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LETTER

Above- and belowground biotic interactions facilitate relocation of plants into cooler environments

Marko J. Spasojevic,^{1*} Susan Harrison,¹ Howard W. Day² and Randal J. Southard³

Abstract

One important but largely unanswered question about floristic responses to climate change is how interactions such as competition, facilitation and plant–soil feedbacks will influence the ability of species to track shifting climates. In a rugged and moisture-limited region that has recently warmed by 2° (Siskiyou Mountains, OR, USA), we planted three species into cooler aspects and elevations than those they currently inhabit, with and without removal of neighbouring plants, and tracked them over 2 years. Two species had higher success in cooler topographic locations, and this success was enhanced by neighbouring plants, which appeared to modulate minimum growing season temperatures. One species' success was also facilitated by the higher soil organic matter found in cooler sites. These results are a novel experimental demonstration of two important factors that may buffer climate change impacts on plants: rugged topography and plant–plant facilitation.

Keywords

climate change, microclimate, plant–plant interactions, plant–soil interactions, serpentine, Siskiyou Mountains, topography.

Ecology Letters (2014)

INTRODUCTION

In mountainous landscapes, rugged topography creates large differences in climatic conditions over short distances, raising the possibility that species may survive rapid climate change through localised movement (Scherrer & Korner 2010; Dobrowski 2011; De Frenne *et al.* 2013). Biogeographic evidence confirms that mountainous landscapes have served as important refugia during past episodes of rapid climate change (Sandel & Dangremond 2012). Moreover, models of climate-driven distributional changes that incorporate this buffering effect of local topography predict far fewer species extinctions than the more standard models that omit this effect (Luoto & Heikkinen 2008).

One key question about biotic responses to climate change is how the movement of species into cooler climate refugia may be either facilitated or inhibited by biotic interactions (Van der Putten *et al.* 2010). For plants, the existing literature on competition and facilitation suggests contrasting possibilities. Experimental evidence indicates that competition tends to be stronger in less stressful environments, while facilitation through the amelioration of abiotic environmental stresses predominates in harsher environments (Goldberg *et al.* 1999; Callaway *et al.* 2002; Brooker *et al.* 2008). Thus, biotic interactions might inhibit the natural or assisted movement of plant species into less stressful, cooler locations if competition predominates. However, some of the strongest evidence for plant facilitation comes from harsh, cold high-elevation environments (e.g., Callaway *et al.* 2002) – perhaps the very locations that may provide cool refugia under climate change.

Thus, it is hard to predict whether competition or facilitation will prevail as species move into cool topographic locations that may have been too harsh in the recent past but are becoming more benign as the climate warms.

Plants may also alter the suitability of cooler sites for other plants via belowground feedbacks. Within generally water-limited climates, cool and moist conditions may be associated with plant species that produce litter that decomposes more slowly, and greater overall litter biomass (Eviner 2004). Nutrient cycling may also be slowed under these conditions (Silver & Miya 2001; Fierer *et al.* 2005). Cool and moist conditions may thus lead to higher soil organic matter, and in turn to higher water retention, macronutrients and cation exchange (Ruiz-Sinoga & Diaz 2010). Enhanced soil fertility in cooler topographic locations may either benefit or inhibit the ability of plant species to move into cooler topoclimates, depending on the relative strengths of direct and indirect (competition- or microbially mediated) effects (Guisan & Thuiller 2005; Kardol *et al.* 2010).

Mountainous regions offer 'natural laboratories' for using relatively small-scale experiments to assess the ability of species to survive climate warming via natural or assisted shifts to cooler microclimates, while avoiding the controversy associated with movement from lower to higher latitudes (Davidson & Simkanin 2008; Hoegh-Guldberg *et al.* 2008). Working in a rugged landscape where recent warming and vegetational change have been documented (see below), we planted seeds of three species currently found at low elevations and/or warm south-facing aspects into cooler topoclimates at higher elevations and on north-facing aspects. We

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assumed that the current distributions of these species might be out of equilibrium with the recently altered climate. We asked: (1) Did these species benefit overall from being in cooler locations? (2) Did aboveground interactions with the surrounding community, as assessed by neighbour removals, help or hinder their success in cooler sites? (3) Did below-ground feedbacks related to variation in soil fertility (organic matter) help or hinder their success in cooler sites?

