable against the model without that variable. To minimise the probability of type I errors resulting from identical tests carried out for multiple response variables, we adjusted *P*-values with the number of models constructed for the number of individuals and relative abundances, respectively.

Similarly, we used a generalised linear mixed-effects model (Poisson distribution with log link) to investigate the effect of *L. polyphyllus* on the number of individuals per bumblebee species. Species, site status (invaded, uninvaded), year (2013, 2014), and species × site status and site status × year interactions were included as fixed explanatory variables, and site-pair was again included as a random factor. Note that other interaction terms were not possible include in the model due to convergence problems. Contrasts (in the *lsmeans* package) were used to determine whether the number of individuals differed between invaded and uninvaded sites for each bumblebee species.

Results

The number of arthropods

The presence of the invasive *L. polyphyllus* reduced arthropod abundance, with the total number of arthropods being on average 45.8% smaller at invaded sites than at uninvaded sites (χ^2 = 18.65, df = 1, P = 0.0002, mean ± SD = 100.5 ± 167.4 and 185.5 ± 44.6, respectively). This pattern was true in both study years (χ^2 = 0.575, df = 1, P = 0.449 for the status × year-interaction). The smaller number of arthropods at invaded sites was mainly due to four arthropod groups (beetles, Diptera, Lepidoptera, ants) that tended to be less abundant in the presence of *L. polyphyllus* (Table 1, Fig. 1a). Bumblebees were the only arthropod group that was more abundant at invaded sites (about double that at uninvaded sites), whereas for the rest of the groups (Hymenoptera (excluding bumblebees and ants), Hemiptera, and Arachnida), abundance did not differ significantly between invaded and uninvaded sites (Table 1, Fig. 1a). The total number of arthropods caught in the traps was higher in 2013 than in 2014 (χ^2 = 16.98, df = 1, P = 0.0004, mean ± SD = 185.2 ± 168.8 and 100.8 ± 39.6, respectively). In particular, Diptera and beetles were more abundant in 2013 than in 2014 (Table 1, mean ± SD per trap = 54.87 ± 27.37 and 28.27 ± 13.45 for Diptera; 100.43 ± 159.67 and 31.47 ± 15.81 for beetles), whereas bumblebees were less abundant in 2013 than in 2014 (mean ± SD per trap = 1.87 ± 1.60 and 6.13 ± 4.26, respectively).

The relative abundances of arthropod groups

The relative abundances of four arthropod groups differed between invaded and uninvaded sites, with Lepidoptera being less common at sites invaded by *L. polyphyllus*, and the opposite being true for bumblebees, Hemiptera, and Arachnida (Table 2, Fig. 1b). Again, these effects remained constant over the two study years (Table 2). However, the relative abundances of many arthropod groups differed between the years; all arthropod groups, except beetles and Diptera, increased in relative abundance in 2014 compared to 2013 (Table 2, results not shown).

Bumblebee richness and number

We observed a total of 11 bumblebee species during the two study years (Fig. 2). Bumblebee richness was higher in 2014 than in 2013 (χ^2 = 8.29, df = 1, P = 0.004, mean ± SD = 2.07 ± 1.51 and 1.13 ± 0.82 species per trap, respectively), but did not differ between invaded and uninvaded sites ($\chi^2 = 0.38$, df = 1, $P = 0.540$ for site status and $\chi^2 = 0.16$, df = 1, $P = 0.688$ for the status × year interaction). However, individual bumblebee species showed different patterns between invaded and uninvaded sites ($\chi^2 = 32.92$, df = 1, $P < 0.001$ for species × site status) in both study years ($\chi^2 = 0.22$, df = 1, $P = 0.640$ for site status × year). *Bombus lucorum* was the most common bumblebee species and also the only species that was more abundant at invaded sites than at uninvaded sites (Fig. 2), accounting for 79.2% and 47.4% of all observed individuals of the genus *Bombus* at these two sites, respectively.

