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POPULATION ECOLOGY - ORIGINAL RESEARCH

Conspecific plant–soil feedback scales with population size in *Lobelia siphilitica* (Lobeliaceae)

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Abstract Plant–soil interactions directly affect plant success in terms of establishment, survival, growth and reproduction. Negative plant–soil feedback on such traits may therefore reduce the density and abundance of plants of a given species at a given site. Furthermore, if conspecific feedback varies among population sites, it could help explain geographic variation in plant population size. We tested for among-site variation in conspecific plant–soil feedback in a greenhouse experiment using seeds and soils from 8 natural populations of *Lobelia siphilitica* hosting 30–330 plants. The first cohort of seeds was grown on soil collected from each native site, while the second cohort was grown on the soil conditioned by the first. Our goal was to distinguish site-specific effects mediated by biotic and/or abiotic soil properties from those inherent in seed sources. Cohort 1 plants grown from seeds produced in small populations performed better in terms of germination, growth, and survival compared to plants produced in large populations. Plant performance decreased substantially between cohorts, indicating strong negative feedback. Most importantly, the strength of negative feedback scaled linearly (i.e., was less negative) with increasing size of the native plant population, particularly for germination and survival, and was better explained by soil- rather than seed-source effects. Even with a small number of sites, our results suggest that the potential for negative plant–soil feedback varies among populations of *L. siphilitica*, and that small populations were more susceptible to negative feedback. Conspecific plant–soil feedback may contribute to plant population size variation within a species' native range.

Keywords Germination · Growth · Survival · Native plants · Soil microorganisms

Introduction

The sessile habit of land plants directly links characteristics of soil with the growth and reproduction of individuals, and consequently with the dynamics of plant populations and the assembly of plant communities (Wardle et al. 2004). The nature of plant–soil interactions is likely to be complex, especially in light of evidence that current plant–soil interactions alter the outcome of future plant–soil interactions, a concept known as 'plant–soil feedback' (Bever et al. 1997). Plant–soil feedback occurs in two steps: plant growth alters or 'conditions' characteristics of the soil, and then this conditioned soil in turn changes the growth rate of the next cohort of plants (Bever et al. 2010). Feedback can be either positive or negative, depending on whether conditioned soil promotes or hinders the establishment and growth of individual plants and, ultimately, populations (Catovsky and Bazzaz 2000; Bonanomi et al. 2005; Casper and Castelli 2007; van der Heijden and Horton 2009; van der Putten 2009). Both positive and negative feedback are thought to be common in nature and are important components of the regulation of population density and plant abundance (Packer and Clay 2000; Bever 2003; Reynolds et al. 2003; Mangan et al. 2010; Liu et al. 2012).

The role of plant–soil feedback has been established as a potentially important factor mediating species co-existence within communities and the spread and impact of invasive

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plant species (reviewed in Kulmatiski et al. 2008; Bever et al. 2010). In addition, species relative abundance has been shown to be associated with susceptibility to negative feedback, with species that are more vulnerable to negative feedback having lower abundance (Klironomos 2002; Mangan et al. 2010). This negative feedback is often attributed to a build-up of soil pathogens with increased virulence (Liu et al. 2012), and escape from co-adapted pathogens mediating negative feedback has been proposed as a mechanism by which plants are able to become invasive outside their native range (Klironomos 2002; Callaway et al. 2008; Reinhart et al. 2010). However, relatively few studies have examined whether the nature of feedback might vary among sites across the native range of a single plant species, and whether site-specific feedback has the potential to explain variation in population size. In one example (van de Voorde et al. 2011), heterospecific feedback (i.e., the effects of soil conditioning by heterospecific plants) on one focal plant species was correlated with field age, potentially explaining reduced abundance of the focal species in older fields. In contrast, several other studies have found that variation in heterospecific feedback effects did not have as strong an influence on plant performance as other environmental characteristics that vary among sites within a species' native range (Harrison and Bardgett 2010; Yelenic and Levine 2011). The studies described above focused on variation in heterospecific feedback among sites across a species native range. However, most seed dispersal and clonal growth occurs near conspecific plants in herbaceous species (Thomson et al. 2011), and conspecific feedback effects are usually among the most strongly negative feedbacks measured for a native plant species (e.g., Klironomos 2002; Kulmatiski et al. 2008; van Grunsven et al. 2010; Harrison and Bardgett 2010; van de Voorde et al. 2011; but see Pregitzer et al. 2010). Our goal here is to document variation among sites in conspecific feedback that could also have a strong effect on broad-scale variation in plant population size. This is a potential component of plant–soil feedback that, to our knowledge, has not been previously examined.

In order for plant–soil feedback to explain variation in population size among sites, feedback itself must be spatially variable. Variation among sites in the propensity for conspecific negative feedback could have multiple underlying causes (Bezemer et al. 2006). Feedback could vary with local nutrient availability, the presence/absence of particular soil microbes (e.g., Reinhart et al. 2003; Lekberg and Koide 2005; Nelson 2004; Dalling et al. 2011), the history of plant–soil interactions at a site (Bartelt-Ryser et al. 2005; Kardol et al. 2007; Grman and Suding 2010; van de Voorde et al. 2011), or plant genotypic variability in either in susceptibility to feedback or influence on soil conditions (Madritch et al. 2006, 2007; Schweitzer et al. 2008; Sthultz et al. 2009; Liu et al. 2012). Most interesting from our perspective is that variation in feedback among sites may be caused by the unique combination of soil conditions and the particular plant populations at each site, such that the particular level of feedback at each site may not be readily explained by soil conditions or plant population characteristics separately. Because of this, experiments designed to distinguish the roles of soil versus plant characteristics on feedback as independent and interactive effects are important for understanding the consequences of spatially variable feedback for plant population size.