MATERIALS AND METHODS

Study system

The Siskiyou Mountains of south-western Oregon (USA) are known for high biodiversity and endemism arising from variation in soils, altitude, topographic relief and biogeographic history (Whittaker 1960; Damschen *et al.* 2010; Fig. S1). This Mediterranean-type climate is strongly moisture limited and over the past 55 years, mean annual and seasonal temperatures in this region have increased by 2°C; precipitation has not significantly changed, but snowpack has declined (Damschen *et al.* 2010; Harrison *et al.* 2010). During this period, the composition of Klamath-Siskiyou plant communities has shifted in a direction consistent with regional warming trends (Damschen *et al.* 2010; Harrison *et al.* 2010). Compared with communities in 1949–1951, present-day communities on serpentine and other soils show lower relative cover by species with northerly biogeographic origins, mesic niches and functional traits conveying low tolerance for moisture stress (Damschen *et al.* 2010; Harrison *et al.* 2010).

Study species

We chose three target species – *Arabis aculeolata* (Greene – Brassicaceae), *Horkelia sericata* (S. Watson – Roseaceae) and *Phacelia corymbosa* (Jeps. – Boraginaceae) – that are perennials, have small geographic ranges and low local abundances, and are restricted to open areas on serpentine soils. Serpentine soils are those that develop on rocks such as peridotite and serpentinite, with high magnesium and iron (Alexander *et al.* 2006). *Arabis* is known to be self-incompatible (Vorobik 1985), no studies have been conducted on *Horkelia*, and the genus *Phacelia* is known to be self-compatible but heavily outcrossing (Moldenke 1976). To our knowledge, pollinators of these three species have never been recorded. However, based on our informal observations of several hundred insect visits, *Horkelia* and *Phacelia* attract diverse Hymenoptera, Diptera and Lepidoptera, and some of their most frequent visitors are widespread generalist bees that range to >2000 m in our study region (*Apis mellifera*, *Bombus vosnesenskii* and *B. mixtus*; S. Harrison, unpublished data). We did not observe any visitation on *Arabis*, in part because most of its flowering season occurs prior to our field season.

In our study area, *Phacelia* ranges from 120 to 1400 m elevation, *Horkelia* from 150 to 950 m, and *Arabis* from 400 to 900 m; towards the upper end of its elevational range, *Phacelia* was only observed on south-facing slopes. These ranges are based on data from 396, 1000 m² plots in the region (ranging from 500 to 2200 m elevation) sampled for

species composition between 2007 and 2009 (Damschen *et al.* 2010; Harrison *et al.* 2010), published elevation ranges (Hickman 1993), and personal observations by the authors.

Experimental design

We planted target species at 18 sites along an elevational transect spanning 432–1320 m. Our sites were located near Cave Junction, Oregon which has a mean annual temperature of 12.1°C and mean annual precipitation of 153 cm with 24% of that falling as snow; 2012 was a typical year for temperature and annual precipitation and 2013 was the driest year on record in southern Oregon (<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?or1448>). Of these sites, 14 were paired north- and south-facing aspects spanning the elevation gradient; one was a high-elevation non-aspect (flat) site, and three were low elevation non-aspect ‘home’ sites where seeds were collected (Fig. 1a). The seed source sites were the locations where these species were most abundant in this area. Plant communities tended to be dominated by grasses at lower elevations and by forbs at higher elevations. At each of the 18 sites, we set up 10 plots consisting of two 0.25 m² subplots (one plot at one site was lost over winter, $n = 179$ plots total). Within each subplot we planted seeds of each species below the soil surface at four locations in a 4 × 4 grid marked with coloured toothpicks. The majority of plots lacked our target species, but at the few sites where target species were present we counted only those individuals that germinated within 2 cm of a toothpick.