Discussion

We discovered that the invasive herb *L. polyphyllus* reduced the total number of arthropods in both study years despite annual differences in arthropod abundance. Similar negative impacts by other invasive plant species have been reported elsewhere (e.g., reviewed by Litt et al. 2014; van Hengstum et al. 2014; Schirmel et al. 2016). In the present study, the reduction in arthropods was mainly due to a decrease in the number of beetles, Diptera, Lepidoptera, and ants at invaded sites. The reduction of these four arthropod groups might be related to the lower overall plant diversity at invaded sites (Valtonen et al. 2006; Ramula and Pihlaja 2012) and the resulting reduced availability of resources (e.g., habitats or nectar) that might be critical to beetles and Lepidoptera in particular (i.e. herbivorous arthropods). For example, small beetles that were frequently found in traps often prefer Apiaceae species, which may have been proportionally less abundant at invaded sites where the vegetation was dominated by the plant invader. Moreover, the lower abundance of nectar-feeding arthropods, such as beetles, Lepidoptera, and some Diptera and ant species, at invaded sites was probably due to the fact that *L. polyphyllus* does not produce nectar as a reward (Haynes and Mesler 1984). In this, our findings concur with those of Valtonen et al. (2006), who observed that *L. polyphyllus* reduced the total number of Lepidoptera on road verges in Finland. Alternatively, the reductions in some of the four arthropod groups at invaded sites might be related to changes in the microclimate or in the complexity of the habitat, with the broad-leaved *L. polyphyllus* possibly increasing habitat humidity and shadiness in the foliage layer. Previous studies have shown that structural changes in the habitat caused by plant invaders may indeed modify the foraging behavior of animals (e.g., Pearson 2009; McKinney and Goodell 2010; Dutra et al. 2011). In the present study, increased shadiness at invaded sites might have been harmful for thermophilic ant species that prefer low vegetation (Kajzer-Bonk et al. 2016), possibly explaining the lower overall abundance of ants.

Despite the negative effect of *L. polyphyllus* on the four arthropod groups (beetles, Diptera, Lepidoptera, ants) in this study, the invader had no effect on Hymenoptera (excluding bumblebees and ants), Hemiptera, or Arachnida. A negligible effect on Hymenoptera and Arachnida could be because these groups are primarily predators that do not directly consume plants for food, but rely on other arthropods. Interestingly, the number of bumblebees was about twice as high at invaded sites compared to uninvaded sites, suggesting that *L. polyphyllus* attracted pollinators by providing pollen resources during its flowering period and might have acted as a magnet species (Molina-Montenegro et al. 2008; Masters and Emery 2015). Window traps used here may have even underestimated bumblebee abundance particularly at the invaded sites where floral resources are abundant (Baum and Wallen 2011). A more detailed inspection of the data revealed that the increased bumblebee abundance was due entirely to the activity of *Bombus lucorum,* which responded to the presence of *L. polyphyllus* more strongly than did other *Bombus* species. Given the fact that *B. lucorum* frequently visits the flowers of *L. polyphyllus* in Finland (Pohtio and Teräs 1995), this observation is not surprising, but shows that the responses of individual species may vary within the same functional group. Similar to our finding, Tiedeken et al. (2016) observed that pollinators (honeybees, solitary bees and bumblebees) were differentially affected by the invasive shrub, *Rhododendron ponticum*. It should be noted, though, that *Bombus* species visiting and pollinating *L. polyphyllus* are likely to vary among countries (Haynes and Mesler 1984; Jakobsson et al. 2015).

Overall, increased bumblebee abundance may be beneficial for plant communities in terms of enhanced pollination services. Previous studies demonstrate that some perennial herbs do indeed receive more pollinator visits when they are growing next to flowering individuals of *L. polyphyllus* than when they are further away (Jakobsson and Padrón 2014; Jakobsson et al. 2015). However, an increase in pollinator visits to local plant species does not necessarily translate into greater total reproductive output if, for example, the plants are not limited by pollen or foreign pollen interferes with fertilization (Hegland and Totland 2008; Masters and Emery 2015), which calls into question the overall benefit of higher pollinator abundance at invaded sites. At least in the plant communities of temperate regions, pollen limitation may be less common than is generally acknowledged (Hegland and Totland 2008). The effects of plant invaders on the reproductive output of native plants might also depend on the density of the plant invader, with positive effects possibly occurring at low invader densities only (Muños and Cavieres 2008). Moreover, Herron-Sweet et al. (2016) previously pointed out that the effects of plant invaders on pollinator communities are likely to vary during the growing season, depending on their blooming time. As we only sampled arthropods during the main flowering season of *L. polyphyllus*, the positive impact of this plant invader on bumblebees is likely to disappear during off-peak flowering, while the negative impact on some arthropod groups would probably still be present.

In contrast to expectations, *L. polyphyllus* had no effect on bumblebee richness in the present study: *B. lucorum* dominated bumblebee communities regardless of the invasion status of a given site. Instead, previous studies have reported that both the abundance and diversity of insect pollinators increased in the presence of some plant invaders (e.g., Lopezaraiza-Mikel et al. 2007; Russo et al. 2016). However, like us, Bartomeus et al. (2008) observed that although two invasive herbs (*Carpobrotus affine acinaciformis* and *Opuntia stricta*) attracted more pollinators than local native species did, there was no effect on pollinator species richness. Taken together, these results indicate that the effects of invasive herbs on pollinator communities are complex and possibly species specific.