This paper describes an investigation of variation in conspecific plant–soil feedback with the expressed goal of explaining population size variation in the native range of *Lobelia siphilitica* (Lobeliaceae). This native perennial is ideal for our study because individual plants produce thousands of passively dispersed seeds (Johnston 1991; Caruso and Yakobowski 2008), and germination is high under sterile conditions (Proell 2009; and unpublished data), yet most populations contain fewer than 100 adults (Caruso and Case 2007; and unpublished data). If germination, establishment, growth, and/or survival in natural populations are generally low, plant–soil feedback at early life-cycle stages may play an important role in regulating population size at a given location.

To test whether conspecific plant–soil feedback is more negative at sites hosting small plant populations, we collected both soil and seeds from native sites varying widely in the number of *L. siphilitica* plants. We used a factorial design to examine both soil-source and seed-source effects on conditioning and feedback in relation to native plant population size. Our approach differs in two fundamental ways from many previous studies of plant–soil feedback (reviewed in Bever et al. 2010), reflecting our focus on regional-scale dynamics of plant populations and variation in conspecific feedback rather than a more 'traditional' focus on plant communities or invasiveness. First, the native soils were collected from microsites in the field that did not contain *L. siphilitica* plants because we wanted to specifically characterize microsites where recruitment of new *L. siphilitica* could occur. Thus, these soils were unconditioned relative to *L. siphilitica,* and instead conditioned by heterospecifics, at the start of the experiment. Second, we did not swap plants from different *L. siphilitica* sites between the conditioning phase and the test phase (as suggested in fig. 1a of Bever et al. 2010) because such swapping would change the focus of our experiment to understanding the consequences of feedback for seed flow between population sites, rather than recruitment within population sites.

Our design specifically allowed us to test: (1) direct effects of seed source, soil characteristics, and seed–soil interactions on plant performance within each cohort,

(2) whether variation in conspecific feedback effects on plant performance between cohorts is mediated through seed sources, soil sources, or the interactive effects of both, and (3) the relationship between field population size and conspecific feedback and/or the direct effects of seed or soil sources.

Materials and methods

Study system

Lobelia siphilitica (Lobeliaceae) is a short-lived herbaceous wildflower native to eastern North America. Plants form a basal rosette upon germination; most bolt and flower within approx. 2–4 months under greenhouse conditions (Case, unpublished data). Peak flowering for this species is typically late July through September; mature fruits can be seen in October and November. Seeds are passively dispersed, and likely to land close to conspecifics. In addition, some plants form clonal rosettes at the base of the inflorescence, which perennate and flower in subsequent years, yielding clonal perennial genets with monocarpic ramets (Beaudoin Yetter 1989).

Soil and seed sources

Eight widely distributed *L. siphilitica* populations across Ohio and West Virginia were chosen as study sites (Table 1). These comprise a subset of the populations used to assess variability in soil microbial communities among sites (Hovatter et al. 2011). In September 2006, we censused the total number of adult (reproductive) plants at each site (Table 1). For 6 of the 8 sites, we censused again in 2007, 2008, and 2009. These populations encompass the range of flowering population sizes typical of *L. siphilitica* (Caruso and Case 2007) and span a wide variety of soil types (Hovatter et al. 2011).

Seeds were collected from 10 randomly selected plants in each of the 8 populations in October 2006. In July 2007, when native seeds were germinating and perennial adult plants were in rosette stage, we collected several liters of soil from 5–7 randomly selected locations within each of the 8 populations. All soil was obtained from the upper 15 cm under plants representative of the plant community at each site, but not under *L. siphilitica* (thus, conditioned by heterospecifics). These microsites would represent potentially available sites for the dispersal and establishment of new *L. siphilitica* plants; thus, feedback measured in these soils could reflect the potential for recruitment of new plants at each site. All population sampling and soil processing was completed within 1 week. Soil was bulked by population, sieved (4 mm) to remove rocks and large woody debris, and mixed with coarse, autoclaved sand in a 3:1 (soil:sand) ratio by volume.

Plant–soil feedback experiment

Plants were grown in two consecutive 8-week cohorts in 2007. In the first cohort, *L. siphilitica* seeds were sown on the heterospecific soil obtained from the field. All eight seed sources and soil sources were crossed in a fully factorial design (64 seed × soil combinations) in five replicate blocks for a total of 320 pots. In the second cohort, soil that had been conditioned by an *L. siphilitica* individual during the first cohort was sown with new *L. siphilitica* seeds from the same population, allowing us to test for within-population feedback due to conspecific soil conditioning.

Table 1 Location and size of eight study populations of *Lobelia siphilitica* in Ohio (*OH*) and West Virginia (*WV*), USA, were used as seed and soil sources for the plant–soil feedback experiment

Population	County, State	Number of *L. siphilitica* plants (2006)	Mean number of *L. siphilitica* plants per year (2006–2009)
Bonnivale (BO)	Wood Co., WV	30	–
Storm Drain (SD)	Fayette Co., WV	44	36
Olive Green (OG)	Guernsey Co., OH	53	–
Pearson (PS)	Lucas Co., OH	61	110
Jennings Woods (JW)	Portage Co., OH	119	89
Apple Creek (AC)	Tuscarawas Co., OH	153	59
Campbell Prairie (CP)	Lucas Co., OH	200	294
Buckwheat (BW)	Preston Co., WV	333	386

Populations are ordered by number of plants in the year that seeds were collected (2006)

Geographic coordinates and results of soil analyses are available in supplementary information for Hovatter et al. (2011); http://esapubs.org/archive/ecol/E092/006/appendix-A.htm)

Cohort 1 (conspecific soil-conditioning phase)

