



The invasive herb *Lupinus polyphyllus* can reduce plant species richness independently of local invasion age

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Abstract The ecological impacts of invasive species may change or accumulate with time since local invasion, potentially inducing further changes in communities and the abiotic environment. Yet, time since invasion is rarely considered when investigating the ecological impacts of invasive non-native species. To examine the effect of time since invasion on the ecological impacts of *Lupinus polyphyllus*, a perennial nitrogen-fixing herb, we surveyed vascular plant communities in the presence and absence of *L. polyphyllus* in young, intermediate, and old semi-natural grassland sites (ca. 5, 10, 15 years representing both time since lupine invasion and plant community age). We analyzed vascular plant community composition, vascular plant species richness, and the cover of

various ecological plant groups and *L. polyphyllus*. In contrast to our hypotheses, we found no change in the mean cover of *L. polyphyllus* (about 35%) with time since local invasion, and an ordination did not suggest marked changes in plant community composition. *L. polyphyllus* was associated with lower species richness in invaded plant communities but this effect did not change with time since invasion. Invaded plant communities were also associated with lower occurrence of generalist, oligotrophic (low-nutrient-adapted) and copiotrophic (nutrient-demanding) species but no temporal dynamics were detected. We conclude that even the intermediate cover of *L. polyphyllus* can reduce plant species richness, but the ecological impact caused by this invader might not dramatically change or accumulate with time since invasion.

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Introduction

Understanding the dynamics of an invasive non-native species is important in invasion biology and for developing best management practices. Whilst it is acknowledged that the ecological impacts and

abundance of non-native species are not stagnant but may vary with time since invasion (Simberloff and Gibbons 2004; Strayer 2012; Flory and Clay 2013; Ortega et al. 2019), empirical data are scant on how the abundance and ecological impacts of non-native species change with time (Strayer et al. 2017; Ortega et al. 2019; Crystal-Ornelas and Lockwood 2020). Previous studies have shown that invasive non-native species can progress from a ‘harmful’ and abundant phase to a ‘harmless’ phase with a lower population size (i.e., boom-bust dynamics) (Elton 1958; Williamson 1996) and, occasionally, populations of invasive non-native species may even collapse spontaneously (e.g., reviewed by Simberloff and Gibbons 2004). For example, boom-bust dynamics have been demonstrated for the perennial herb *Heracleum mantegazzianum* (giant hogweed) in the Czech Republic: its cover declined with time since local invasion and native plant communities started to recover ~ 30 years thereafter (Dostál et al. 2013). Here we investigate impacts of the harmful non-native herb *Lupinus polyphyllus* (garden lupine) on vascular plant communities of semi-natural grasslands in relation to time since lupine invasion.

Boom-bust dynamics could be caused by an array of factors (reviewed by Strayer et al. 2017), including a weakening of the mechanisms that initially led to the organism’s invasion success: enemy release (Elton 1958; Keane and Crawley 2002), novel weapons (Callaway and Aschehoug 2000), and the resulting increased competitive ability (Blossey and Nötzold 1995). Firstly, enemies and competitors may accumulate during invasion as they arrive from the invader’s native range, and local species adapt to compete with the non-native species or attack the new host (Carroll et al. 2005; Hawkes 2007; Diez et al. 2010; Flory and Clay 2013; Stricker et al. 2016). For example, Dostál et al. (2013) linked the decline of *H. mantegazzianum* to the accumulation of enemies, and specifically to negative plant-soil feedbacks. Secondly, native species may evolve to tolerate the novel weaponry of non-native species, e.g., allelochemicals in plants (Callaway et al. 2005; Oduor 2013). Besides native competitors and enemies, non-native species also continue to evolve. As an example, the production of allelochemicals may decrease with time since invasion, as Lankau et al. (2009) has demonstrated for the invasive *Alliaria petiolata* (garlic mustard) and Gruntman et al. (2017) for *Impatiens glandulifera*

(Himalayan balsam). Yet, it is unclear how frequently and during what timeframe such changes in species interactions occur, or whether the extent of these changes is sufficient to cause boom-bust dynamics.