Since the present study is observational, different confounding factors might have influenced the results. However, the fact that the effect of *L. polyphyllus* on the number and relative abundance of the eight target arthropod groups remained constant over the two study years indicates that the results are robust. In other words, the abundance of beetles, Diptera, Lepidoptera, and ants are lower at sites invaded by *L. polyphyllus* than at uninvaded sites, while the opposite is true for bumblebees and *B. lucorum* in particular. We note, though, that all invaded sites included in the present study represented large invasions, often consisting of hundreds of quadrats of *L. polyphyllus*, and our results may not apply to small invasions. For example, Fenesi et al. (2015) detected that the effect of the invasive herb *Solidago canadensis* on the abundance of some pollinator groups depended on the relative cover of this plant invader, and the same might apply to our study species. We also primarily focused on the abundance of different arthropod groups rather than their diversity and therefore, the diversity impacts of *L. polyphyllus* (if any) on arthropods other than bumblebees remain to be assessed. Moreover, our main interest was in flying and foliage arthropods, and different types of traps would have been needed to sample ground-dwelling arthropods more efficiently. Still, the sampling used is unlikely to violate our main finding of reduced arthropod abundance at invaded sites, as Tanner et al. (2013) observed that foliage- and ground-dwelling arthropods showed qualitatively similar responses to the presence of the invasive herb *Impatiens glandulifera*.

Taken together, the present study demonstrates that the invasive herb *L. polyphyllus* generally has a negative impact on its associated arthropod fauna in terms of a lower abundance of beetles, Diptera, Lepidoptera, and ants. These results, together with previous findings on the negative impact of this plant invader on plant communities (Valtonen et al. 2006; Ramula and Pihlaja 2012), indicate that *L. polyphyllus* tends to reduce the number of co-occurring species across different trophic levels. Such changes in species abundances may extend up to higher trophic levels (Schirmel et al. 2016) and might have consequences for local communities at a large scale.

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Table 1 Results from generalised linear mixed-effect models used to examine the effect of the invasive herb *Lupinus polyphyllus* on the number of individuals per arthropod group at five paired study sites over two summers. Site-pair was included as a random effect in the models. The likelihood ratio test was used to assess the significance of the fixed explanatory variables ($P < 0.05$ in bold after adjusting P-values by the number of models)

No. individuals	Source	df	χ^2	P
Bumblebees	Status (invaded, uninvaded)	1	28.25	**<0.001**
	Year (2013, 2014)	1	69.39	**<0.001**
	Status × Year	1	0.22	0.999
Ants	Status	1	7.31	0.062
	Year	1	2.62	0.949
	Status × Year	1	0.03	0.999
Other Hymenoptera	Status	1	7.37	0.090
	Year	1	1.51	0.999
	Status × Year	1	0.40	0.999
Beetles	Status	1	8.16	**0.039**
	Year	1	7.64	0.052
	Status × Year	1	0.72	0.999
Diptera	Status	1	13.52	**0.002**
	Year	1	30.71	**<0.001**
	Status × Year	1	0.01	0.999
Hemiptera	Status	1	0.54	0.999
	Year	1	1.42	0.999
	Status × Year	1	0.12	0.999
Lepidoptera	Status	1	40.44	**<0.001**
	Year	1	1.42	0.999
	Status × Year	1	0.01	0.999
Arachnida	Status	1	4.52	0.326
	Year	1	3.54	0.507
	Status × Year	1	6.53	0.088

Table 2 Results from generalised linear mixed-effect models used to examine the effect of the invasive herb *Lupinus polyphyllus* on the relative abundance of different arthropod groups at five paired study sites over two summers. Site-pair was included as a random effect in the models. The likelihood ratio test was used to assess the significance of the fixed explanatory variables (P < 0.05 in bold after adjusting P-values by the number of models)