In May 2007, 200 seeds were bulked from the 10 maternal plants from each population, using an equal number of seeds from each. Each batch of seeds was placed between two layers of sterile wet filter paper in a clean plastic Petri dish and subjected to 8 weeks of vernalization at 4 °C to break seed dormancy (Dudle et al. 2001). We filled 3.5-in (c.9-cm) square pots (BFG Supply, Xenia, OH, USA) with the sieved field-collected soil from a single population soil source, and planted five seeds, all from a single population seed source, into each pot. To keep experimental seedlings separated from seedlings emerging from native soil seed banks, we cut drinking straws into 1-cm rings, placed five rings on the surface of the soil in each pot, and put one *L. siphilitica* seed into each ring. This allowed us to monitor the experimental seeds that were placed on the surface of the soil, and remove any additional seedlings germinating within each pot. Pots were randomized within each block, weeded daily to remove all non-experimental seedlings, and top watered daily to saturation with distilled water. Each pot was placed in its own drain dish, so that there was no contact among pots.

We recorded seedling emergence daily for 2 weeks, when pots were thinned, leaving only the largest *L. siphilitica* seedling in each pot (hereafter referred to as the ‘focal plant’). Thus, germination was scored as the percentage of all five seeds that had emerged in each pot by week 2. All other traits were recorded biweekly, but only for the focal plant in each pot. We counted total leaf number and measured rosette diameter to the nearest mm with digital calipers on each focal plant at 2-week intervals until harvesting. Focal plants that suffered mortality were noted during each biweekly census. We refer to the last census in which a focal plant was alive as ‘survival’ because this is the minimum age of the plant when it died.

At week 8, we completely removed all focal plants (after measuring) and all soil from each pot. The soil was homogenized with gloved hands in clean plastic containers and placed back into its original pot; this conditioned soil was used in Cohort 2. After each pot and plant was processed, gloves were changed and all mixing containers were rinsed with water, cleaned with a mixture of 95 % ethanol and bleach, and dried before proceeding to the next pot.

Cohort 2 (test phase for conspecific feedback)

At the start of Cohort 1 (July 2007), 200 additional seeds from the same 10 maternal plants were transferred to cold treatment (4 °C) for 8 weeks of vernalization. After all plants from Cohort 1 had been harvested, the entire procedure (planting, monitoring, and harvesting) was repeated as above using the homogenized, conditioned soil recovered from Cohort 1 as substrate. Soils were put back into the same pots, and planted with the same population seed source as in Cohort 1 (i.e., we did not change the seed × soil combinations between cohorts). Cohort 1 pots were reassigned to the same block for Cohort 2, but their positions within blocks were re-randomized.

Statistical analysis

Direct effects on plant response traits

We used mixed-model analyses of variance (ANOVA) in JMP v.9.0 (SAS Institute 2010) to look for sources of variation in germination (percent of seedlings emerging within first 2 weeks), maximum plant diameter (largest of the biweekly measurements), maximum leaf number (highest of the biweekly leaf counts), and survival (age at death of each focal plant) during each 8-week cohort. Three-way ANOVAs on each of the four plant response traits included soil source, seed source, cohort, and all interactions as fixed effects. Block was included as a random effect, nested within the soil × seed term, to represent individual pots, which were not independent between cohorts. Separate ANOVAs by trait were justified given highly significant effects of soil, seed, and cohort on all plant response traits in a MANOVA (all effect $P < 0.0001$). Pots with no germination ($n = 122$) were included as zeros for the analysis of germination, but were recorded as ‘missing’ for analysis of all other plant responses. Because three soil × seed combinations were entirely missing in Cohort 2 (i.e., there was no germination in any of the replicate pots), we could test for the three-way interaction only on percent germination.

Feedback effects

To assess plant–soil feedback between cohorts, we calculated feedback indices for each pot as the difference in each trait value between Cohorts 1 and 2 (similar to comparison between growth periods by Kardol et al. 2006). For example, if a pot had 80 % germination in Cohort 1 and 20 % germination in Cohort 2, germination feedback would be $C2 - C1 = -60$; if plants survived for 8 weeks in C1 and only 3 weeks in C2, then survival feedback would be $C2 - C1 = -5$. This best represents the change in performance within each pot and, unlike feedback metrics using ratios (C2/C1) or proportional change [(C2 − C1)/C1; see Table 1 in Brinkman et al. 2010], allowed us to include the empty pots in the analysis. This is important for two reasons. First, C1 empty pots showing C2 germination represent positive feedback, making the C2 − C1 analysis of negative feedback more conservative than using ratios or proportions. Second, using the difference permits quantitative assessment of the strength of complete negative feedback (i.e., when C2 germination was zero). Nevertheless, to assess consistency among various potential feedback indices, feedback analyses were performed with both the difference (C2 − C1) and ratio (C2/C1), with and without empty pots. Correlations between feedback metrics were positive and highly statistically significant ($r_p = 0.92$ for germination, 0.52 for rosette diameter, 0.92 for leaf number, 0.89 for survival; all $P < 0.0001$), and the results from each analysis were qualitatively the same (data not shown). Therefore, we present here the analyses based on C2 − C1 including empty pots.

We performed two-way ANCOVAs on the feedback index for each trait to look for the fixed effects of seed source, soil source, or an interaction effect on the intensity of plant–soil feedback; block was included as a random effect. One potential weakness in two-phase feedback studies, particularly when plants are grown in pots under greenhouse conditions, is that nutrients may be depleted by Cohort 1 plants during the conditioning phase, increasing the likelihood of observing negative feedback in the second phase (Brinkman et al. 2010). Assuming that larger plants could potentially use up more nutrients from the soil during the conditioning phase compared to smaller plants, we included Cohort 1 plant size as a covariate in each analysis. Cohort 1 plant size was represented by the first principal component (PC1) of Cohort 1 maximum rosette diameter and leaf number, accounting for 88.7 % of the variation in the data. An additional way to assess whether nutrient depletion could be contributing to apparent feedback is to run correlations between Cohorts 1 and 2 for each plant size variable (Brinkman et al. 2010). Therefore, we also ran between-cohort correlations for each trait. Negative correlations (e.g., pots with larger Cohort 1 plants having smaller Cohort 2 plants) would be consistent with the possibility that the larger plants depleted soil nutrients during the conditioning phase, while positive or no correlation would be evidence against this.