The ecological impact of a non-native species is dependent on its abundance (e.g., Hejda et al. 2009). However, a non-native species could also become locally more harmful with time since invasion even if its abundance does not increase because some species modify or engineer the invaded ecosystem, its food web and physical resources, nutrient cycles, hydrology and disturbance regimes (Crooks 2002; Levine et al. 2003; Simberloff 2011; Strayer 2012). For instance, *Morella (Myrica) faya*, a nitrogen-fixing shrub, doubled the nitrogen and water content of canopies compared to native forests in nitrogen-poor areas of Hawaii (Asner and Vitousek 2005). Moreover, invasive non-native species can alter the physical structure of ecosystems through major changes in species composition (Williamson 1996). Initially, species richness increases due to a lag between introduction of a non-native species and extinction of the negatively impacted native species. Such an extinction lag is particularly pronounced among plants (Sax et al. 2002; Gilbert and Levine 2013). Extinction is rare and the process is slow, since invasive non-native plants increase extinction probability of affected plants through metapopulation dynamics (Gilbert and Levine 2013). Nevertheless, older invasions can show a decrease in native plant species richness compared to more recent invasions (Gaertner et al. 2009). Marked changes in community composition then cause concurrent changes in nutrient and energy flows, and vice versa (Simberloff 2011).

In its invaded range, *L. polyphyllus* (hereafter lupine) is associated with declines in both vascular plant and insect species richness in various open habitats such as grasslands, sparse forests, road verges and wastelands in Northern Europe (Valtonen et al. 2006; Ramula and Pihlaja 2012; Ramula and Sorvari 2017) and nutrient-poor acidic, mesic or wet grasslands in Central Europe (Thiele et al. 2010a; Hejda et al. 2019; Hansen et al. 2020). The magnitude of ecological impact depends on environmental conditions and species composition of the invaded plant community (Thiele et al. 2010a; Čuda et al. 2017). For example, lupine-associated reduction in plant diversity was greater in ruderal grasslands than in managed grasslands (Thiele et al. 2010a), and low-growing

plant species appeared to be more vulnerable to the presence of lupine than taller plants (Valtonen et al. 2006; Thiele et al. 2010a). Such a decline in plant species may be linked to lupine shading (Valtonen et al. 2006) or may indicate an overall asymmetrical competition for light and space (Thiele et al. 2010a). However, *Lupinus* species may also increase nitrogen and organic matter content of soils (Evans et al. 1987; Titus 2009). Thereby, lupine can lead to changes in plant community composition such as an increased number of nitrogen-demanding plant species and a decreased number of species with low nitrogen demand (Thiele et al. 2010a), decreased species richness and increased biomass (Maron and Jefferies 2001; Gosling 2005). Furthermore, *Lupinus* species excrete quinolizidine alkaloids that hinder seed germination and the growth of other plants (Wink 1983; Muzquiz et al. 1994; Loydi et al. 2015; Lytinen and Lindström 2019). If the ecological impacts of lupines accumulate or the invader's abundance changes over time, species composition may shift with time since invasion.

To our knowledge, local temporal dynamics of lupine invasions have not been studied, but some lupine stands do disappear with time (S. Ramula, H. Setälä, pers. obs.). This suggests that the ecological impacts of lupine may indeed vary in relation to time since local lupine invasion and might be related to a weakening of mechanisms that initially lead to its invasion success (i.e., boom-bust dynamics). Currently, the species has a few aboveground herbivores in Finland; it is consumed by the native generalist snail *Arianta arbustorum* and the moth *Agonopterix nervosa* (M. Prass, pers. obs.). Additionally, for the first time in Finland, we detected a lupine aphid from North America, *Macrosiphum albifrons* (M. Prass, D.J. Kotze, H. Setälä, pers. obs.), which can lower its seed production (Beuthin 2012). Plant-soil feedbacks have not been studied on lupine, but the accumulation of belowground enemies is probable.

Here, we investigate vascular plant communities of dry to mesic semi-natural grasslands in southern Finland in the presence and absence of the invasive lupine in young, intermediate, and old sites (ca. ≤ 5 , 10, ≥ 15 years, respectively, representing both time since lupine invasion and plant community age). Our research questions were: (1) How does the abundance of lupine change with time since local invasion? (2) How do the vascular plant community and plant

species richness differ with community age depending on the presence and abundance of lupine, and more specifically, (3) which kinds of plant species are most sensitive to lupine invasion? To answer the latter question, we divided individual plant species into ecological groups based on preferred soil moisture and nutrient levels. Firstly, based on the concept of boom-bust dynamics and our observations in the field, we hypothesized that the cover of lupine would start to decline in older stands. If, however, there is no such decline in lupine cover with time since invasion, we, secondly, expected that its impact on local plant communities would accumulate. Thus, when comparing lupine-invaded and uninvaded plant communities, species composition and plant species richness would differ more with time since lupine invasion. Furthermore, due to the shading and fertilizing impact of lupine, we expected that compared to uninvaded communities, lupine-invaded plant communities would become more dissimilar with time due to the following changes: the cover of nutrient-demanding species (copiotrophs) would increase, while covers of low-growing species of dry habitats and low-nutrient habitats (oligotrophs) would decline (Thiele et al. 2010a).

