

IDEA AND PERSPECTIVE

Phenotypic variation in nurse traits and community feedbacks define an alpine community

Richard Michalet,^{1,2*} Sa Xiao,^{1,3}
Blaise Touzard,¹ David S. Smith,²
Lohengrin A. Cavieres,⁴ Ragan M.
Callaway⁵ and Thomas G. Whitham²

Abstract

Much is known about facilitation, but virtually nothing about the underlying genetic and evolutionary consequences of this important interaction. We assessed the potential of phenotypic differences in facilitative effects of a foundation species to determine the composition of an Alpine community in Arizona. Two phenotypes of *Geum rossii* occur along a gradient of disturbance, with ‘tight’ competitive cushions in stable conditions and ‘loose’ facilitative cushions in disturbed conditions. A common-garden study suggested that field-based traits may have a genetic basis. Field experiments showed that the reproductive fitness of *G. rossii* cushions decreased with increasing facilitation. Finally, using a dual-lattice model we showed that including the cost and benefit of facilitation may contribute to the co-occurrence of genotypes with contrasting facilitative effects. Our results indicate that changes in community composition due to phenotypic differences in facilitative effects of a foundation species may in turn affect selective pressures on the foundation species.

Keywords

Common-garden experiment, community feedbacks, community genetics, cost of facilitation, dual-lattice model, facilitation, foundation species, physical disturbance.

Ecology Letters (2011) 14: 433–443

INTRODUCTION

Biotic interactions are a major component of community genetics (reviews by Whitham *et al.* 2003, 2006; Johnson & Stinchcombe 2007; Wade 2007; Hughes *et al.* 2008), as demonstrated by many studies of interactions across trophic levels. However, studies of interactions *within* trophic levels have not yet played a major role in studies of community genetics (Bailey *et al.* 2009). Furthermore, most studies of organisms within a trophic level have focused on competition or allelopathy (Booth & Grime 2003; Lankau & Strauss 2007; Bossdorf *et al.* 2009; Lankau 2009; Silvertown *et al.* 2009; Whitlock *et al.* 2010). Facilitative interactions also have strong effects on community and ecosystem properties, including diversity, structure, productivity and stability (Mulder *et al.* 2001; Michalet *et al.* 2006; Callaway 2007; Kéfi *et al.* 2007; Brooker *et al.* 2008; Cavieres & Badano 2009), but few studies have explored the genetic basis of these interactions (Callaway *et al.* 1991; Rudgers & Maron 2003; Proffitt *et al.* 2005; Crutsinger *et al.* 2010) or tested evolutionary questions associated with facilitation (but see Day & Young 2004; Ehlers & Thompson 2004; Valiente-Banuet *et al.* 2006).

An important context in which to address genetically based variation in facilitation is that of ‘bi-directional’ interactions, that is, the effects of benefactors on beneficiaries *and* beneficiaries on benefactors. This deficit exists in part because we also know much less about the effects of beneficiary species on their facilitators (i.e.

community feedbacks) than about the effects of the facilitators (Callaway 2007; Bronstein 2009; but see Pugnaire *et al.* 1996a,b; Holzapfel & Mahall 1999; Travis *et al.* 2005, 2006). The relationship between facilitators and beneficiaries can be mutualistic (+, +), antagonistic (+, –) or commensal (+, 0) (Callaway 2007), indicating that feedback effects of beneficiaries have substantial potential to affect genetically based variation in many different ways. Progress towards understanding the evolutionary importance of facilitation requires measurements of the fitness costs and benefits associated with facilitation (Bronstein 2009) in the context of these feedbacks and the underlying genetic basis of these interactions.

Here we focus on the facilitative effects of an alpine species with a ‘cushion’ morphology, *Geum rossii*, which appears to be a foundation species, i.e., a species that structure a community by ameliorating abiotic stress and creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes (Ellison *et al.* 2005). We assessed how the costs and benefits of facilitation experienced by the foundation species (i.e. community feedbacks) may affect its fitness, and thus act as a selection pressure that may drive genetic differentiation in the nurse, and in turn how phenotypic variation in the foundation species affects the distribution and survival of other species in the community. In an alpine system in Northern Arizona, we observed that *G. rossii* facilitated a large number of other species. Importantly, we also observed pronounced trait variation among *G. rossii* individuals in the field, and that this trait

¹University Bordeaux 1, UMR INRA 1202 BIOGECO, 33405 Talence, France

²Department of Biological Sciences; and Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, Arizona 86011 USA

³MOE Key Laboratory of Arid and Grassland Ecology, School of Life Science, Lanzhou University, CN-730000 Lanzhou, China

⁴Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepcion, Instituto de Ecología y Biodiversidad-IEB, Concepcion 4070043, Chile

⁵Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA

*Correspondence: E-mail: r.michalet@ecologie.u-bordeaux1.fr

variation appeared to correspond with the distribution and abundance of other species within the cushion. Interspecific facilitation has been widely documented in alpine communities, where stress and physical disturbance are strong limiting factors for plant survival and growth (Choler *et al.* 2001; Callaway *et al.* 2002; Cavieres *et al.* 2006). This alpine community is a highly suited system for testing evolutionary questions associated with facilitation, as it is easily amenable to manipulation, is characterized by substantial variation in abiotic stress at small spatial scales, and there are easily distinguished phenotypes that vary in the degree to which they facilitate other species. We assessed the genetic basis of facilitation by integrating field observations, removal experiments, a greenhouse and common-garden experiment and a spatially explicit modelling approach.

MATERIAL AND METHODS

Study system

Our study sites were located on Humphreys Peak, the highest of a group of ancient volcanic mountains known as the San Francisco Peaks (Northern Arizona, USA, 3852 m a.s.l., 35°20'47" N, 111°40'41" W). The climate is continental with *c.* 700 mm of rainfall per year on the peaks (556 mm at the Flagstaff weather station, 2100 m a.s.l.), with predominantly summer rainfall. Mean annual temperature is 7.6 °C at Flagstaff and thus close to 0 °C at the peaks, when applying a lapse rate of 0.5 °C per 100 m of elevation (Michalet *et al.* 2003). Our model species, *Geum rossii* (R. Br.) Ser. var. *turbinatum* (Rydb.) C.L. Hitchc. (Alpine avens, Rosaceae), is a common alpine species throughout the Rocky Mountains of North America. At the peaks, *G. rossii* is the most abundant plant of the alpine communities. Other species include grasses such as *Agropyron scribneri*, *Bromus ciliatus*, *Festuca ovina* var. *brachyphylla* and forbs such as *Cerastium beeringianum*, *Penstemon whippleanus*, *Polemonium viscosum*, *Thlaspi montanum* and the endangered *Senecio franciscanus*. *Geum rossii* forms circular to elliptic cushions of varying sizes (20 cm to 1 m diameter) occurring from timberline (3550 m a.s.l.) to the summit. Each cushion is formed of several rosettes tightly connected by short rhizomes and individual cushions are spatially discrete with no connections between them. Thus, each cushion has the potential to be genetically distinct from its neighbours. Cushions typically produce many yellow flowers with viable seeds each year (see results), but no seedlings were observed during the summers of 2008, 2009 and 2010, suggesting the dominance of clonal reproduction. Most other species of the plant community are primarily found within cushions.

We observed that two distinct morphological phenotypes of cushions occurred in the system, 'tight' cushions with very few or no other species within the cushions and 'loose' cushions with a very open internal stem and with many other species within the cushions. A second general observation was that there were more flowers being produced by tight cushions than loose cushions, suggesting a potential reproductive cost to loose *G. rossii* cushions. Tight cushions clearly occurred in the most stable conditions, on shallow organic soils on large rocks within scree slides, whereas loose cushions were more present on fine-textured mineral soils (volcanic ashes and gravels) where physical disturbance is high. Both microhabitats and corresponding cushion types may be found within a few metres of each other. These patterns suggest the occurrence of a single population with different phenotypes growing side by side depending on the level of physical disturbance.