Average feedback indices were calculated to capture variation from three sources: (1) average soil-source feedback index was the mean feedback on each of the eight soil sources averaged across all seed sources, (2) average seed-source feedback index was the mean feedback on each of the eight seed sources across all soil sources, and (3) average site-specific feedback index was the mean feedback for each of the eight paired soil and seed sources from the same original population site.

Average site-specific feedback presents a unique case, where seeds are matched with soil from their original population sites. This is useful as an estimate of the levels of feedback that natural populations would likely experience at the original population site, but confounds the effects of soil characteristics and those associated with the seed sources. Thus, we ran two additional analyses to dissect the causes of site-specific feedback. First, we regressed average site-specific feedback against average soil- and seed-source feedback indices for each trait. Significant relationships would indicate which source (soil vs. seed) was likely driving the site-specific feedback effects. Second, we ran nested ANOVAs on each of the four feedback indices to test whether matched soils and seeds performed differently in terms of feedback compared to seeds and soils paired from different sites (i.e., a ‘home’ vs. ‘away’ effect). The model included a fixed effect (matched vs. unmatched), a random effect of block, and two random nested effects accounting for variation among the ‘away’ sites: (1) soil source nested within the matching effect represents the performance of each seed source on its native soil vs. all other soils; and (2) seed source nested within the matching effect represents a differential effect of one particular soil source on seeds from the same site relative to seeds from other sites.

Variation in plant traits or plant–soil feedback with population size

Significant effects of seed or soil sources in the ANCOVAs indicate whether those source populations differed from each other, but not whether plant responses to native soil conditions or plant–soil feedback were correlated with the size of source populations in the field. We used separate linear regressions of population size against the least-squares means for each plant response, and against size-adjusted least-squares means for each feedback index. We ran the regressions for all eight populations using population size in 2006; this census is most representative of factors that may have affected the seeds that were produced during that season. To test consistency of the patterns observed during the experiment, we repeated the regressions using the average plant population size from 2006 to 2009 at the six sites for which we had these additional population size data. Note that second-order polynomial regressions were tested and all were non-significant, thus only results of linear regressions are shown.

Results

Direct effects of soil and seed source on plant responses

Soil-source versus seed-source direct effects

Soil source directly affected three of the four plant responses—maximum diameter, leaf number, and survival (Table 2; Fig. 1); the effect on germination was only marginally significant (but see below). Seed-source effects

Table 2 Effects of soil, seed source, cohort, and interactions on four plant responses: percent germination, maximum diameter (mm), maximum leaf number, and survival (weeks)

ANOVA model fixed effects	Percent germination ($df = 256$)	Maximum diameter ($df = 214$–238)	Maximum leaf number ($df = 234$–282)	Survival ($df = 266$–318)
Soil source ($df = 7$)	1.9†	22****	15****	8.6****
Seed source ($df = 7$)	30****	1.7†	1.1	3.5***
Soil × seed ($df = 49$)	0.5	0.7	0.9	1.0
Cohort ($df = 1$)	498****	637****	590****	242****
Soil × cohort ($df = 7$)	3.6***	18****	3.6***	4.6****
Seed × cohort ($df = 7$)	6.7****	0.6	0.7	2.2*
Soil × seed × cohort ($df = 49$)	0.6	–	–	–

Block nested within soil × seed was included as a random effect in each model. Empty pots were included as zeros for percent germination ($n = 320$ pots per cohort) and missing for all other traits ($n = 302$ and 216 plants per cohort). The three-way interaction could only be tested for percent germination because some soil × seed combinations were entirely missing from cohort 2 (see text for details)

Values are *F* statistics. Parenthetical values for ANOVA model indicate numerator degrees of freedom (*df*) for each effect; denominator *df* are given for each variable