Relative abundance	Source	df	χ^2	P
Bumblebees	Status (invaded, uninvaded)	1	28.25	**<0.001**
	Year (2013, 2014)	1	69.39	**<0.001**
	Status × Year	1	1.96	0.999
Ants	Status	1	3.26	0.568
	Year	1	7.71	**0.044**
	Status × Year	1	0.09	0.999
Other Hymenoptera	Status	1	0.49	0.999
	Year	1	25.03	**<0.001**
	Status × Year	1	0.15	0.999
Beetles	Status	1	2.37	0.999
	Year	1	2.37	0.987
	Status × Year	1	0.98	0.999
Diptera	Status	1	0.19	0.537
	Year	1	3.39	0.402
	Status × Year	1	0.37	0.999
Hemiptera	Status	1	22.39	**<0.001**
	Year	1	17.06	**<0.001**
	Status × Year	1	3.26	0.569
Lepidoptera	Status	1	17.26	**<0.001**
	Year	1	10.55	**0.009**
	Status × Year	1	0.01	0.999
Arachnida	Status	1	11.45	**0.006**
	Year	1	10.09	**0.012**
	Status × Year	1	7.15	0.060

Figure legends

Fig. 1 (a) The number of individuals per arthropod group and (b) the relative abundance of different arthropod groups in the presence and absence of the invasive herb *Lupinus polyphyllus* (mean ± SE, n = 5 paired sites). Stars indicate statistically significant differences between invaded and uninvaded sites for a given arthropod group ($P < 0.05$, generalised linear mixed-effects models). Abbreviations are Bumble = bumblebees, Hymeno = Hymenoptera (excluding bumblebees and ants), Hemipt = Hemiptera, Lepidop = Lepidoptera

Fig. 2 The number of individuals per bumblebee (*Bombus*) species in the presence and absence of the invasive herb *Lupinus polyphyllus* (mean ± SE, n = 5 paired sites). A star indicates a statistically significant difference between invaded and uninvaded sites for a given species ($P < 0.05$, contrasts)