To assess aboveground biotic interactions we used removal treatments. Each subplot was randomly assigned to control or neighbour+litter removal. In the neighbour+litter removal subplots, all live and dead aboveground biomass was removed in 2011, prior to the experiment, and removal was regularly maintained in 2012 and 2013.

Site characterisation

To characterise the underlying geology and soil of each site, we dug soil pits and collected several rocks from the bottom of each soil pit. Rocks were analysed using thin-section microscopy and X-ray diffraction. We sampled soils from the top 15 cm at four locations in each plot, bulked them and analysed them for nitrogen (N), carbon (C), phosphorus (P; Weak Bray and Sodium Bicarbonate), potassium (K), magnesium (Mg), calcium (Ca), cation exchange capacity (CEC, cations and CEC by ammonium acetate method), soil organic matter (OM, by loss on ignition) and pH (analysis was done by A & L Western Laboratories, Modesto, CA., USA). Because soil OM was strongly correlated with nitrogen ($r^2 = 0.98$) and phosphorus ($r^2 = 0.96$) in our data, and because it has been found to strongly link plant productivity to soil fertility in water-limited Mediterranean climates (Ruiz-Sinoga & Martinez-Murillo 2009; Ruiz-Sinoga & Diaz 2010), we focus on OM to describe soil fertility. Our key results were qualitatively unchanged if we used the first principal component of all soil variables.

Slope (in degrees) was measured in the centre of each plot using a clinometer laid on the ground. Soil moisture was mea-

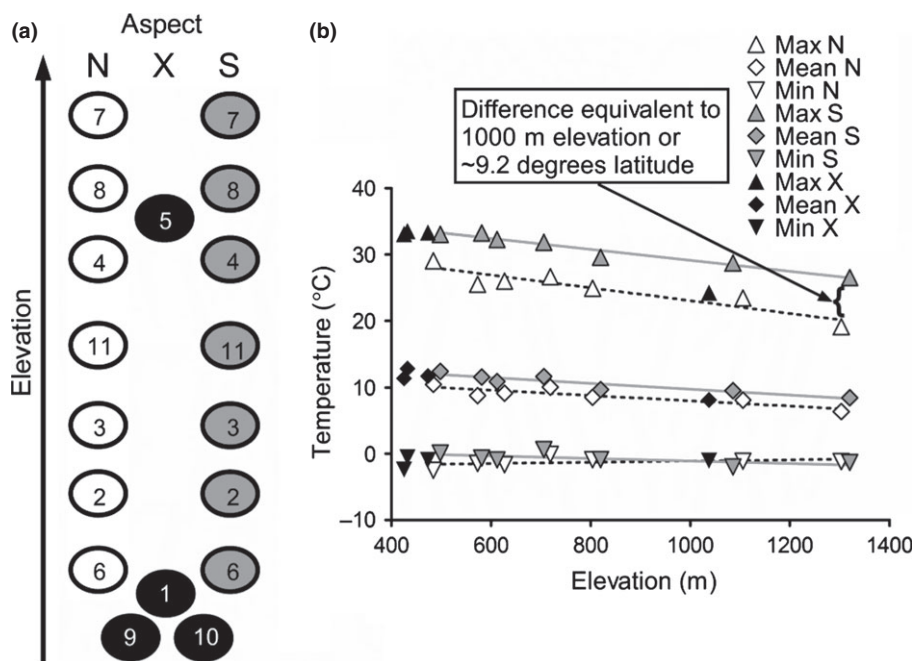


Figure 1 (a) Schematic of site setup along the elevational gradient N: north-facing aspects; S: south-facing aspects; X: non-aspect flat sites. Numbers in schematic correspond to map site numbers in Figure S1. (b) Differences in average daily mean, minimum and maximum temperature among sites.

sured in each subplot to a depth of 15 cm using a Field Scout TDR (Spectrum Technologies, Aurora, IL, USA). Soil strength was quantified as the force (in g) required to pull over a nail buried 2 cm deep in each plot using a 500 g field scale. Canopy density was quantified using a densiometer held at waist height above each plot. Number of trees and shrubs was quantified as the number of trees or shrubs that, if they fell over, would be able to touch a given plot.