Greenhouse and common-garden experiment

To evaluate whether loose and tight cushion morphologies were due to genetic differences or a plastic response to different environments, clones of the two cushion types were collected in the field and grown for 2 years in similar environmental conditions. The experiment was conducted first in a greenhouse during the winter of the first year and then in an outdoor common garden during the first and second growing seasons. In early October 2008, we collected 33 cushions (hereafter genotypes) of both types between 3650 m and 3800 m a.s.l. Samples included short stems and roots but no leaves because frost killed leaves before the harvest in the field. Each cushion was planted in a 2-L pot in a soil-less mix of peat moss, perlite, and vermiculite in a 1 : 1 : 1 proportion. All pots were installed in a greenhouse and watered two to three times a week. Greenhouse temperatures ranged from 21 to 26 °C. In early November all genotypes had made new green leaves. At this point we separated each genotype into 10–15 individual rosettes. Each rosette was planted into a separate pot (total $n = 900$). At this time we measured the number and size of leaves, stems and roots of each rosette. Pots were then randomly placed on benches within the greenhouse and temperatures were adjusted to range between 16 and 24 °C. Plants were watered two to three times per week and fertilized every 2 weeks with a balanced 20–20–20 water-soluble fertilizer at 120 ppm nitrogen. In early May 2009, all rosettes were planted in a random arrangement in a common garden located at 2800 m a.s.l. at the Nature Conservancy's Hart Prairie Reserve. The soil of the site was plowed before transplanting and all regrowth of other species was removed from around the *G. rossii* individuals each week. The site was fenced to exclude deer and elk. Plants were watered every 4 days during dry periods. In both the greenhouse and the common garden, each month, from November 2008 to August 2009, we measured leaf and flower numbers and the size of the longest leaf for all transplants. Living and dead leaves were counted at each date to calculate relative leaf number production during the first year of the experiment [(final number of living leaves + total number of dead leaves – initial number of living leaves)/initial number of living leaves]. During the second year of the experiment we only calculated total leaf number production (number of living and dead leaves in August 2010), as all individuals had no living leaves at the beginning of the growing season. Additionally, leaf lifespan was measured in the greenhouse between February and April 2009 on at least five randomly chosen rosettes of each genotype, by tagging one young leaf with a ring surrounding the petiole. To assess the differences in palatability among phenotypes, we also measured aphid colonization on *G. rossii* in the greenhouse during an aphid outbreak in March 2009. Three simple classes of aphid colonization were made (0, no aphid; 1, less than 10 aphid individuals; 2, more than 10 individuals).

All data were analysed with one-way ANOVAS with cushion morphology (i.e. loose vs. tight) as independent factor. For the first year, replicates of each genotype were averaged before ANOVAS and genotypes with less than five survivors were excluded from analyses. For the second year, because survival was very low (less than 15%) and most of the genotypes had less than five survivors; ANOVAS were conducted on all survivors, regardless of genotypes. Dependent variables were checked for normality and log-transformed (leaf length, relative leaf number production) or arcsinroot-transformed (survival, leaf lifespan, aphid colonization and flower production) before ANOVAS. All ANOVAS and regressions were carried out with JMP 8.0.2 (SAS Institute, Cary, NC, USA).

Field patterns and removal experiment

To quantify the frequency of each cushion type, in October 2010 we sampled 100 cushions along six, 10-m long transects located between 3650 m and 3800 m a.s.l. and measured their density of rosettes and flower production. On each cushion we randomly sampled a circular plot that was 20 cm in diameter (314 cm²) and counted the number of *G. rossii* rosettes and their number of flowers within the plot. We regressed the number of flowers against the number of rosettes and used this diagram to separate the 100 cushions in three categories, tight cushions, loose cushions and intermediate cushions, with a main importance given to rosette density. Cushions with a density of rosettes higher than 5 dm⁻² (up to 7) and a flower production higher than 7 flowers per dm² were classified as tight cushions, whereas cushions with a density of rosettes lower than 4 dm⁻² and a flower production lower than 13 flowers per dm² were classified as loose cushions. All other cushions were considered as intermediate, that is, mainly cushions with 4–5 rosettes per dm², but also few cushions with less than 4 rosettes per dm² but more than 13 flowers per dm² and few cushions with more than 5 rosettes per dm² but less than 7 flowers per dm².

To measure the strength of associations between *G. rossii* cushions and beneficiary species, and thus the potential for *G. rossii* to be a foundation species, we randomly selected 160 individual cushions between 3650 m and 3800 m a.s.l. We measured the maximum and minimum axes of the horizontal area of each cushion, calculated cushion area, and randomly selected in the close vicinity of each cushion (less than a metre) an 'open' plot of the same area. We counted all individuals of each vascular species growing within the cushions and within the open paired plots. We also quantified the percentage cover of cushions and open area on ten 20-m long linear transects.

We also conducted a removal experiment to quantify differences in facilitative and competitive effects between both cushion types. Two target species, naturally occurring in both cushion types, were chosen to measure these effects, *F. ovina* var. *brachyphylla* and *P. viscosum*. In mid-June 2009 we randomly selected 60 tight cushions and 60 loose cushions between 3650 m and 3800 m a.s.l. For each type 30 cushions included one discrete individual of *F. ovina* and the 30 other cushions one individual of *P. viscosum*. For half of the cushions we removed by hand the aboveground parts of *G. rossii* within a circular area 15 cm in diameter. In mid-June 2009 and late August 2010 we measured the height, number of ramets and number of flowering heads of all target individuals. For the three variables we calculated the relative increment during the experiment as: (final performance value – initial performance value)/initial performance value.

We assessed the cost of facilitation for *G. rossii* cushions first by testing for significant relationships between the total density of beneficiary species within cushions and the production of flowers by cushions, and the species richness of beneficiaries within cushions and the production of flowers by cushions. In early October 2008 we selected 50 cushions that appeared to exhibit a large range of beneficiary densities and beneficiary species richness. This haphazard sampling included both tight and loose cushions, as well as intermediate forms, but was only based on the range of beneficiary densities to be conservative. On each cushion we randomly sampled a circular plot that was 20 cm in diameter (314 cm²) and counted all beneficiary individuals by vascular species and the number of *G. rossii* flowers within the ring. To assess the effect of this cost on the fitness

of the nurse, we collected all seeds from each of the 50 *G. rossii* cushions, overwintered them under the snow at NAU until February 2009 and then sowed the seeds in pots in the greenhouse. Seeds germinated from 3 to 8 days after sowing and the number of emerged seedlings was counted for each of the 50 samples. Additionally, we conducted a removal experiment to fully test the hypothesis that beneficiary species reduce the flower production of loose cushions. In mid-June 2009 we randomly selected 12 sites between 3650 m and 3800 m a.s.l., with at least 100 m between sites. At each site we randomly selected six loose cushions and three tight cushions and removed all beneficiary species growing within a circular plot that was 20 cm in diameter (314 cm²) in half of the selected loose cushions. In early August 2010 we counted the number of flowers produced by all cushions within the previously delimited circular plot.

To assess the importance of *G. rossii* cushions for species richness at the scale of the whole community (cushions and open areas between cushions), we calculated species accumulation curves for the 160 cushion samples and for the 160 paired samples in the open areas. As our protocol included samples that varied in area, these curves were constructed using sample-based rarefaction techniques to avoid biases due to the sequence in which samples were added to the curves. For each microhabitat we generated a species X samples matrix, where each cell (i, j) indicated the presence (1) or absence (0) of the i species in the j sample. From these matrices, 5000 re-samples with replacement were randomly drawn for each sample size, and the Mao-Tau expected richness estimation and its 95% confidence interval were calculated. The average values of species richness were then plotted against the respective sample size to construct a species accumulation curve for each microhabitat. Significant differences were assumed if confidence intervals did not overlap at the asymptote of the species accumulation curves (Gotelli & Colwell 2001). The rarefaction analyses were performed with the software EstimateS v. 8.2 (Colwell 2000).

For the removal of *G. rossii* experiment we analysed relative increment in height, ramet number and flowering head number of the targets, but not survival which approached 100%. For each dependent variable we conducted a three-way ANOVA, with target species, cushion type and removal as independent variables.

The 50 measurements for the cost of facilitation were analysed with simple regression by plotting the number of flowers and emerged seeds of *G. rossii* against the number of species and number of individuals of beneficiary species. For the removal of beneficiary species experiment we compared the flower production of each of the three cushion types (removed loose, control loose and control tight cushions) with a one-way ANOVA followed by a *post hoc* Tukey test. The three values of flower number of each cushion type per site were averaged before the ANOVA.