Significance: † $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$

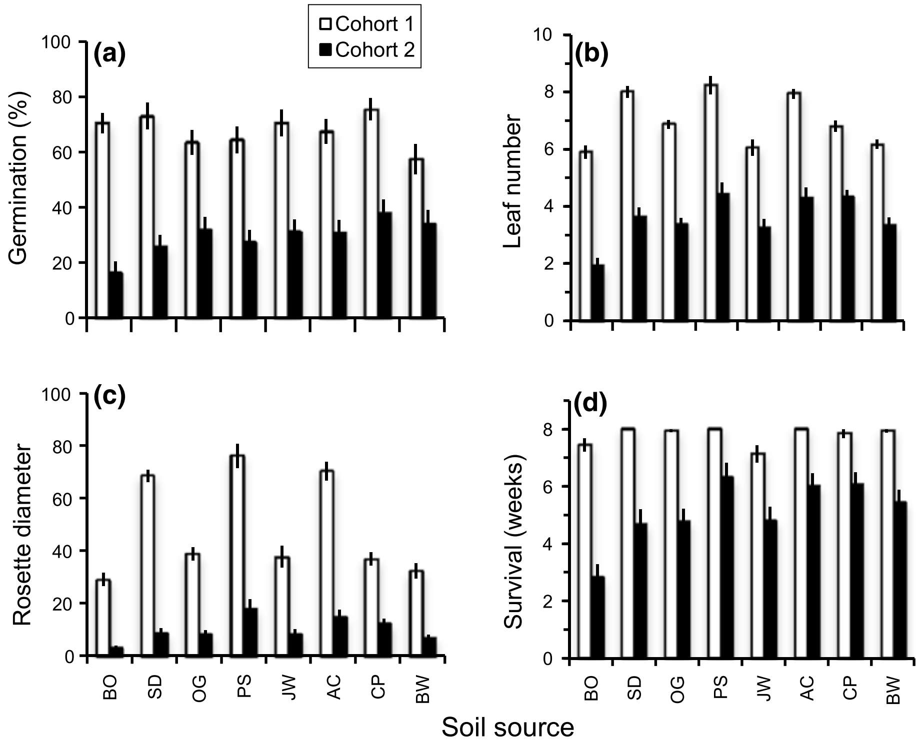

Fig. 1 Comparison of four plant response traits between Cohort 1 and Cohort 2 of *Lobelia siphilitica*. Values are means ± 1SE for each soil source (i.e., averaged across all seed sources). Sites are ranked in order of plant population size (*left* to *right*); see Table 1 for source population codes

were significant for percent germination and survival, but not the metrics of plant size. The significant cohort effect represents a substantial reduction in means for all plant responses from Cohort 1 to Cohort 2, attesting to strong negative feedback overall (Figs. 1, 2). The effect of soil source differed between the two cohorts for all four traits (i.e., significant soil × cohort interactions; Fig. 2), while the seed source effect differed between cohorts only for germination and survival (Table 2). We detected no significant soil × seed source interactions.

Variation of direct effects with plant population size

Although plant responses varied by soil source, there was no correlation between soil-source population size and any of the average plant responses in Cohort 1 (linear regressions, all $P > 0.05$; Fig. 1). In contrast, average values for all four plant traits in Cohort 1 were significantly negatively related to the size of the populations where seeds were collected, meaning that seeds produced in smaller populations had higher percent germination, and produced plants with larger rosettes, more leaves, and higher survival in Cohort 1 ($r^2 = 0.58$–0.73, all $P < 0.02$). When seeds and soils were matched by site, negative relationships between average trait values and population size were also significant in Cohort 1 for percent germination ($r^2 = 0.50$, $n = 8$, $P = 0.05$) and survival ($r^2 = 0.60$, $n = 8$, $P = 0.021$). In the case of both seed-source and site-specific effects, these relationships were driven by poorest germination, growth, and survival of seeds from the single largest population (Buckwheat), and highest germination, growth, and survival of seeds from the two smallest populations (Bonnivale and Storm Drain). Mahalanobis distance indicated that Buckwheat was an outlier; there were huge gaps between average values for Buckwheat plant responses and those for all other seed sources. When Buckwheat values were excluded from the analysis, all of these regressions between average plant responses and population size became non-significant. Excluding the Buckwheat population of seeds strengthened the direct effect of soil source on percent germination in the ANOVAs (soil source effect on germination: $F = 2.8$, $P = 0.0069$); however, all other patterns of statistical significance shown in Table 2 were unchanged. Regardless, seeds from the two smallest populations performed best in Cohort 1.

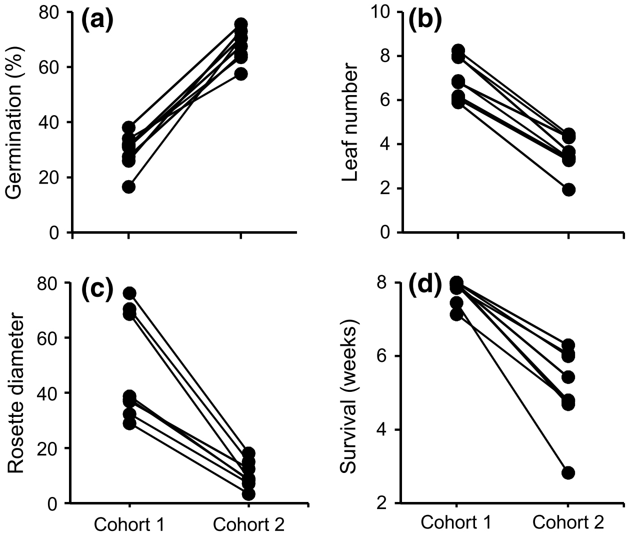

Fig. 2 Trait means for two cohorts of *Lobelia siphilitica* plants grown on eight soil sources. Each point is the mean of all plants growing on each soil source; **a** percent germination ($n = 40$ plants per site per cohort); **b** total leaf number, **c** rosette diameter, and **d** survival ($n = 23$–40 plants per site per cohort). All four traits showed significant soil source × cohort interaction effects (see Table 2)

Conspecific plant–soil feedback

Soil-source versus seed-source effects on feedback

After adjusting for the effects of Cohort 1 plant size, we detected significant effects of soil source and seed source on the feedback indices of percent germination, maximum diameter, maximum leaf number, and survival, but no significant soil × seed interactions (Table 3). Although feedback indices calculated for individual pots ranged from positive (meaning plants in Cohort 2 performed better) to negative (plants in Cohort 1 performed better), the majority (66–91 %) of plants in Cohort 2 experienced negative feedback on each of the four plant responses. These patterns of significance were identical to those that were not adjusted for C1 plant size (i.e., two-way ANOVAs without the plant size covariate; data not shown), suggesting that feedback intensity did not scale with C1 plant size in our experiment. Additionally, all correlations between maximum diameter and leaf number between cohorts were positive ($r = 0.25$–0.37, $n = 200$ plants, all $P < 0.0003$),

Table 3 Effects of soil source, seed source, and interaction effects on feedback indices of percent germination, maximum diameter (mm), maximum leaf number, and survival (weeks)

ANCOVA model fixed effects	Feedback index			
	Germination	Diameter	Leaf number	Survival
Soil source (*df* = 7, 252)	3.9***	6.0****	9.0****	9.1****
Seed source (*df* = 7, 252)	5.8****	2.2*	11.1****	5.6****
Soil × seed (*df* = 49, 252)	0.7	1.0	1.0	1.0
PC plant size (*df* = 1, 252)	6.7*	690****	242****	57****

Feedback was calculated for each pot as the difference in trait value between Cohorts 1 and 2 (all $n = 320$; see text for details). In each ANCOVA, block was included as a random effect, and the first principal component (PC) of plant size was included as a covariate

Values are *F* statistics

Significance: † $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$

indicating that negative feedback was not being driven by nutrient depletion alone.