Material and methods

Study species

Lupinus polyphyllus Lindl. (Fabaceae) is a short-lived perennial nitrogen-fixing herb, native to western areas of North America (Fremstad 2010). It is invasive in many European countries as well as in southern Australia and New Zealand (Global Invasive Species Database 2020). The species was introduced to Finland for ornamental purposes but escaped into natural habitats more than a hundred years ago and is now common, especially in southern parts of the country (Lampinen and Lahti 2019). Lupines can grow up to 50–120 cm tall (Mossberg et al. 2005) and produce large quantities of seeds (Ramula 2014), which disperse ballistically up to a few meters from the parent individual and may remain viable in the soil seed bank for decades (Fremstad 2010). Lupines can form dense stands ($> 70\%$ cover) and thrive in a variety of open habitats (see above) but, in Finland, it frequently occurs in nutrient-poor, well-drained and

ruderal habitats (Mossberg et al. 2005; Fremstad 2010; Ramula and Pihlaja 2012).

Study system

The study was conducted in the Lahti area, southern Finland, where the first confirmed record of lupine is from 1936 (Erkamo 2020). Lupines were still rare in the 1980's but currently occur widely across the city of Lahti (Hovi Antti, unpublished results). According to the Köppen climate classification, Lahti is on the boundary between a warm-summer humid continental climate (i.e., class Dfb) and subarctic climate (i.e., Dfc), meaning that the monthly mean temperature of the coldest month is under $-3\text{ }^{\circ}\text{C}$ and approximately four months average above $10\text{ }^{\circ}\text{C}$, and with no significant difference in precipitation between summer and winter (Kottek et al. 2006).

Since lupine commonly occurs in well-drained open habitats in the study region, we selected 18 gravelly or sandy semi-natural grassland sites, which were partially invaded by lupine (i.e., invaded locality) and for which it was possible to estimate time since lupine invasion (Online Resource 1). Distance between individual sites (i.e., nearest neighbor) varied between 220 and 9250 m (mean = 2700 m). We did not select sites based on the cover of lupine in the invaded localities. Time since lupine invasion was estimated using a combination of on-site visits and information from local residents (i.e., first sightings of lupine), and yearly aerial photographs of the Lahti city map portal (2018) (i.e., visual disturbance). While we cannot fully exclude the possibility of lupine occurring in these invaded localities earlier, we consider this unlikely based on lupine sightings or previous land cover (e.g., forest). Both lupine-invaded and uninvaded localities were disturbed once. For example, the entire site was cleared from forest for urban development in the surrounding area. Alternatively, a building or a road was demolished from or built at the site, and the heavy machinery used significantly disturbed the vegetation within the entire site. Care was taken that the selected lupine-invaded and uninvaded localities of sites experienced similar disturbance and that both invaded and uninvaded localities had similar environmental conditions (see below). As the vegetation was significantly disturbed, a secondary succession process began at the study sites. Based on our information, we assume that the seeds of lupine were

accidentally introduced during the disturbance event (e.g., with the machinery) and thus, time since lupine invasion coincides with plant community age. The cover of annual plants was low at all sites and did not differ between the young, intermediate and old plant communities ($p = 0.402$, LR = 1.82, df = 2, a generalized linear mixed-effects model, presence-absence data; mean cover = 0.6%, 0.2% and 0.1%, respectively). This implies that the vascular plant communities were rather well-developed, which allowed us to better study the effect of time since invasion per se. Besides lupine, no other significant dominating non-native or native species were present in the studied plant communities (Online Resource 2). The investigated vascular plant communities did not contain any species of special conservation interest.

Based on the information above, we classified the 18 study sites as young ($n = 7$), intermediate ($n = 7$) or old ($n = 4$) (i.e., respectively, ca. ≤ 5 , 10, ≥ 15 years since disturbance and lupine-invasion). We were only able to find four suitable old sites and could not locate lupine stands older than 20 years. To investigate the impact of lupine on plant community composition and vascular plant species richness with time since local invasion, we surveyed vegetation in lupine-invaded and uninvaded localities (i.e., lupine not present) of each site from mid-July to early August 2018. At each site, we examined plant communities within 10 randomly placed 1 m^2 quadrats: five within a lupine-invaded locality (mean lupine cover \pm SD = $35 \pm 19\%$) and five in an uninvaded locality ≥ 10 m away from the lupine-invaded locality. Distance between individual sample quadrats was at least 1 m. Size of the lupine-invaded localities varied between $150 - 1800\text{ m}^2$ (mean = 530 m^2) (Online Resource 1). All vascular plant species were recorded and identified to species level where possible, following Hämet-Ahti et al. (1998) and Mossberg et al. (2005). Plant species abundance was estimated as absolute percentage cover (i.e., the proportion of the quadrat covered by a given species) as precisely as possible. This measure thus reflects changes in plant population abundances enabling us to investigate which kind of species are most sensitive to lupine invasion.