Modelling

We used a spatially explicit modelling approach to theoretically assess how the costs and benefits of facilitation for a foundation nurse species may affect its fitness and act as selective pressures that are likely to drive genetic differentiation in the nurse. We used a dual-lattice model (Travis *et al.* 2005, 2006) with *G. rossii* and the dependent species living in two overlapping two-dimensional lattices of similar sizes (200 × 200 cells). Each *G. rossii* individual occupied 25 cells (5 × 5 square area) on the first lattice, whereas each individual of the dependant species occupied one cell in the second lattice. We defined

the neighbourhood of *G. rossii* as the Moore neighbourhood, which includes the eight immediate neighbours of a given individual *G. rossii*: north, northeast, east, southeast, south, southwest, west and northwest. For the beneficiary species, we assumed that the dispersal distance of their propagules was the same as for *G. rossii*, creating a neighbourhood of a 11×11 square area including 120 neighbours around each individual. When reproduction occurred, an individual produced propagules that were identical to the parents. The total number of these propagules equalled the reproductive rate rf_i of the *G. rossii* and the reproductive rate rb_i of the beneficiary species. Both types of propagules were dispersed sequentially to one of the neighbours that was randomly selected from the parent's neighbourhood, and the propagules could only establish in empty cells.

In both lattices there was a linear gradient of increasing physical disturbance (parameter D), ranging from 0 (no disturbance) at the left end of the lattices to 1 (maximum disturbance) at their right end. We used a 'wraparound' (torus) approach to avoid edge effects (Yamamura et al. 2004). As the disturbance level was 0 at the left edge of the lattice and the highest at the right edge of the lattice, the wraparound was not conducted at the horizontal direction but only at the vertical direction (Travis et al. 2005, 2006).

In the *G. rossii* lattice there were 40 different genotypes that differed in their competitive ability, p_i , which was defined as the ability of the propagules of one genotype's individual to exclude the propagules of another *G. rossii* individual. Because the propagules of *G. rossii* individuals could only establish in empty patches, the propagule of the individual having the largest p_i value will occupy an empty patch when competing with other individuals. However, as observed in the field and following Grime (1974), we assumed that there is a tradeoff between a genotype's competitive ability and tolerance to disturbance. Thus, with increasing disturbance the survival rate of *G. rossii* genotypes with a high p_i value will decrease more than that of genotypes with a low competitive ability. We modelled this as:

$$sf_i = sf_{\max} - a \times p_i \times D,$$

where sf_{\max} is the maximum survival rate of the genotype occurring in the absence of disturbance; a is a constant, which is larger than 0 and represents the effect of disturbance on a genotypes' survival rate.

Because our field observations showed that most beneficiary species occurred only within *G. rossii* cushions, we assumed for simplicity that the survival rate of beneficiary species is 0 when there is no cushion individual in the corresponding cells of the *G. rossii* lattice. Thus in our model there was a second tradeoff between a genotype's competitive and facilitative abilities, and thus the survival rate of the beneficiary species will decrease with increasing competitive ability of a genotype:

$$sb_i = sb_{\max} - g \times p_i.$$

Here sb_{\max} is the maximum survival rate of the beneficiary species occurring under the most facilitative conditions, that is, within a *G. rossii* genotype with $p_i = 0$; g is a constant representing the intensity of this facilitative effect. For simplicity we assumed that the reproductive rate rb_i of the beneficiary species was the same.

To quantify the impact of beneficiary species on *G. rossii* (feedback effects) we included within the model both a cost and a benefit of facilitation for *G. rossii*. For the cost of facilitation, consistent with our field measurements presented next, we assumed that beneficiary species have a negative effect on the reproductive rate rf_i of the *G. rossii* and this negative effect will increase with decreasing

genotype's competitive ability (p_i) and increasing the number of individuals of beneficiary species (nfb).

Thus, rf_i can be defined as:

$$rf_i = rf_{\max} - c \times (1 - p_i) \times nfb,$$

where rf_{\max} is the maximum reproductive rate of the *G. rossii* occurring when there are no beneficiary species and c is a constant which is larger than 0 and indicates the intensity of the cost of facilitation. Although we did not observe obvious patterns of potential benefits for cushions that hosted other species, for the sake of modelling complete feedback processes among *G. rossii* and other species we assumed that grasses within cushions may help to anchor the cushions on the highly unstable substrate of slopes and thereby decrease cushion's mortality. This positive effect of the beneficiary species on the *G. rossii* was modelled to increase with increasing disturbance (D), to increase with a genotype's decreasing competitive ability (p_i) and to increase with increases in the number of individuals of beneficiary species (nfb).

Thus, including the benefit of facilitation, sf_i is now defined as:

$$sf_i = sf_{\max} - a \times p_i \times D + b \times (1 - p_i) \times nfb \times D.$$

Here b is a constant which is larger than 0 and indicates the intensity of one potential benefit of facilitation for the benefactor. For simplicity, we assumed that all beneficiary species have a similar positive effect on *G. rossii*. Please see the Supporting Information for more details of our model.

RESULTS

In the greenhouse, several lines of evidence suggested that the observed differences between tight and loose phenotypes are genetically based. At the date of transplanting, early November 2008, there were significant differences among cushion phenotypes for both the size of the stems and the longest leaf ($P < 0.001$ and $P < 0.01$, respectively), but not for the size of the roots, number of stems, leaves and roots ($P > 0.1$). Tight phenotypes had longer stems and leaves than loose phenotypes, as observed in the field (data not shown). In the first year of the experiment, differences in leaf length in the greenhouse were still significant 5 months after transplanting ($P = 0.003$; Table 1), with 20% longer leaves for tight cushions as

Table 1 Greenhouse and common-garden (leaf length and relative leaf number production in August) results for leaf traits and aphid colonization of the two cushion phenotypes during the first year of the experiment

Variable	Trait values		Morphology effect
	Tight mean and SE	Loose mean and SE	<i>F</i> and <i>P</i> values
Leaf length (cm), March	7 (0.27)	5.9 (0.24)	3.12 (0.003)
Leaf length (cm), August	5.7 (0.31)	5.8 (0.32)	0.05 (0.821)
Relative leaf number production in August [(final number - initial number)/initial number]	12.6 (0.95)	16.5 (1.20)	7.98 (0.007)
Leaf lifespan (days), February–April	63.04 (2.7)	54.7 (2.5)	2.09 (0.042)
Aphid colonization (classes), March	1.28 (0.05)	1.47 (0.05)	2.79 (0.007)

Significant effects are indicated in bold.

compared with loose cushions. However, 8 months after transplanting, in August 2009 in the common garden, there were no differences in leaf length among cushion types. There were also significant differences in leaf production among cushion types but, in contrast to leaf length, these differences remained significant until the end of the first year of experiment (Table 1). Loose phenotypes produced 30% more leaves than tight phenotypes ($P = 0.007$; Table 1). Additionally, there were significant differences in leaf lifespan and aphid colonization among cushion types ($P = 0.042$ and 0.007 , respectively). Fast-growing loose phenotypes had a 15% shorter leaf lifespan and were slightly more colonized by aphids in the greenhouse than the slow-growing tight phenotypes (Table 1).

In the common garden during the second year of the experiment, survival was very low, but survival did not differ among cushion types ($12.4 \pm 1.8\%$ for tight phenotypes vs. $10.4 \pm 1.4\%$ for loose phenotypes). However, leaf production was still significantly 30% higher for loose phenotypes than for tight phenotypes (22.6 ± 1.6 leaves for loose phenotypes, $N = 49$ vs. 17.8 ± 1.2 for tight phenotypes, $N = 55$; $P = 0.022$). Additionally, and consistent with field measurements, flower production was three times higher for tight phenotypes than for loose phenotypes (0.65 ± 0.2 flower for the former vs. 0.22 ± 0.1 for the latter; $P = 0.051$).