We measured temperature at each site using iButton temperature data loggers (Maxim Integrated, San Jose, CA, USA). Loggers were placed in PVC housings resting on the soil surface, and recorded air temperature every 2 h from October 2011 to October 2012. For each site we calculated the mean daily minimum, mean and maximum temperature. To measure how neighbour removals influenced growing season temperatures, at four plots at each site, we placed iButtons into white cloth tea bags and placed them on the soil surface in the centre of each subplot under any existing vegetation from June to September 2013.

Population success

We surveyed our target species for germination and first year survival monthly from April 2012 to October 2012. We visited plots every 3–4 weeks and recorded the location and number of individuals that germinated and marked individuals that were still present and alive at the end of the growing season. We resurveyed our plots monthly from April 2013 to October 2013 to assess second year survival and growth.

Biomass is correlated with fitness in perennial species (Sultan 2001) and several syntheses of demographic data have suggested that survival is much more important for population dynamics of perennials than reproduction (Silvertown

et al. 1992; Franco & Silvertown 1996). Thus, we used as our principal response variable the summed biomass of surviving individuals in each subplot, termed ‘population success’. We quantified biomass using allometric relationships on all plants alive in October. We measured longest leaf, leaf number and plant height on 20 individuals of each species found outside our plots and harvested these individuals to ground level, dried them at 60°C for 3 days and weighed them. We then regressed biomass against all variables and chose the relationship with the highest r^2 value to estimate biomass: *Phacelia*: longest leaf $r^2 = 0.64$; *Horkelia*: longest leaf $r^2 = 0.80$; *Arabis*: leaf number $r^2 = 0.74$. We then summed the estimated biomass of surviving individuals for each species in each subplot for both 2012 and 2013. We quantified overwinter survival as the proportion of individuals surviving the 2012 growing season that were alive at the beginning of the 2013 growing season.

Statistical analyses

Environmental variation

To determine how abiotic and biotic conditions differed between our sites, we tested for differences in microclimate (average site minimum, mean and maximum temperatures) and soil fertility (OM) among north- and south-facing aspects and along our elevational gradient. We used a generalised linear model to test how each environmental variable was influenced by aspect, elevation and the interaction between aspect and elevation. When a significant effect of aspect was found, we then tested for a significant difference between north and south-facing aspects using contrasts. In all instances we tested for both linear and non-linear relationships and selected the best fit using Akaike’s Information Criteria (AIC; Crawley

2007). All analyses were performed in JMP version 10 (SAS Institute Inc., Cary, NC).

Plant success in cooler environments

To test whether first or second year population success or overwinter survival was higher in cooler environments under unaltered conditions (competitors present), we used a generalised linear mixed model (GLMM) with site as a random factor; sites with no aspect (3 home and 1 high elevation) were at unique sites, and adjacent north- and south-facing aspects were at the same site. We first tested how population success was influenced by aspect, elevation and the interaction between aspect and elevation. When a significant effect of aspect was found, we then tested for a significant difference between north- and south-facing aspects using contrasts. For this analysis, we only included control subplots where there were surviving individuals. We then explored specific local factors that could influence first and second year population success and overwinter survival (slope, soil strength, soil moisture, canopy density, number of trees) using a stepwise forward selection model including each of the above local factors, and selected the model with the lowest AIC score.