Soil variables

To account for possible differences in soil conditions between or within sites and to examine soil variables in relation to the composition of vascular plant communities, we took soil samples on 1 November 2018. We collected six soil samples at each site from 0 to 10 cm depth at randomly selected locations (≥ 3 m apart): three of the soil samples were collected under lupines in the invaded locality and three samples from the uninvaded locality. The three samples were pooled and mixed well, resulting in one 0.5 L soil sample each for lupine-invaded and uninvaded localities at each site. Stones ($\emptyset > 1.5$ cm) and plant material were removed from the soil. The samples were stored at 4 °C until analyzed two weeks later for soil pH, moisture, organic matter (OM), ammonium (NH₄), nitrate (NO₃) and phosphate (PO₄) content. Soil pH was measured from a suspension of air-dried soil and distilled water (1:5 v/v) (ISO 10390 standard). Soil moisture and OM content (i.e., loss on ignition) were measured following standard SFS3008: air-dried soil was dried in a 105 °C oven for 2 h and later for 2 h at 550 °C, respectively. Water-soluble soil nutrients were extracted in distilled water (SFS-EN 13652 standard) and measured using a QuickChem Lachat 8000 flow injection analysis system (LACHAT Instruments Inc., Loveland, CO, USA) according to standards 10-115-01-1-Q for phosphate, 10-107-06-1-F for ammonium and HPLC K101-NO3-140407 for nitrate.

Based on visual data comparison, the lupine-invaded and uninvaded localities had rather similar environmental conditions regarding soil pH, soil moisture, OM, NO₃, NH₄ and PO₄ (Online Resource 3). Regarding site age, soil pH was similar across all age categories, while soil moisture, OM, NO₃, NH₄ and PO₄ were similar at young and intermediate sites but were higher at old sites (Online Resource 3). This latter observation implies that several soil variables potentially confounded the effect of time since invasion (see “[Discussion](#)” section) and could not be included in mixed-effect models used to investigate the effects of locality and site age (see “[Data analyses](#)” section).

Data analyses

To evaluate the effect of lupine on vascular plant species representing different ecological groups, we ascertained species traits following Hämet-Ahti et al. (1998) and NatureGate (2020). Species were characterized according to their preference for soil moisture (dry habitat, mesic, wet habitat) and soil nutrient levels (copiotroph, oligotroph), or were classified as generalists if the species occurred in a wide range of conditions (i.e., not meeting the criteria above, being mutually exclusive) (Online Resource 2). These groups were chosen based on expected changes in plant communities: lupine-invasion is expected to create a lush cover (see “[Introduction](#)” section) that may reduce the cover of low-growing dry habitat species, and increase the nitrogen content of the soil, which, in turn, may increase the cover of copiotrophic species and decrease the cover of oligotrophic species. We summed the covers of individual species into ecological groups based on the traits listed above (Online Resource 4) because we were not interested in the effect of lupine on individual species per se but on species trait groups. We also calculated vascular plant species richness per locality ($n = 36$). Lupine was excluded from species richness and ecological group analyses to evaluate changes in the invaded plant community.

All analyses were performed in R (R Core Team 2018). We used generalized linear mixed-effects models (GLMMs, `glmmTMB` package in R; Magnusson et al. 2019) to evaluate changes in response variables (i.e., vascular plant species richness, cover of lupine and ecological plant groups) relative to site age. GLMM models included site age (young, intermediate, old), locality (lupine-invaded, uninvaded), and their interaction as fixed categorical explanatory variables. We dropped the interaction term from models when it was non-significant ($p > 0.05$), whereas age and locality were always retained in a model as variables of interest (except for the model on lupine, where locality was removed). We included a nested random effect in the models (i.e., locality nested within site) to account for the non-independence of multiple observations per lupine-invaded and uninvaded locality (i.e., five quadrats per locality) and site (i.e., two localities per site).