The mean cover of *G. rossii* cushions was 15.3% of which 45% were comprised by loose cushions, 40% by tight cushions and 15% by intermediate cushions. Thus, intermediate forms were less frequent than both loose and tight phenotypes. Several lines of evidence support our hypothesis that *G. rossii* is a foundation species. First, although the mean cover of *G. rossii* cushions was very low, the accumulated species richness was 60% higher within the cushions than in the open (16 species in cushions vs. 10 in the open, respectively; 16 total species), and this pattern of positive associations between beneficiary species and *G. rossii* cushions was highly significant (non-overlapping 95% confidence intervals; Fig. 1). Second, even though cushions represented only 15.3% of the total ground cover, they supported all the species found in this alpine community; no species were found only in the open. Furthermore, most of the species that occurred in open areas reached higher densities within cushions than in the open (data not shown). The only species that was found at much higher densities in the open than in cushions was the endangered *S. franciscanus*. Third, six species were

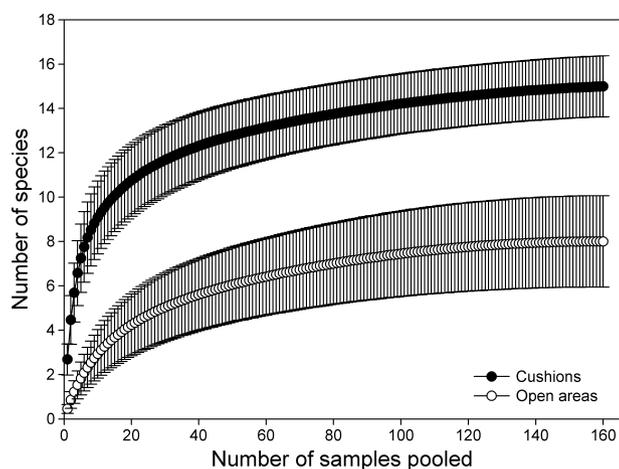


Figure 1 Estimated species richness ($\pm 95\%$ confidence intervals) from rarefaction curves for 160 cushions (solid symbols) and open areas (empty symbols).

only found in cushions indicating that more than a third of the plant community is dependent upon cushions for their survival.

The removal of *G. rossii* from around the two target species showed that both cushion types had contrasting effects on beneficiary species (Fig. 2). For ramet number there was a significant three-way interaction between the target, removal and cushion type treatments ($P < 0.05$), with a strong positive removal effect for *P. viscosum* in the tight cushions only, but no removal effect in either cushion type for *F. ovina* (Fig. 2a). For height there was a highly significant negative effect of cushion removal in both cushion types and for both target species ($P < 0.0001$; Fig. 2b). The same tendency occurred for flower head number, but removal was not significant (data not shown). Together these results show that loose cushions were stronger facilitators than tight cushions.

There was a highly significant negative relationship between the number of beneficiary species (species richness) within *G. rossii* cushions, and the flowering intensity of these cushions (Fig. 3a) suggesting a substantial cost to cushions for facilitating other species. A similar relationship was observed for the density of beneficiary individuals (Fig. 3b). Cushions hosting zero or one species (i.e. tight

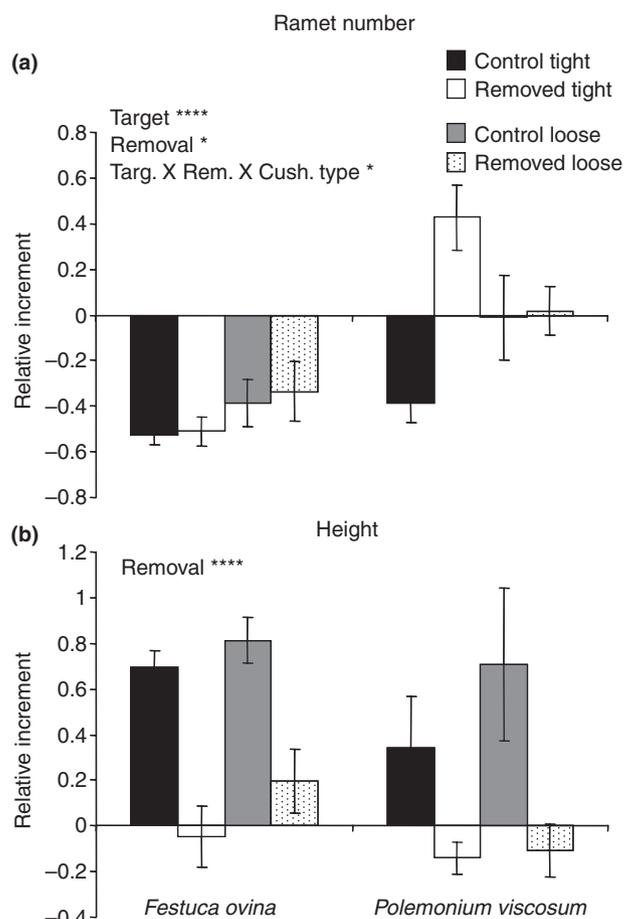


Figure 2 Mean relative increment (± 1 SE) in ramet number (a) and height (b) of the two target species (*Festuca ovina* var. *brachyphylla* and *Polemonium viscosum*) in the cushion removal treatment and control and for tight and loose cushions. Mean relative increment during the experiment is calculated as: (final performance value – initial performance value)/initial performance value. Only significant effects of the three treatments and their interactions are provided for each dependent variable.

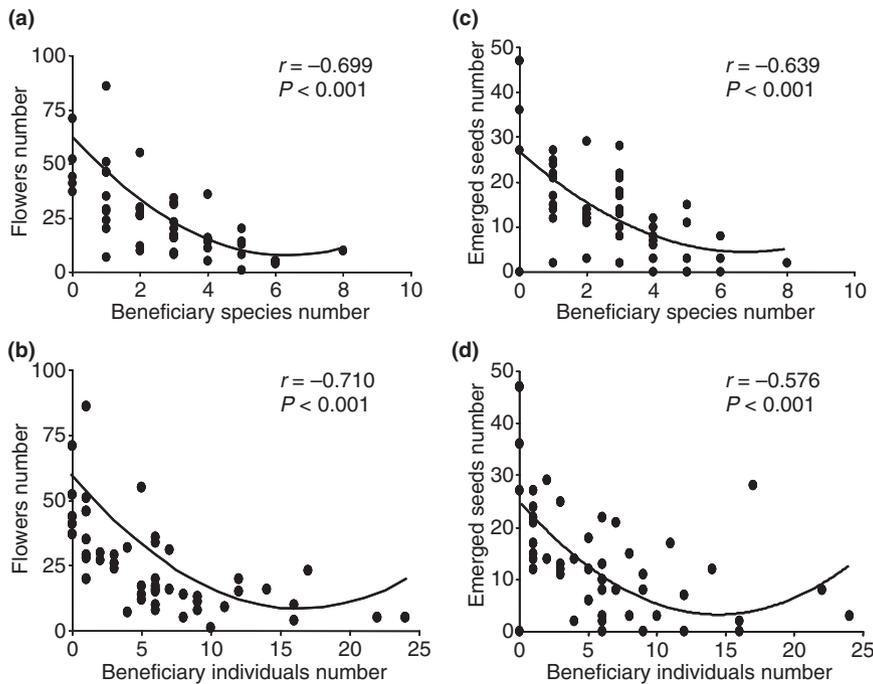


Figure 3 Relationships between the number of beneficiary species and of beneficiary individuals and *Geum rossii* fitness [number of flowers (a and b, respectively) and number of emerged seeds (c and d, respectively)].

cushions) had a mean of 15 flowers per dm² of cushion area; whereas cushions hosting > 5 species (i.e. loose cushions) produced a mean of 5 flowers per dm² of cushion area (Fig. 3a). This negative relationship between species richness and density of beneficiaries within *G. rossii* and flower production by *G. rossii* was further supported by the seed germination experiment. The number of emerged seeds from *G. rossii* plants with many beneficiaries was five times lower than the number of emerged seed from plants with few or no beneficiaries (Fig. 3c,d) indicating that facilitating many other species substantially decreased seed quality.

Consistent with field patterns suggesting a cost to facilitation, the removal of beneficiary species within loose cushions significantly increased flower production by *G. rossii* ($P < 0.001$; Fig. 4). Loose cushions with beneficiaries removed produced two times more flowers than controls, but still produced significantly fewer flowers than tight cushions (Fig. 4).

Our modelling results indicated that with increasing physical disturbance there is a decrease in a mean genotype's competitive ability in each of the four scenarios incorporated into the model

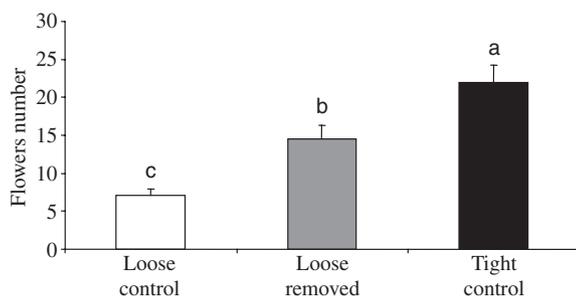


Figure 4 Effect of removal of beneficiary species on flower production of loose *Geum rossii* cushions and comparison with tight cushions. Shared letters above bars indicate no significant difference as determined from a *post hoc* Tukey test ($P < 0.05$).