Average site-specific feedback on germination (Fig. 3a) and maximum rosette diameter (Fig. 3c) scaled linearly with average soil-source feedback on these traits. In contrast, none of the average site-specific feedback indices scaled significantly with average seed-source feedback (all $P > 0.05$; Fig. 3b, d), although the relationship for maximum diameter was marginally significant. This suggests that soils likely mediate more feedback effects on germination and rosette size than do seed-source effects. Site-specific feedback on leaf number and survival did not significantly scale with either soil- or seed-source effects (all $P < 0.05$).

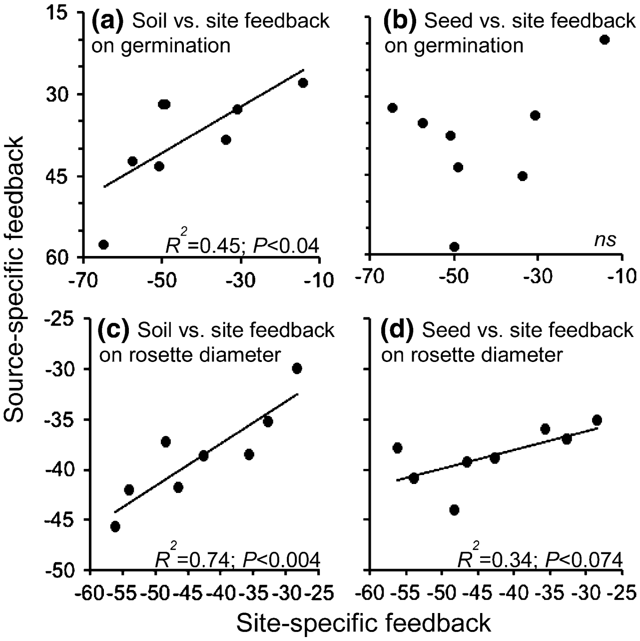

Fig. 3 Average site-specific feedback indices for **a**, **b** germination, and **c**, **d** maximum diameter against **a**, **c** soil-source feedback, and **b**, **d** seed-source feedback. Values toward the *lower left* indicate greater negative feedback, i.e., a greater average reduction in the plant response trait between cohorts 1 and 2 (see text for details). Regression statistics are provided for significant relationships; $n = 8$ population sites

Finally, feedback indices did not differ between ‘home’ and ‘away’ sites for any of the plant responses (all ANOVA $P > 0.50$), providing no evidence for local adaptation of seeds to their particular soil source. This result is consistent with the lack of any soil-by-seed interactions in any of the previous analyses (Tables 2, 3).

Variation of feedback with plant population size

Although feedback indices varied significantly when averaged by soil and seed sources (Table 3), there was no explicit effect of population size on feedback on any plant response (linear regressions, all $P > 0.05$). However, when soils and seeds were matched, we found evidence for greater average negative feedback on both germination (Fig. 4a) and survival (Fig. 4b) at sites hosting smaller populations in 2006. This effect was consistent across the following 3 years for germination (Fig. 4c) but not survival (not shown), although the trend was consistent for survival, with the two largest populations experiencing the least negative feedback.

Discussion

Using an experimental ‘soil-conditioning’ approach, we found that conspecific plant–soil feedback has the potential to contribute to population size variation of a single species, while direct effects of soil or seed sources did not. Conspecific feedback was negative at all sites, but was significantly more negative at sites hosting small plant populations.

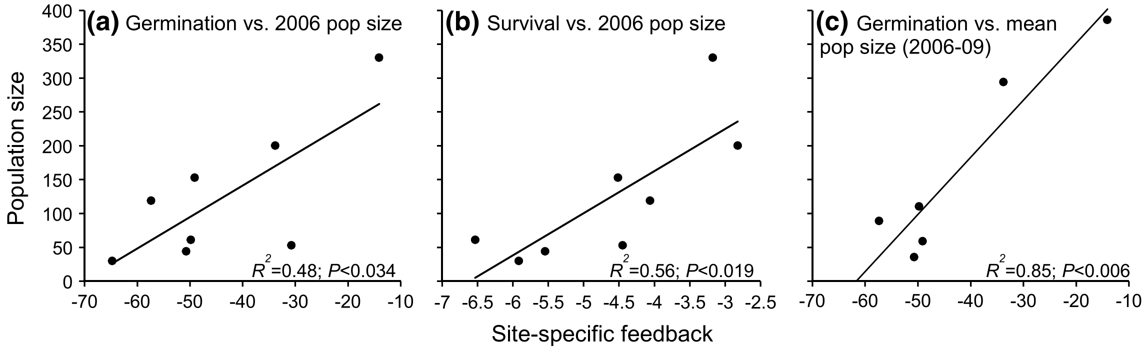

Fig. 4 Relationships between average site-specific feedback and source population size for **a**, **c** germination and **b** survival. **a**, **b** Show population size at all eight sites in 2006 (the year that seeds were collected); **c** shows the mean population size across 4 years (2006–2009) for six of the sites. *Values to the left* indicate greater negative feedback, i.e., a greater average reduction in the plant response trait between cohorts 1 and 2 (see text for details). Regression statistics are provided for significant relationships

Furthermore, the intensity of feedback on germination and survival scaled monotonically with natural plant population size. Based on our examination of the source of feedback effects in this sample of population sites, we suggest that variation in soil characteristics may contribute significantly to population size variation in *L. siphilitica*.