As the GLMMs above focused on the presence and absence of lupine, we conducted an additional analysis

with data from the lupine-invaded localities only (i.e., a subset of data) to explicitly investigate the effect of lupine cover (%) on plant communities; such an effect could have been masked by larger differences between lupine-invaded and uninvaded localities. These additional GLMM models could only be conducted for response variables with sufficient data (< 30% zeros, see below; i.e., species richness, cover of dry habitat species and generalist species), and they included site age (a categorical variable), lupine cover (a continuous variable) and their interaction as fixed explanatory variables. As before, we removed the interaction term from models when it was non-significant ($p > 0.05$). The random effect included site to account for the five observations (i.e., quadrats) at each site. The explanatory variables included in the model were not associated (i.e., lupine cover was not explained by site age, $\chi^2 = 5.49$, $df = 2$, $p = 0.064$; Kruskal-Wallis H test).

Data exploration for the mixed-effects models followed the protocol of Zuur et al. (2010). Species richness was analyzed with a Poisson, log-link GLMM and plant cover with a beta, logit-link GLMM. If our data showed zero-inflation, we followed recommendations by Zuur and Ieno (2016): if the data included < 5% zeros, we truncated the data following the transformation of Smithson and Verkuilen (2006). If the data included ca. 5–30% zeros, we applied a zero-altered beta model. If the data had $\geq 30\%$ zeros, we only analyzed the presence/absence of an ecological group using a binomial distribution. Data exploration revealed two extreme outliers in the generalist group, which we removed due to potentially faulty data entry. Model assumptions were verified by plotting residuals versus fitted values.

To visually examine the effects of lupine invasion on plant community structure in relation to site age (after first removing lupines from the data), we employed non-metric multidimensional scaling (NMDS) using the Bray–Curtis dissimilarity index based on the cover of individual plant species (vegan package in R; Oksanen et al. 2019). Species cover data were averaged across quadrats within each locality per site. We then fitted six soil variables (soil pH, moisture, OM, NH_4 , NO_3 and PO_4 content) to the ordinations (using the *envfit* function based on 999 permutations) to assess their significance in relation to plant communities.

Results

The cover of lupine did not vary in relation to site age (Table 1, Online Resource 5). On average, vascular plant species richness was 16% lower in lupine-invaded localities than in uninvaded localities (Table 1, Fig. 1a), but did not differ in relation to site age (Table 1). In lupine-invaded localities, vascular plant species richness decreased with increasing lupine cover (Table 1, Fig. 1b). Overall, the presence or cover of copiotrophic, oligotrophic and generalist plant species tended to be lower in lupine-invaded localities than in uninvaded localities (Table 1, Fig. 1c–f, Online Resource 5), while the other ecological groups considered were not affected (Table 1). In general, site age was not associated with any trends in the cover of ecological plant groups (Table 1), albeit in lupine-invaded localities, the cover of dry habitat species was higher at intermediate-aged sites (Online Resource 5). The interaction between site age and lupine invasion was non-significant in all models and was thus dropped (Table 1, $p > 0.05$, see “Material and methods” section), suggesting that the observed patterns between lupine-invaded and uninvaded localities did not change with site age.

Likewise, visual assessment of the NMDS revealed that lupine-invaded vascular plant communities were not markedly different from uninvaded communities (Fig. 2), as the lupine-invaded localities could not be distinguished from uninvaded localities in ordination space. Uninvaded localities of young sites were associated with generalists such as the grassland species *Agrostis gigantea* (black bent) and *Veronica officinalis* (heath speedwell) (Online Resource 6), which were less abundant in lupine-invaded localities of young sites. No other vascular plant species was distinguishably associated with lupine-invaded or uninvaded localities (Online Resource 6). Overall, plant communities correlated with soil pH (Fig. 2). In particular, high soil pH was associated with *Leucanthemum vulgare* (ox-eye daisy), *Centaurea jacea* (brown knapweed), *Leontodon sp.* (hawkbits), *Pilosella sp.* and *Hieracium sp.* (hawkweeds) (Online Resource 6). However, fewer species occurred at higher soil pH levels than at lower pH levels (Online Resource 6).