(Fig. 5). This allows us to hypothesize that disturbance might act as a strong selective pressure creating dominance by tight genotypes in the most stable substrate conditions (left end of the lattice, i.e. left end of the disturbance axis on Fig. 5) and dominance of loose genotypes in the most disturbed substrates (right end of the lattice). However, the four curves have different slopes because the inclusion of either the cost or benefit of facilitation had different effects on the dominance of each cushion type at different positions along the physical disturbance gradient. When including the cost of facilitation (blue and green curves) there was a strong increase in the dominance of genotypes with a high competitive ability (tight genotypes) in conditions with minimal disturbance (disturbance range: 0.1–0.2; Fig. 5a), as compared with the two other scenarios (with no cost). This suggests that facilitation may act as a negative selective pressure on loose genotypes (i.e. the best facilitators) when disturbance is low. In contrast, when including the benefit of facilitation (red and green curves) there is a strong increase in frequency of genotypes with a low competitive ability (loose genotypes) in highly disturbed conditions (disturbance range: 0.5–0.6; Fig. 5b), as compared with the two other scenarios (with no benefit). This suggests that facilitation may conversely act as a positive selective pressure for loose genotypes when disturbance is high. Thus, when including both the cost and benefit of facilitation to *G. rossii* the population strongly shifts from dominance by highly competitive genotypes (tight phenotypes) to dominance by highly facilitative genotypes (loose phenotypes) along a short gradient of increasing disturbance (green curve with the strongest inflexion point in Fig. 5), as observed in the field.

DISCUSSION

Our field measurements and experiments showed the importance of the role of facilitation in this alpine community, but that different phenotypes of *G. rossii* had contrasting facilitative effects on other species, and the strongest facilitators (the loose phenotypes) experienced a strong negative feedback on their reproductive fitness.

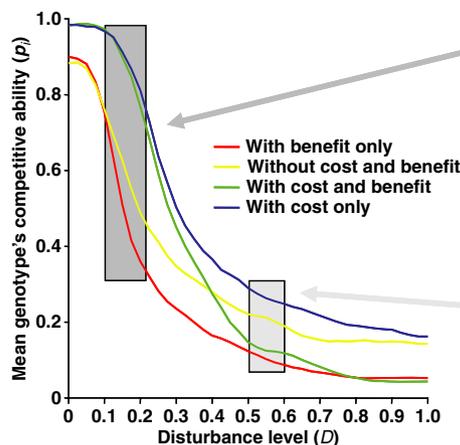


Figure 5 Modelling results with left panel showing variation in mean genotype's competitive ability (p) along the disturbance gradient (D) under four scenarios: (i) red curve shows benefit only; (ii) yellow curve shows no cost or benefit; (iii) green curve shows cost and benefit; and (iv) blue curve shows cost only). The right panels show, for each of the four scenarios, the frequency of genotypes of increasing competitive ability at two positions along the disturbance gradient: (a) $D = 0.1$ – 0.2 ; (b) $D = 0.5$ – 0.6 .

Our greenhouse and common-garden results showed that the two different phenotypes of *G. rossii* conserved most of their traits after 2 years of growth in similar environmental conditions, suggesting genotypic differentiation within this foundation species. Finally, using a spatially explicit model, we showed that the inclusion of both the cost and benefit of facilitation in this system contributes to explaining the occurrence of a strong shift in dominance from highly competitive genotypes to highly facilitative ones along a short gradient of physical disturbance. In combination, these results suggest that facilitation may act as a selective pressure on the fitness of the foundation species and thus has the potential to affect genetic differentiation within the species. As facilitation and competition in alpine systems vary in relative importance along much larger gradients of physical stress and productivity correlated with elevation (Callaway *et al.* 2002), our results also suggest the possibility of shifts in selective pressures along these same gradients.

Positive associations and facilitation

Cushion species are common in alpine communities and their low stature and compact form is adaptive to the severe environmental conditions (low temperatures, excessive radiation and high physical disturbance) of these extreme habitats (Körner 2003; Cavieres & Badano 2009). Several studies have documented positive effects of cushion plants on the diversity of alpine and arctic communities (Arroyo *et al.* 2003; Cavieres *et al.* 2006; LeRoux & McGeoch 2008). However, positive associations are not always evidence of facilitation. For example, in water-limited ecosystems a number of removal experiments have demonstrated that, although positively associated, plants in vegetated patches may compete for soil resources, at least when mature (Maestre *et al.* 2003; Michalet 2006; Forey *et al.* 2010). In contrast, in alpine communities it has been shown that positive associations are generally good evidence of facilitation, as measured in removal experiments (Choler *et al.* 2001; Kikvidze *et al.* 2005).

In our removal experiment we found, for both phenotypes, strong facilitative effects of the cushions on the height of both target species. However, for the ramet number of one target species, we found strong competitive effect of the tight cushions but no effect of the

loose cushions. This higher competitive effect of tight cushions is consistent with our field observations showing a lower density of beneficiary species within the tight cushions (Fig. 3). Previous studies have shown that phenotypic architectural variation in foundation species may induce contrasting facilitative (and competitive) effects on other plant species (Callaway *et al.* 1991; Rudgers & Maron 2003; Proffitt *et al.* 2005; Crutsinger *et al.* 2010). Additionally, plant genetic diversity may also have other positive within-trophic level effects such as increasing community stability or productivity through niche complementarity processes (Booth & Grime 2003; Crutsinger *et al.* 2006; Hughes *et al.* 2008).

The costs and benefits of facilitation

We found evidence for a cost of facilitation for *G. rossii*. First, our field measurements showed that the reproductive fitness of *G. rossii* cushions hosting up to five species beneath their canopy were five times lower than that of cushions hosting zero or one species. Second, the removal of beneficiary species from loose cushions significantly increased their flower production. These competitive effects of beneficiary species on the facilitator *G. rossii* in the highly disturbed microhabitats of the loose cushions may be similar to patterns described along primary successional gradients, where late-successional species otherwise facilitated in pioneer conditions might outcompete their benefactor through time (Clements 1916; Walker & Chapin 1987). However, in our system, because beneficiary species were very rarely found alone, such competitive exclusion of the benefactor likely leads also to the death of the beneficiary species due to excessive stress conditions, which is consistent with models of Travis *et al.* (2005) and Xiao *et al.* (2009).

With the exceptions of models (Travis *et al.* 2005, 2006), we are not aware of any facilitation study which addressed reciprocal effects other than Pugnaire *et al.* (1996a,b) and Holzapfel & Mahall (1999). Our experimental results are consistent with those of Holzapfel & Mahall (1999) who found overall positive net effects of shrubs on annuals, and negative net effects of annuals on shrubs in the Mojave Desert. For the leguminous shrub *Retama sphaerocarpa*, Pugnaire *et al.* (1996a) showed that shrubs facilitating the understory herb *Marrubium vulgare*

benefited from sheltering herbs beneath their canopy. Pugnaire *et al.* (1996b) showed in the same system that this mutualistic interaction was a process emerging through succession with increasing age of the shrub, consistent with niche construction theory (Wilson & Agnew 1992; Laland *et al.* 1999).

In contrast to the study by Pugnaire *et al.* (1996a), we did not observe obvious field patterns suggesting the occurrence of a benefit of facilitation for the nurse *G. rossii*. However, our study examined effects of facilitation on flower numbers and it is possible that a benefit may exist if it acts on *G. rossii*'s survival. For example, most of the beneficiary species are grasses, which may anchor *G. rossii* in disturbed slopes with their deep rooting system and decrease cushion's mortality rate induced by the disturbance. If *G. rossii*'s individuals that do not receive a benefit from facilitation die, then it may be difficult to detect any potential benefit. Further experiments should be conducted to assess any potential of benefits from facilitation, and in particular the removal of grasses within very small loose cushions in highly disturbed slopes. However, it is worthwhile addressing through modelling the potential impact of such benefit on *G. rossii*.