Direct effects of soils and seed sources do not scale with plant population size

Plant responses in the first cohort reflect direct effects of soil characteristics, including soil conditions at the original population site (soil-source effects), and/or the genotypic composition of the original plant population (seed-source effects). Both types of direct effects significantly affected plant success. Although these direct effects could theoretically provide a more parsimonious explanation for variation in plant population size than feedback effects, we found no evidence supporting this explanation. Direct effects of soil source were not significantly related to plant population size, whereas direct effects of seed-source actually scaled negatively with plant population size.

Although soil source clearly affected all measures of plant success, there was no evidence that starting soil conditions varied in a way predictable by natural variation in *L. siphilitica* population size. This result suggests that variation in nutrient availability, chemical or physical composition of soils, or even patterns of heterospecific soil conditioning before the start of the experiment, did not translate into consistently low or high success. Most studies of heterospecific feedback show high variability in its effect on a focal species depending on the identity of heterospecifics (Bonanomi et al. 2005; Casper and Castelli 2007; Brandt et al. 2009; van der Heijden and Horton 2009; van de Voorde et al. 2011). Although detailed studies of plant communities at our study sites could determine the potential for particular heterospecifics to affect *L. siphilitica*, we used soil samples representative of the entire community at each site in this experiment. We collected and bulked soils from microsites that should be most available for new recruits, thus the effect we observed should meaningfully represent the net outcome of future interactions between *L. siphilitica* seeds and a range of local heterospecific microsites.

In a concurrent study on these same population sites, we documented significant variation in native soil microbial communities and physicochemical characteristics among sites (Hovatter et al. 2011). Soil-borne pathogens, nutrient levels, and other physical and chemical aspects of the soil environment have been previously found to affect seedling establishment and plant growth in other plant species (Packer and Clay 2000; Villagra and Cavagnaro 2005; Bonanomi et al. 2005; Travlos et al. 2007; Wilcke et al. 2008; Laliberte et al. 2008; Pregitzer et al. 2010; Liu et al. 2012). Further experiments would be necessary to determine which of these factors is most important in determining direct site effects on *L. siphilitica* traits. Regardless, it is remarkable that direct effects of soil source on plant performance did not scale with population size variation, especially given that conspecific feedback was strongly correlated with population size across this wide geographic range, and was likely to be soil mediated.

Seed-source effects in Cohort 1, reflecting site-specific properties of the plants that produced them, scaled negatively with population size, but were limited to percent germination and survival. There are many possible causes of seed-source effects, ranging from local adaptation of genotypes (Joshi et al. 2001; Pregitzer et al. 2010; Smith et al. 2012) to the likelihood of a seed being inbred (Keller and Waller 2002). In general, small populations of plants are expected to contain less genotypic diversity, have lower adaptive potential, and have a greater likelihood of inbreeding relative to large populations (Ellstrand and Elam 1993; Keller and Waller 2002; Leimu et al. 2006). Therefore, plant success might be expected to be lowest for seeds from small population sites (Menges 1991). Thus, our finding that Cohort 1 plant success was lowest in our largest population and highest in the two smallest populations begs explanation. Although we could not identify the underlying causes of seed-source effects in our study, we detected no significant seed × soil interactions, and no evidence for any ‘home-site’ advantage or local adaptation to particular soils. Interestingly, concurrent studies on these same populations showed that even under soil-free conditions (i.e., Petri dishes in growth chambers), percent germination was highest in smallest populations, and germination was also insensitive to inbreeding (Proell 2009). Further studies of the relationship between population size and individual plant success are clearly warranted.

Small populations were more susceptible to conspecific negative feedback

Previous studies have shown that differences among *species* in susceptibility to negative feedback can explain variation in relative abundance at particular sites (Klironomos 2002; Mangan et al. 2010). However, to our knowledge, variation in conspecific negative feedback has not previously been considered as a mechanism responsible for the regulation of natural population size across a single species’ native range. We observed a monotonic, positive relationship between average site-specific feedback and native plant population size, with seeds and soils from smaller population sites experiencing greater negative feedback. Again, these patterns were particularly apparent in the two traits likely to be linked directly to population size—germination and survival. When we dissected the source of these site-specific effects, we found that variation associated with soil, not seed source, was more likely responsible. In the case of germination, the monotonic relationship between negative feedback and population size was even stronger when considering plant population size in the 3 years following the experiment, suggesting that these results are meaningful with respect to the near-term trajectory of natural populations.

We have several reasons to conclude that more negative feedback in small population sites was driven by feedback with soil microorganisms, and not nutrient limitation. First, there was no relationship between C1 plant responses and soil-source population size, suggesting that if there was variation in nutrient availability among sites, it did not translate into predictable variation in plant responses. Second, all of our analyses of feedback were conducted using least-squares means corrected for C1 plant size, and we still observed a strong relationship between feedback and population size. Note also that the relationships between feedback and population size were identical when we did not correct for C1 plant size (data not shown), suggesting that the intense feedback was not the result of nutrients being disproportionately depleted during the conditioning phase. Finally, the strongest relationship between feedback and population size was observed for percent germination. Germination success is not as affected by soil nutrient availability as are growth and survival. If nutrient limitation was the key mediator of feedback, we should have observed stronger patterns with resource-dependent plant responses.