Table 1 Likelihood-ratio test results of the GLMMs to examine the effects of lupine and site age on lupine cover, vascular plant species richness, and the covers of ecological groups

Response variable	Explanatory variable	LR _{df}	<i>p</i> value
<i>Lupinus polyphyllus</i>	Site age (3 levels)	2.09 ₂	0.351
	Lupine (present, absent)	5.11 ₁	0.024
Species richness	Site age	0.85 ₂	0.652
	Lupine cover	4.44 ₁	0.035
Subset: lupine-invaded localities	Site age	1.07 ₂	0.585
<i>Ecological groups according to preferred moisture levels</i>			
Dry habitat species (PA)	Lupine	2.81 ₁	0.094
	Site age	4.24 ₂	0.120
Dry habitat species (presence only)	Lupine	0.99 ₁	0.317
	Site age	2.85 ₂	0.240
Dry habitat species (PA)	Lupine cover	1.40 ₁	0.237
	Site age	2.94 ₂	0.230
Dry habitat species (presence only)	Lupine cover	1.94 ₁	0.164
	Site age	6.83 ₂	0.033
Mesic habitat species (PA)	Lupine	1.53 ₁	0.216
	Site age	5.11 ₂	0.078
<i>Ecological groups according to preferred nutrient levels</i>			
Copiotrophic species (PA)	Lupine	4.34 ₁	0.037
	Site age	4.14 ₂	0.126
Oligotrophic species (PA)	Lupine	3.73 ₁	0.053
	Site age	3.02 ₂	0.220
<i>Generalist species</i>			
Full dataset	Lupine	3.97 ₁	0.046
	Site age	2.20 ₂	0.333
Subset: lupine-invaded localities	Lupine cover	0.07 ₁	0.778
	Site age	0.13 ₂	0.933

Data with 5–30% zeros were analyzed with a zero-altered model and data with $\geq 30\%$ zeros were only analyzed as presence/absence (PA). The abundance of wet habitat species was too low to be analyzed. “Lupine” denotes the presence or absence of lupine, while “lupine cover” denotes the subset of data from lupine-invaded localities. “Site age” represents both time since lupine invasion and plant community age. The random effect included locality nested within site, or only site for the subset data of lupine-invaded localities. Bold values represent statistical significance at *p* value < 0.05 after dropping the non-significant interaction between the two fixed variables. Detailed GLMM results can be found in Online Resource 5

Discussion

Time since invasion is rarely considered when investigating the impacts of invasive non-native species, although boom-bust dynamics is an established concept (e.g., Strayer et al. 2017) and impacts of invasive non-native species can accumulate or change with time since local invasion (e.g., Gaertner et al. 2009; Strayer 2012; Ortega et al. 2019). Yet, in contrast to our expectations, lupine invasions revealed neither boom-bust dynamics of *Lupinus polyphyllus*, nor a

change in its impacts. Vascular plant species richness was lower in the presence of lupine, but this effect did not change with site age (i.e., both time since invasion and plant community age). Furthermore, the composition of lupine-invaded and uninvaded plant communities was generally similar. In contrast to our expectations, the cover of dry habitat species was not lower in lupine-invaded localities. Both oligotrophic (low-nutrient-adapted) and copiotrophic (nutrient-demanding) species occurred less frequently in lupine-invaded localities, although we expected that