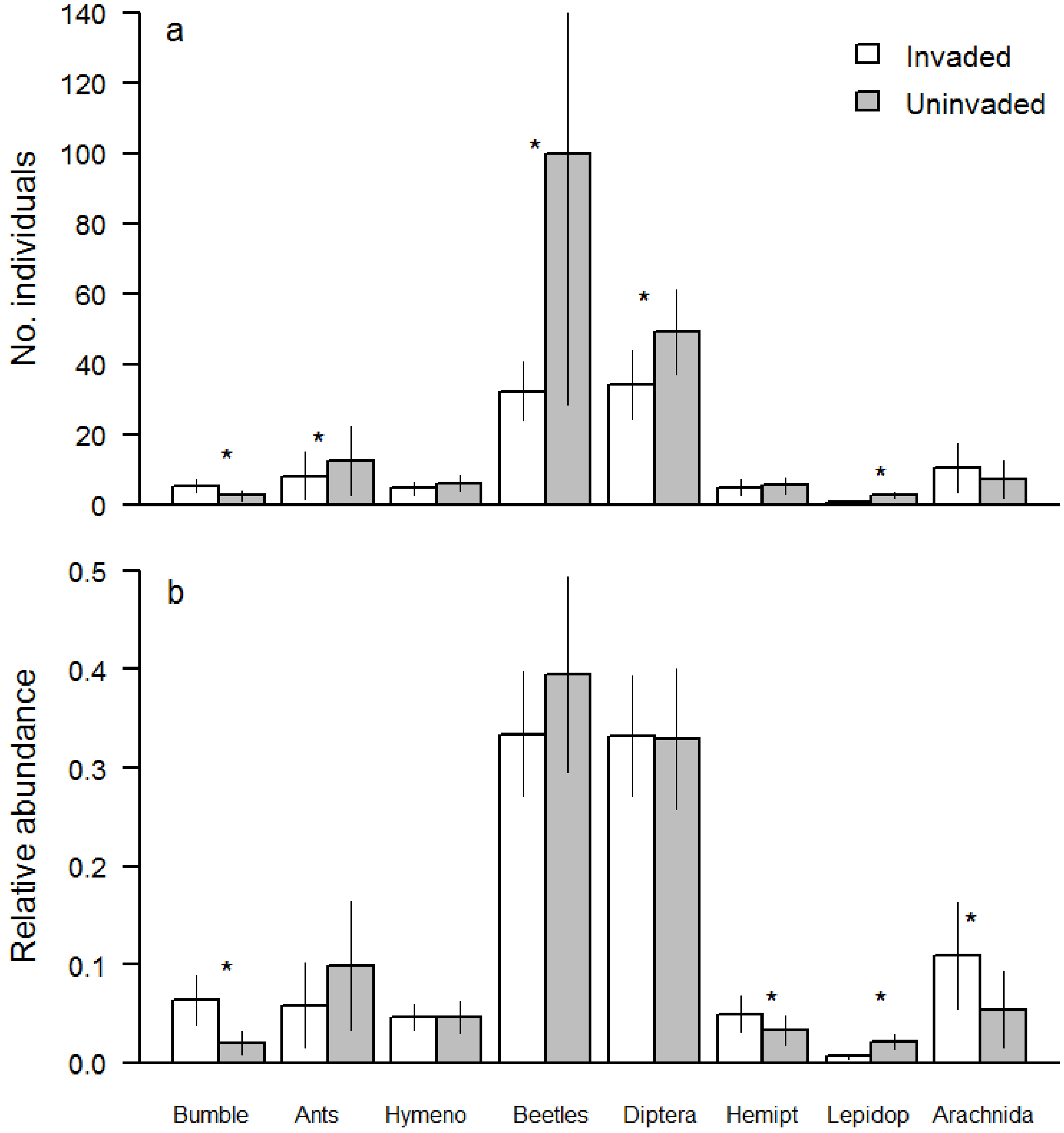
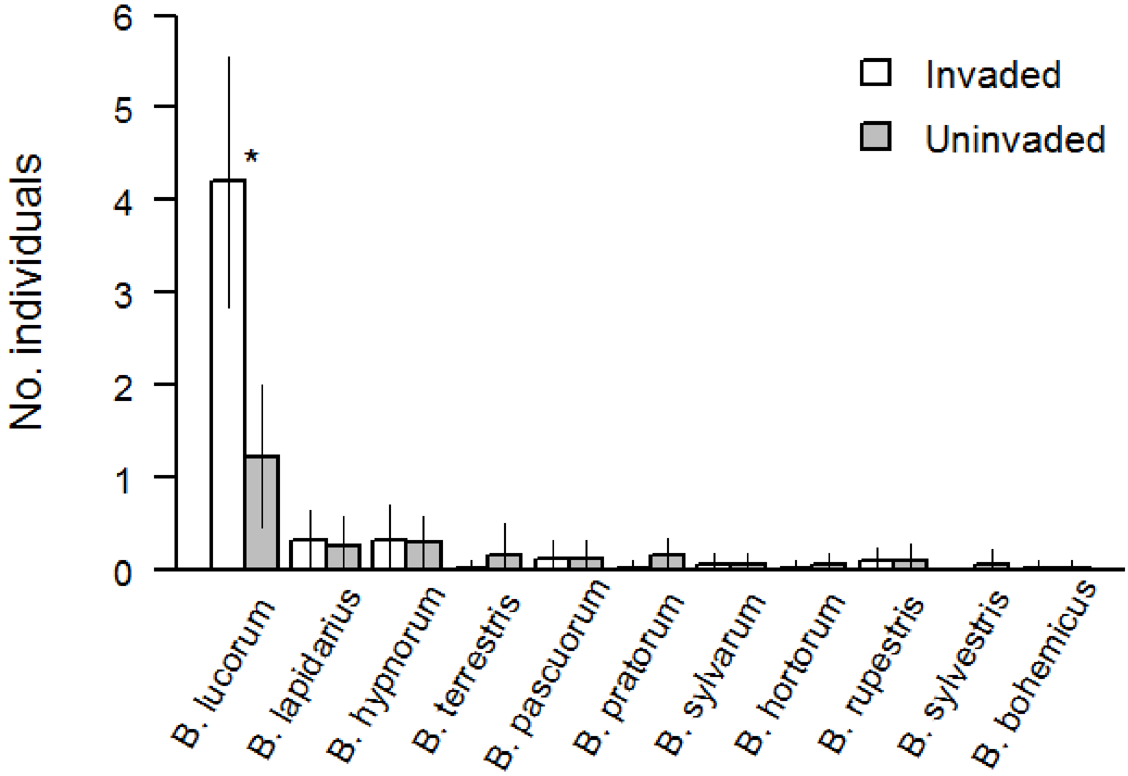

a
b
Invaded
Uninvaded
No. individuals
Relative abundance
140
120
100
80
60
40
20
0
0.5
0.4
0.3
0.2
0.1
0.0
Bumble
Ants
Hymeno
Beetles
Diptera
Hemipt
Lepidop
Arachnida

Fig. 1



No. individuals
6
5
4
3
2
1
0
*
Invaded
Uninvaded
B. lucorum
B. lapidarius
B. hypnorum
B. terrestris
B. pascuorum
B. pratorum
B. sylvarum
B. hortorum
B. rupestris
B. sylvestris
B. bohemicus

Fig. 2