Phenotypic differentiation within the nurse *Geum rossii*

Phenotypic variability among populations experiencing different environmental conditions can be due to phenotypic plasticity, genetic difference or maternal effects (Roach & Wulff 1987; Monty *et al.* 2009). Common gardens are commonly used to separate the effects of plasticity from that of genetic differences (Clausen *et al.* 1940; Roach & Wulff 1987; Schmid & Dolt 1994) and maternal effects are thought to be eliminated by producing second generations of the phenotypes in question in common conditions. Schmid & Dolt (1994) showed that maternal effects for *Solidago altissima* were greatly reduced after one growing season and eliminated after two growing seasons.

We did not exclude maternal effects, but of three traits measured during two growing seasons (leaf and flower production and leaf length) we found that two traits remained significantly different among *G. rossii* morphological types at the end of the experiment (leaf and flower production) and one showed no significant differences (leaf length). As in the field, tight cushions still had longer leaves than loose cushions until April of the first year, but this difference vanished during the first summer to remain no longer significant until the end of our experiment. Because harvested rhizomes from tight cushions were bigger than those of loose cushions, this early difference in the common garden as well as that observed in natural environmental conditions could be due to differences in storage among cushion types related to the environmental conditions of their respective microhabitats. In contrast, leaf production remained higher for loose cushions than for tight cushions after 2 years. Furthermore, loose cushions had shorter leaf lifespans and higher aphid colonization rates in the greenhouse than tight cushions. These differences in traits suggest an 'exploitative' strategy for loose cushions vs. a 'conservative' strategy for tight cushions (MacArthur & Wilson 1967; Grime 1974). These differences are consistent with the higher frequency of tight cushions in physically stable conditions and the higher frequency of loose cushions in highly disturbed conditions, as well as the higher competitive ability of tight cushions (MacArthur & Wilson 1967). This is also consistent with studies showing local adaptation and biotype formation in response to disturbance (Solbrig & Simpson 1974, 1977).

Different growth rates between tight and loose cushions may also be due to an age-related decline in vigour of clonal material among cushion types, as shown by Thompson *et al.* (1991) for *Spartina anglica*. However, Thompson *et al.* (1991) showed that the lower growth rate of successional mature populations was associated with a decrease in survival and flowering fitness in greenhouse conditions. In contrast, in our study there were no differences in survival between the slow-growing tight cushions and the fast-growing loose cushions and the former had a much higher reproductive fitness in the field than the latter. As in the field, flower production was higher for tight cushions than for loose cushions during the second year of the common-garden experiment. Other common-garden studies have demonstrated a genetic basis of similar tradeoffs among populations between resource acquisition or phenological rate and size at maturity (Weber & Schmid 1998; Rowland 2001; Hangelbroek *et al.* 2003).

Our common-garden results suggest a genetic basis for the observed differences in flower production, resource utilization and tolerance to disturbance among cushion types. However, because maternal effects cannot be excluded in our study, reciprocal transplants and genetic structure analysis should be conducted to further test the adaptive significance of the observed phenotypic variation in *G. rossii*.

Including genetic-based costs and benefits within a dual-lattice model

Our models simulating the long-term dynamics of sympatric populations of different genotypes showed that facilitation has the potential to act as a strong selective pressure on *G. rossii* under particular sets of conditions. In conditions of low disturbance, tight cushions appeared to be favoured in the long-term compared with loose cushions because the reproductive rate of the latter is strongly decreased by the negative effect of the beneficiary species (the cost of facilitation), as observed in the field. In contrast, in conditions of high physical disturbance, and at least as hypothesized in our model, loose cushions might be favoured over tight genotypes because their survival rate has the potential to be enhanced by the positive effect of the beneficiary species (the benefit of facilitation). These contrasting effects of facilitation that favour the population dynamics of different genotypes in different environmental conditions enhance the effect of physical disturbance on selecting for slow-growing tight genotypes in stable conditions and fast-growing loose genotypes in disturbed conditions, as shown by the enhanced steepness of the curve including both the cost and benefit of facilitation in our model (Fig. 5).

An interesting improvement of our models could be to modify the parameters of the model to increase the contribution of both the cost and benefit of facilitation in shaping the shift in relative frequency of each phenotype along the physical disturbance gradient. For instance, the contribution of the feedback effects of facilitation may be too subtle as the shift in dominance of the two phenotypes along the gradient also occurs without any feedback effects of facilitation (yellow curve in Fig. 5). This is due to the important contribution given in our model to the tradeoff between competitive ability and tolerance to disturbance. However, further field and common-garden experiments are certainly needed to realistically quantify the relative contribution of environmental vs. biotic selective pressures to the long-term dynamic of this *G. rossii* population. For simplicity our model assumed that all cost and benefit functions are linear, whereas nonlinear functions maybe more biologically reasonable and realistic,

in particular to take into account density-dependant effects of beneficiary species (Chu *et al.* 2008). Such improvements may increase the steepness of the curve including both the cost and benefit of facilitation in our model.

The extent to which such contrasting selective pressures may contribute to sympatric genetic differentiation, that is, when gene flow is possible as in our case, has been widely addressed in the literature and referred as evolutionary branching by Doebeli & Dieckmann (2000) or evolutionary diversification (Day & Young 2004). Doebeli & Dieckmann (2000) stressed that evolutionary branching has been found in a number of across-trophic levels models including mutualistic or predator–prey interactions. Sympatric genetic differentiation has been shown to also occur in contrasting habitat conditions (Choler *et al.* 2004; Freeland *et al.* 2010), but in plant–plant interactions most emphasis has been placed on competition (Miller 1995; Rice & Knapp 2008; Liancourt & Tielbörger 2009; Thorpe *et al.*, in press). Day & Young (2004) and others (Callaway 2007; Brooker *et al.* 2008; Bronstein 2009) suggest that facilitation may also be important in the evolutionary diversification of some taxa, but most empirical evidence comes from microbial experiments (Turner *et al.* 1996; Travisano & Rainey 2000). Our models, in part supported by our field and common-garden experiments, strongly suggest high potential of plant–plant facilitation for evolutionary diversification. We consider that the most challenging issue for future researches will be to assess, through modelling and field experiments, the relative contribution of environmental and biotic drivers in driving this genetic differentiation.

The potential for using facilitation in the study of community evolution

Five key findings emerged from our studies that are potentially important to the study of community evolution (i.e. a genetically based change in the ecological interactions that occur between species over time; Whitham *et al.* 2006). First, our findings from the field argue that through facilitation, *G. rossii* is a foundation species in this alpine community. Second, as facilitation increased, the reproductive fitness of *G. rossii* strongly declined due to the competitive effect of beneficiary species on loose *G. rossii* phenotypes. This argues that there is an important cost of facilitation for the foundation species, which may provide an important feedback of the community on the fitness of individual cushion genotypes. Third, our greenhouse and common-garden results suggest a genetic basis to the predominant cushion phenotypes (tight and loose); after 2 years of growth in similar environmental conditions, the two phenotypes retained most of their respective traits. Fourth, under different disturbance regimes, tight and loose phenotypes growing in close proximity exhibit different fitness, and support different communities. Fifth, in agreement with our field and common-garden studies, using a spatially explicit model, we showed that the inclusion of both the cost and benefit of facilitation within this system contributes to produce a shift in frequency from highly competitive phenotypes to highly facilitative ones along a short gradient of physical disturbance.

Together, these results suggest that facilitation may act as a selective pressure that favours loose phenotypes in disturbed environments, and tight phenotypes in more stable environments. If these architectural-based phenotypes are genetically based as has been shown in other plant studies (e.g. Bailey *et al.* 2004), then they are subject to natural selection and as they change so may their dependent communities. Although our findings show that the two cushion phenotypes support

different communities, they may also have unknown effects on the genetics of species in the dependent community. Thus, if different cushion phenotypes favour different genotypes of the dependent plant species or their associated species (e.g. mycorrhizal mutualists and pollinators), the potential for genetically based facilitation to alter community evolution is strongly suggested. Although not yet examined with studies of facilitation, several studies have found that populations of herbivores are adapted to individual host plant genotypes (Mopper *et al.* 2000; Evans *et al.* 2008). This may extend to multiple trophic levels. Stireman *et al.* (2005, 2006) showed that multiple herbivores and their parasitoids are genetically differentiated on two closely related sympatric species of *Solidago*, which suggests that host plants can affect species' evolution at multiple trophic levels.