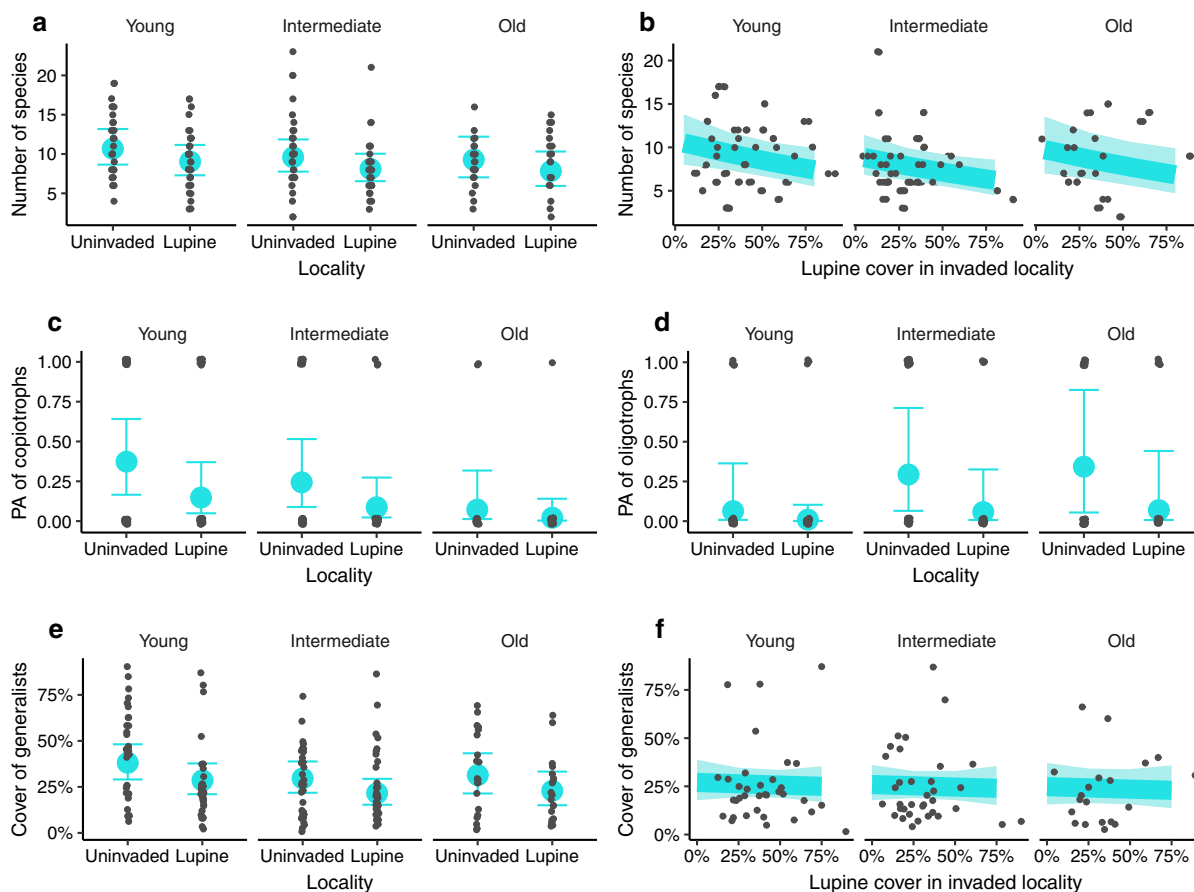


Fig. 1 GLMM-predicted plant cover or presence-absence (PA; 1 and 0, respectively) for vascular plant richness (**a**, **b**) and for different ecological groups (**c**–**f**) at uninvaded and lupine-invaded (Lupine) localities of young, intermediate and old sites (mean \pm 95% CI, denoted in blue). In **b**, **f**, darker blue bands represent the mean value and lighter blue bands the confidence

interval. Site age represents both time since lupine invasion and plant community age (i.e., time since disturbance). The confidence intervals are based on fixed explanatory variables only. Black dots represent raw data on the cover or presence-absence of the response variable

copiotrophic species would have been facilitated by lupine.

Although lupine cover did not change with time since invasion, we were unable to locate populations older than 20 years. Indeed, Williamson (1996) as well as Simberloff and Gibbons (2004) claimed that boom-bust dynamics is uncommon. Yet, Davis (2009) and Lockwood et al. (2013) stated the opposite. Dostál et al. (2013) found a slow continuous decrease in the cover of the perennial invasive herb, *Heracleum mantegazzianum*: from ca. 66% to 54% at 11- to 48-year-old populations, respectively. Others have found either no difference in the density of invasive herbs (Hazelton et al. 2015) or a slow gradual increase with time since invasion (Mitchell et al. 2011; Ortega

et al. 2019). Thus, we do not see support for boom-bust dynamics in invasive herbs, although most data records, like ours, cover relatively short time spans.

We did not observe an accumulation of ecological impacts of lupine on vascular plant communities. Similar to Valtonen et al. (2006) and Ramula and Pihlaja (2012), we found fewer vascular plant species in lupine-invaded localities and at higher lupine cover, but the difference between lupine-invaded and uninvaded localities remained similar irrespective of site age. Given that lupine abundance remained unchanged over time, this result is not surprising (e.g., Hejda et al. 2009). Vascular plant species richness may increase rapidly during the first years since disturbance (e.g., Cseceserits and Rédei 2001; Ruprecht 2005). However,