Although we cannot unambiguously parse the effects of specific components of the soil environment without further experimentation, we predict that the mechanisms are likely to involve soil biota, as has been found elsewhere (reviewed in Bever et al. 2010; Brinkman et al. 2010). In a companion study conducted at these same native population sites, we found distinct microbial communities and regional patterns in community composition in soils beneath *L. siphilitica* plants compared to soils taken from just a few centimeters away where this species was absent (Hovatter et al. 2011). This implies that conditioning by *L. siphilitica* alters soil communities, and potentially the abundance of species-specific enemies that may be mediating negative feedback. However, our current results indicate that there are also inherent differences among sites in the microbial community, causing some soils to induce greater negative feedback on *L. siphilitica*. Based on work in other systems, it seems likely that such differences are related to the geographic distributions of pathogens among population sites (Klironomos 2002; Reinhart et al. 2010; Liu et al. 2012). Alternatively, although we did not see direct effects of heterospecific-conditioned soil scaling with *L. siphilitica* population size, differences among the plant communities surrounding *L. siphilitica* may influence the soil microbial community such that the propensity for conspecific negative feedback is variable among sites. Additional studies will be necessary to address the causes of variation in conspecific feedback, and may be an important step in understanding population size variation within a species' native range.

The fact that feedback on germination success was most predictive of population size suggests that seed pathogens may be a key factor regulating *L. siphilitica* population dynamics. Future inoculation studies would be helpful in establishing a role for various soil biota, including seed pathogens, in affecting individual plant success (Brinkman et al. 2010). If variation in feedback regulates germination success among sites, then it has the potential to explain how population size of species like *L. siphilitica* could be so small (fewer than 100 individuals; Caruso and Case 2007) relative to their exceedingly high seed production (Johnston 1991; Caruso and Yakobowski 2008). In addition to producing clonal basal rosettes, the small seeds of common North American *Lobelia* species, including *L. siphilitica* and its sister taxa, are passively dispersed, and given the field stature of all North American species is <2 m (E. Knox, personal communication), they should have among the most limited seed dispersal distances (Thomson et al. 2011). Thus, seeds should frequently encounter soil environments conditioned by neighboring conspecifics. This increases the importance of our finding that conspecific feedback was more strongly negative at small population sites.

Evolutionary consequences of conspecific plant–soil feedback in natural populations

We do not have explicit demographic data for *L. siphilitica* populations, thus we do not know how sensitive population dynamics are to variation in germination success relative to other demographic parameters, such as growth, flowering, seed production, or clonality. However, it seems reasonable to assume that among-site variation in germination success, whatever the cause, could influence the evolutionary trajectory of populations independently of its effect on plant population size.

Soils are clearly agents of natural selection on plants, and in several cases have resulted in local adaptation of genotypes to their native soil conditions (Schweitzer et al. 2008; Pregitzer et al. 2010; Smith et al. 2012 and references therein). At a regional scale, such effects could potentially influence patterns of gene flow among sites, and not just between extreme soil types like serpentine versus non-serpentine (Sambatti and Rice 2006). Gene flow does not occur unless seeds containing ex situ genetic material are recruited into an adult population. Thus, the likelihood of gene flow is related to the successful recruitment of seeds, which can be differentially affected by both seed and soil sources (Pregitzer et al. 2010; Schweitzer et al. 2011;

Liu et al. 2012). Soil sources affect locally dispersed seeds as well as any seeds dispersed to a site from any other sites. Seed-source effects will be important for locally dispersed seeds as well as those dispersing to any other population site, whether large or small. Site-specific effects account for feedback on seeds that are dispersed locally at their own population site, which is particularly common in passively dispersed herbaceous plants (Thomson et al. 2011), such as *L. siphilitica*. If the site-specific feedback effects that we observed for germination persist, then *L. siphilitica* populations that are currently small might be expected to stay small, regardless of whether it is components of the soil or the plants that is driving the feedback effect. The translation of this effect into population size variation would then depend on how frequently seeds encounter soil conditioned by conspecifics versus heterospecifics, the latter of which did not vary according to *Lobelia* population size in our study. Our result showing that soil variation is contributing more heavily to site-specific feedback than are seed-source effects suggests that small populations should experience less gene flow through seeds. Seeds may disperse to these sites, but something in the soils may prevent immigrant seeds from establishing. In contrast, seeds dispersing to larger population sites may be more likely to be recruited.

Finally, we suggest further investigation into how plant–soil feedback could influence evolution in species, such as *L. siphilitica*, that are comprised of separate sexes. In the same way that individual genotypes may foster particular soil communities (Schweitzer et al. 2008), there is evidence from other systems that plants of different sexes can interact differently with various soil conditions, both abiotic (Freeman et al. 1976; Cox 1981; Dawson and Ehleringer 1993; Eppley 2005; Ashman 2006) and biotic (Varga and Kytöviita 2010; Vega-Frutis et al. 2013). There is also evidence that alternate sexes produce seeds with differential germination and survival (e.g., Eppley 2001; Delph and Mutikainen 2003; Chang 2006). To our knowledge, there have been no explicit studies of sex-differential susceptibility to plant–soil feedback, but such studies would be of interest in order to fully appreciate the role of plant–soil feedback in the evolution of dimorphic plant species. In gynodioecious *L. siphilitica*, small populations tend to contain more female plants than larger populations (Caruso and Case 2007), meaning that some of the connection between sex expression and population size may in fact be mediated by differences in plant–soil interactions. Further studies following plants of each sex would be fruitful.

Conclusions

Although feedback is common in nature, and is known to be an important component of the regulation of population density and plant abundance, we have shown its potential to contribute to variation in natural population size of a single species in its native range. Although based only on a small sample of study sites, this study provides evidence of regional-scale variation in conspecific negative feedback that is likely mediated by biotic components in the soil environment of *L. siphilitica* soils, and is correlated with population size. These results may have implications for further field and manipulative experiments that could test mechanisms behind patterns in population size variation and may contribute to conservation efforts of low-abundance species.

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