ACKNOWLEDGEMENTS

We acknowledge the University of Bordeaux 1 for funding the sabbatical year of the first author in Northern Arizona University and the Post-Doc grant of Sa Xiao. This research was also supported by the National Science Foundation FIBR grant DEB-0425908, the Andrew W. Mellon Foundation, the National Natural Science Foundation of China (grants 40901019, 31000203 and 31000178), the National Outstanding Youth Foundation of China (grant 30625008), the National Basic Research Program of China (973 Program) (grant 2007CB108902), and the P05-002 F ICM and CONICYT PFB-023 grants from Chile. We acknowledge the Nature Conservancy for hosting the common-garden at Hart Prairie and the US Forest Service. We are very grateful to Brad Blake and Phil Patterson for their important contribution in the Greenhouse of NAU, to Neil Chapman for his warm welcome at Hart Prairie and to Jenna Monroy and Ryan Jacobs for their help in the common-garden and the field. We also would like to thank Alice and Antoine Michalet for their help in the greenhouse and Emile Michalet and Edith Schaffter for their help in the field and the common-garden.

REFERENCES

- Arroyo, M.T.K., Cavieres, L.A., Peñaloza, A. & Arroyo-Kalin, M.A. (2003). Positive associations between the cushion plant *Azorella monantha* (Apiaceae) and alpine plant species in the Chilean Patagonian Andes. *Plant Ecol.*, 169, 121–129.
- Bailey, J.K., Bangert, R.K., Schweitzer, J.A., Trotter, R.T. III, Shuster, S.M. & Whitham, T.G. (2004). Fractal geometry is heritable in trees. *Evolution*, 58, 2100–2102.
- Bailey, J.K., Schweitzer, J.A., Ubeda, F., Koricheva, J., LeRoy, C.J., Madritch, M.D. *et al.* (2009). From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. *Proc. Roy. Soc. B-Biol. Sci.*, 264, 1607–1616.
- Booth, R.E. & Grime, J.P. (2003). Effects of genetic impoverishment on plant community diversity. *J. Ecol.*, 91, 721–730.
- Bossdorf, O., Shuja, Z. & Banta, J.A. (2009). Genotype and maternal environment affect belowground interactions between *Arabidopsis thaliana* and its competitors. *Oikos*, 118, 1541–1551.
- Bronstein, J.L. (2009). The evolution of facilitation and mutualism. *J. Ecol.*, 97, 1160–1170.
- Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G. *et al.* (2008). Facilitation in plant communities: the past, the present, and the future. *J. Ecol.*, 96, 18–34.
- Callaway, R.M. (2007). *Positive Interactions and Interdependence in Plant Communities*. Springer, Dordrecht.
- Callaway, R.M., Nadkarni, N.M. & Mahall, B.E. (1991). Facilitation and interference of *Quercus douglasii* on understory productivity in central California. *Ecology*, 72, 1484–1499.

- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R. et al. (2002). Positive interactions among alpine plants increase with stress. *Nature*, 417, 844–848.
- Cavieres, L.A. & Badano, E.I. (2009). Do facilitative interactions increase species richness at the entire community level? *J. Ecol.*, 97, 1181–1191.
- Cavieres, L.A., Badano, E.I., Sierra-Almeida, A., Gómez, S. & Molina-Montenegro, M.A. (2006). Positive interactions between alpine plant species and the nurse cushion plant *Laretia acaulis* do not increase with elevation in the Andes of central Chile. *New Phytol.*, 169, 59–69.
- Choler, P., Michalet, R. & Callaway, R.M. (2001). Facilitation and competition on gradients in alpine plant communities. *Ecology*, 82, 3295–3308.
- Choler, P., Erschbamer, B., Tribsch, A., Gielly, L. & Taberlet, P. (2004). Genetic introgression as a potential to widen a species' niche: insights from alpine *Carex curvula*. *Proc. Natl. Acad. Sci.*, 101, 171–176.
- Chu, C.J., Maestre, F.T., Xiao, S., Weiner, J., Wang, Y.S., Duang, Z.H. et al. (2008). Balance between facilitation and resource competition determines biomass–density relationships in plant populations. *Ecol. Lett.*, 11, 1189–1197.
- Clausen, J., Hiesey, W.M. & Keck, D.D. (1940). *Experimental Studies on the Nature of Species. I. Effect of Varied Environments on Western North American plants*. Carnegie Institution of Washington Publication 520, Washington DC, USA.
- Clements, F.E. (1916). *Plant Succession: An Analysis of the Development of Vegetation*. Carnegie Institution of Washington Publication 242, Washington DC, USA.
- Colwell, R.K. (2000). *EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples*. University of Connecticut, Storrs, CT.
- Crutsinger, G.M., Collins, M.D., Fordyce, J.A., Gompert, Z., Nice, C.C. & Sanders, N.J. (2006). Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science*, 313, 966–968.
- Crutsinger, G.M., Strauss, S.Y. & Rudgers, J.A. (2010). Genetic variation within a dominant shrub species determines plant species colonization in a coastal dune ecosystem. *Ecology*, 91, 1237–1243.
- Day, T. & Young, K.A. (2004). Competitive and facilitative evolutionary diversification. *Bioscience*, 54, 101–109.
- Doebeli, M. & Dieckmann, U. (2000). Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *Am. Nat.*, 156, 77–101.
- Ehlers, B.K. & Thompson, J. (2004). Do co-occurring plant species adapt to one another? The response of *Bromus erectus* to the presence of different *Thymus vulgaris* chemotypes. *Oecologia*, 141, 511–518.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R. et al. (2005). Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.*, 9, 479–486.
- Evans, L.M., Allan, G.J., Shuster, S.M., Woolbright, S.A. & Whitham, T.G. (2008). Tree hybridization and genotypic variation drive cryptic speciation of a specialist mite herbivore. *Evolution*, 62, 3027–3040.
- Forey, E., Touzard, B. & Michalet, R. (2010). Does disturbance drive the collapse of biotic interactions at the severe end of a diversity–biomass gradient? *Plant Ecol.*, 206, 287–295.
- Freeland, J.R., Biss, P., Conrad, K.F. & Silvertown, J. (2010). Selection pressures have caused genome-wide population differentiation of *Anthoxanthum odoratum* despite the potential for high gene flow. *J. Evol. Biol.*, 23, 776–782.
- Gotelli, N.J. & Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.*, 4, 379–391.
- Grime, J.P. (1974). Vegetation classification by reference to strategies. *Nature*, 250, 26–31.
- Hangelbroek, H.H., Santamaria, L. & Boer, T.D. (2003). Local adaptation of the pondweed *Potamogeton pectinatus* to contrasting substrate types mediated by changes in propagule provisioning. *J. Ecol.*, 91, 1081–1092.
- Holzapfel, C. & Mahall, B.E. (1999). Bidirectional facilitation and interference between shrubs and annuals in the Mojave desert. *Ecology*, 80, 1747–1761.
- Hughes, A.R., Inouye, B.D., Johnson, M.T.J., Underwood, N. & Vellend, M. (2008). Ecological consequences of genetic diversity. *Ecol. Lett.*, 11, 609–623.
- Johnson, M.T. & Stinchcombe, J.R. (2007). An emerging synthesis between community ecology and evolutionary biology. *Trends Ecol. Evol.*, 22, 250–257.
- Kéfi, S., Rietkerk, M., Alados, C.L., Pueyo, Y., Papanastasis, V.P., ElAich, A. et al. (2007). Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature*, 449, 213–217.
- Kikvidze, Z., Pugnaire, F.I., Brooker, R.W., Choler, P., Lortie, C.J., Michalet, R. et al. (2005). Linking patterns and processes in alpine plant communities: a global study. *Ecology*, 86, 1395–1400.
- Körner, Ch. (2003). *Alpine Plant Life*, 2nd edn. Springer, Berlin.
- Laland, K.N., Odling-Smee, F.J. & Feldman, M.W. (1999). Evolutionary consequences of niche construction and their implications for ecology. *Proc. Natl. Acad. Sci.*, 96, 10242–10247.
- Lankau, R. (2009). Genetic variation promotes long term coexistence of *Brassica nigra* and its competitors. *Am. Nat.*, 174, 40–53.
- Lankau, R.A. & Strauss, S.Y. (2007). Mutual feedbacks maintain both genetic and species diversity in a plant community. *Science*, 317, 1561–1563.
- LeRoux, P. & McGeoch, M. (2008). Spatial variation in plant interactions across a severity gradient in the sub-Antarctic. *Oecologia*, 155, 831–844.
- Liancourt, P. & Tielbörger, K. (2009). Competition and a short growing season lead to ecotypic differentiation at the two extremes of the ecological range. *Funct. Ecol.*, 23, 397–404.
- MacArthur, R.H. & Wilson, E.O. (1967). *Island Biogeography*. Princeton University Press, Princeton, NJ.
- Maestre, F.T., Bautista, S. & Cortina, J. (2003). Positive, negative, and net effects in grass–shrub interactions in Mediterranean semiarid grasslands. *Ecology*, 84, 3186–3197.
- Michalet, R. (2006). Is facilitation in arid environments the result of direct or complex interactions. *New Phytol.*, 169, 3–6.
- Michalet, R., Rolland, C., Joud, D., Gafta, D. & Callaway, R.M. (2003). Associations between canopy and understory species increase along a rainshadow gradient in the Alps: habitat heterogeneity or facilitation? *Plant Ecol.*, 165, 145–160.
- Michalet, R., Brooker, R.W., Cavieres, L.A., Kikvidze, Z., Lortie, C.J., Pugnaire, F.I. et al. (2006). Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecol. Lett.*, 9, 767–773.
- Miller, T.E. (1995). Evolution of *Brassica rapa* L. (Cruciferae) populations in intra- and interspecific competition. *Evolution*, 49, 1125–1133.
- Monty, A., Lebeau, J., Meerts, P. & Mahy, G. (2009). An explicit test for the contribution of environmental maternal effects to rapid clinal differentiation in an invasive plant. *J. Evol. Biol.*, 22, 917–926.
- Mopper, S., Stiling, P., Landau, K., Simberloff, D. & Van Zandt, P. (2000). Spatio-temporal variation in leafminer population structure and adaptation to individual oak trees. *Ecology*, 81, 1577–1587.
- Mulder, C.P.H., Uliassi, D.D. & Doak, D.F. (2001). Physical stress and diversity–productivity relationships: the role of positive interactions. *Proc. Natl. Acad. Sci.*, 98, 6704–6708.
- Proffitt, C.E., Chiasson, R.L., Owens, A.B., Edwards, K.R. & Travis, S.E. (2005). *Spartina alterniflora* genotype influences facilitation and suppression of high marsh species colonizing an early successional salt marsh. *J. Ecol.*, 93, 404–416.
- Pugnaire, F.I., Haase, P. & Puigdefabregas, J. (1996a). Facilitation between higher plant species in a semiarid environment. *Ecology*, 77, 1420–1426.
- Pugnaire, F.I., Haase, P., Puigdefabregas, J., Cueto, M., Clark, S.C. & Incoll, L.D. (1996b). Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. *Oikos*, 76, 455–464.
- Rice, K.J. & Knapp, E.E. (2008). Effects of competition and life history stage on the expression of local adaptation in two native bunchgrasses. *Restor. Ecol.*, 16, 12–23.
- Roach, D.A. & Wulff, R.D. (1987). Maternal effects in plants. *Annu. Rev. Ecol. Evol. Syst.*, 18, 209–235.
- Rowland, D.L. (2001). Diversity in physiological and morphological characteristics of four cottonwood (*Populus deltoides* var. *wislizenii*) populations in New Mexico: evidence for a genetic component of variation. *Can. J. For. Res.*, 31, 845–853.
- Rudgers, J.A. & Maron, J.L. (2003). Facilitation between coastal dune shrubs: a non-nitrogen fixing shrub facilitates establishment of a nitrogen-fixer. *Oikos*, 102, 75–84.
- Schmid, B. & Dolt, C. (1994). Effects of maternal and paternal environment and genotype on offspring phenotype in *Solidago altissima* L. *Evolution*, 48, 1525–1549.
- Silvertown, J., Biss, P.M. & Freeland, J. (2009). Community genetics: resource addition has opposing effects on genetic and species diversity in a 150-year experiment. *Ecol. Lett.*, 12, 165–170.
- Solbrig, O.T. & Simpson, B.B. (1974). Components of regulation of population of dandelions in Michigan. *J. Ecol.*, 62, 473–486.