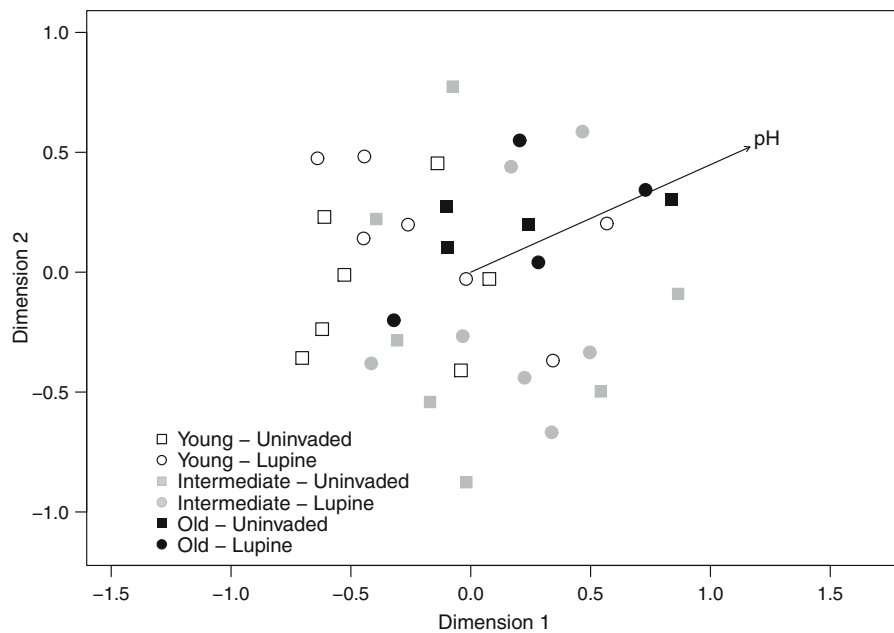


Fig. 2 Non-metric multidimensional scaling (NMDS) ordination showing similarity of vascular plant communities between lupine-invaded (Lupine) and uninvaded localities at young ($n = 7$), intermediate ($n = 7$) and old sites ($n = 4$) (ca. ≤ 5 , 10, ≥ 15 years). Site age refers both to time since lupine

invasion and plant community age (i.e., time since secondary succession was initiated by disturbance). NMDS is based on species cover data (Bray–Curtis dissimilarity index) without lupine. Only significant environmental variables were plotted ($p < 0.05$)

here the vascular plant communities contained few annual plant species even in young plant communities (Online Resource 4). This suggests that the plant communities were rather well-developed in both lupine-invaded and uninvaded localities, which may explain why species richness did not significantly change with time. At our study sites, lupine appeared to spread into disturbed soils achieving a rather constant cover immediately after the disturbance. Such a rapid establishment may indicate a higher benefit from priority effects compared to native plants, subsequently limiting post-establishment competition among plant species (Körner et al. 2008; Dickson et al. 2012). Thus, it seems that under the secondary succession scenario considered here, time since lupine invasion had a negligible effect on the vascular plant communities. Still, future studies should investigate the impact of lupine and its temporal dynamics under diverse environmental scenarios.

Valtonen et al. (2006) observed a clear effect of the presence of lupine on the vascular plant community composition, while Ramula and Pihlaja (2012) and we did not. Valtonen et al. (2006) and Thiele et al. (2010a) found a decrease in low-growing but not in tall plant

species in the presence of lupines, which indicates that lupines may generate a shadier microhabitat not suitable for low-growing dry grassland plants. We did not find a decrease in dry habitat species in lupine-invaded localities. The discrepancies between previous findings and the present study could be explained by several factors, e.g., lupine cover, confounding environmental conditions or yearly variation. Here, generalist, oligotrophic and copiotrophic species occurred more frequently in uninvaded localities, while we expected a higher occurrence of copiotrophic species in lupine-invaded localities. Furthermore, generalist species were not reduced at higher lupine cover in invaded localities. Thus, it is possible that these patterns arose from differences in soil variables (see “Material and methods” section) despite our efforts to standardize environmental conditions. Alternatively, these ecological groups may have been reduced by the presence of lupine in invaded localities (e.g., allelopathy or shading).

The average lupine cover in the present study was lower, ca. 35%, than we expected based on previous findings in Finland: 66% and 69% (Ramula and Pihlaja 2012; Valtonen et al. 2006, respectively).

Understandably, a higher dominance leads to a stronger ecological impact (e.g., Ortega and Pearson 2005; Thiele et al. 2010b). The impact is likely to also vary between habitats and environmental variables (Thiele et al. 2010b). Even though mature plants are drought-tolerant (Robson et al. 2008), we cannot reject the possibility that the lower cover of lupines in our study was caused by exceptionally dry and hot weather conditions: May–August saw a record number of hot and dry days since 1959 (Finnish Meteorological Institute 2019). However, since we did not find evidence for an accumulation of impacts, we believe that the observed cover is not exceptional but characteristic for such dry to mesic semi-natural grassland habitats and disturbance patterns. Indeed, in its native range, lupine appears to prefer moister habitats, yet it occurs across a wide range of habitats (Robson et al. 2008). We conclude that whilst lupine may reduce species richness even with intermediate cover (i.e., ca. 35%), the ecological impact caused by lupine might not change or accumulate with time since invasion.

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Data availability This article contains online supplementary material, which is available to authorized users.

Code availability Can be provided upon request by the corresponding author.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication All authors have approved the contents of this paper and have agreed to the submission policies of Biological Invasions.

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