- Solbrig, O.T. & Simpson, B.B. (1977). A garden experiment on competition between biotypes of the common dandelion (*Taraxacum officinale*). *J. Ecol.*, 65, 427–430.
- Stireman, J.O., Nason, J.D. & Heard, S.B. (2005). Host-associated genetic differentiation in phytophagous insects: general phenomenon or isolated exceptions? Evidence from a goldenrod-insect community. *Evolution*, 59, 2573–2587.
- Stireman, J.O., Nason, J.D., Heard, S.B. & Seehawer, J.M. (2006). Cascading host-associated genetic differentiation in parasitoids of phytophagous insects. *Proc. Natl. Acad. Sci.*, 273, 523–530.
- Thompson, J.D., McNeilly, T. & Gray, A.J. (1991). Population variation in *Spartina anglica* C. E. Hubbard. *New Phytol.*, 117, 115–128.
- Thorpe, A.S., Aschehoug, E.T., Atwater, D.Z. & Callaway, R.M. (in press). Interactions among plants and evolution. *J. Ecol.*
- Travis, J.M.J., Brooker, R.W. & Dytham, C. (2005). The interplay of positive and negative species interactions across an environmental gradient: insights from an individual-based simulation model. *Biol. Lett.*, 1, 5–8.
- Travis, J.M.J., Brooker, R.W., Clark, E.J. & Dytham, C. (2006). The distribution of positive and negative species interactions across environmental gradients on a dual-lattice model. *J. Theor. Biol.*, 241, 896–902.
- Travisano, M. & Rainey, P.B. (2000). Studies of adaptive radiation using model microbial systems. *Am. Nat.*, 156, 35–44.
- Turner, P.E., Souza, V. & Lenski, R.E. (1996). Tests of ecological mechanisms promoting the stable coexistence of two bacterial genotypes. *Ecology*, 77, 2119–2129.
- Valiente-Banuet, A., Rumebe, A.V., Verdú, M. & Callaway, R.M. (2006). Modern Quaternary plant lineages promote diversity through facilitation of ancient Tertiary lineages. *Proc. Natl. Acad. Sci.*, 103, 16812–16817.
- Wade, M.J. (2007). The co-evolutionary genetics of ecological communities. *Nat. Rev. Genet.*, 8, 185–195.
- Walker, L.W. & Chapin, F.S. III (1987). Interactions among processes controlling successional change. *Oikos*, 50, 131–135.
- Weber, E. & Schmid, B. (1998). Latitudinal population differentiation in two species of *Solidago* (Asteraceae) introduced into Europe. *Am. J. Bot.*, 85, 1110–1121.
- Whitham, T.G., Young, W.P., Martinsen, G.D., Gehring, C.A., Schweitzer, J.A., Shuster, S.M. *et al.* (2003). Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology*, 84, 559–573.
- Whitham, T.G., Bailey, J.K., Schweitzer, J.A., Shuster, S.M., Bangert, R.K., LeRoy, C.J. *et al.* (2006). A framework for community and ecosystem genetics: from genes to ecosystems. *Nat. Rev. Genet.*, 7, 510–523.
- Whitlock, R., Grime, J.P. & Burke, T. (2010). Genetic variation in plant morphology contributes to the species-level structure of grassland communities. *Ecology*, 91, 1344–1354.
- Wilson, J.B. & Agnew, A.D.Q. (1992). Positive-feedback switches in plant communities. *Adv. Ecol. Res.*, 23, 263–336.
- Xiao, S., Michalet, R., Wang, G. & Chen, S.Y. (2009). The interplay between species' positive and negative interactions shapes the community biomass–species richness relationship. *Oikos*, 118, 1343–1348.
- Yamamura, N., Higashi, M., Behera, N. & Wakano, J.Y. (2004). Evolution of mutualism through spatial effects. *J. Theor. Biol.*, 226, 421–428.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Data S1 Details of model.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Editor, Francisco Lloret

Manuscript received 2 December 2010

First decision made 10 January 2011

Manuscript accepted 1 February 2011