Aboveground interactions

To examine the role of aboveground biotic interactions, we calculated the relative interaction intensity as the log response ratio (logRR) of population success (first year, overwinter survival and second year) in control subplots divided by population success in neighbour+litter removal subplots (Goldberg *et al.* 1999). We then used the same GLMM as above to test how logRR was influenced by aspect and elevation. For this analysis we included both control and neighbour+litter removal subplots where there were surviving individuals. We then explored specific local factors that may be influencing logRR using the same stepwise analysis as above (we present the patterns for raw population success in neighbour removal plots in Figure S2).

Belowground feedbacks

To examine the role of belowground feedbacks, we used the same GLMM as above to analyse population success, but included soil OM in the model as a continuous variable, as well its interactions with aspect and elevation. If a significant effect of OM was found we then used GLMM to test if the residuals from this model were influenced by aspect and elevation. If the residuals of OM are not significantly influenced by aspect or elevation, then we conclude the influence of these two factors on population success is due to OM alone; however, if there is a significant relationship with aspect or elevation, then microclimate is important independently of its effects on soil OM.

RESULTS

Environmental variation

Maximum annual temperature was significantly influenced by aspect ($F_{2,12} = 31.83$, $P < 0.001$) and elevation ($F_{1,12} = 43.25$, $P < 0.001$), with no significant interaction ($F_{2,12} = 3.08$,

$P = 0.08$). It averaged $\sim 7^{\circ}\text{C}$ greater on south-facing aspects than on north-facing aspects, equivalent to a ~ 1000 m elevation gain or an increase of $\sim 9.2^{\circ}$ latitude. Mean annual temperature was significantly influenced by aspect ($F_{2,12} = 12.17$, $P = 0.001$) and elevation ($F_{1,12} = 59.46$, $P < 0.001$) with no significant interaction ($F_{2,12} = 1.06$, $P = 0.37$), and was greater on south-facing aspects than on north-facing aspects. Minimum annual temperature was not influenced by aspect ($F_{2,12} = 0.65$, $P = 0.62$) or elevation ($F_{1,12} = 0.02$, $P = 0.86$). Minimum temperatures were approximately 0.5°C higher in control subplots than in neighbour+litter removal subplots ($F_{1,111} = 15.12$, $P < 0.01$); mean and maximum temperature were not influenced by treatment.

Based on thin-section microscopy and X-ray diffraction, the underlying lithology of all sites was dominated by massive-scale serpentinite. Nonetheless, organic matter content significantly increased with elevation ($F_{1,174} = 9.29$, $P = 0.003$) and there was a significant effect of aspect ($F_{2,174} = 20.63$, $P < 0.0001$) with overall higher OM on north-facing than on south-facing aspects ($F_{1,166} = 39.40$, $P < 0.001$). There was no significant interaction between aspect and elevation on OM ($F_{2,174} = 2.88$, $P = 0.06$).

Plant success in cooler environments

Two of the three species benefited from being planted into cooler topographic microclimates. First year population success of *Phacelia* in control subplots was significantly greater at higher elevations and on north-facing aspects (Table 1, Fig. 2a). In contrast, both overwinter survival and second year population success of *Phacelia* were not significantly influenced by elevation or aspect (Table 1, Fig. 2d and g). However, *Phacelia* only survived to the second year at three higher elevation sites on north- or non-aspect sites (Fig. 2g).

First year population success of *Horkelia* was greater at higher elevations and on north-facing aspects (Table 1, Fig. 3b). Overwinter survival of *Horkelia* was not significantly influenced by elevation but was significantly influenced by aspect, with greater overwinter survival at non-aspect sites than on north- or south-facing aspects (Table 1, Fig. 2e). Second year population success of *Horkelia* was again significantly higher at higher elevations and was significantly influenced by aspect with a significant elevation by aspect interaction where success was higher at high elevation flat and north-facing aspects (Table 1, Fig. 2h).

First year population success of *Arabis* exhibited a non-linear (unimodal) response to elevation in the control plots but was not significantly influenced by aspect (Table 1, Fig. 2c). Overwinter survival of *Arabis* was not influenced by elevation or aspect (Table 1, Fig. 2f) and no individual of *Arabis* survived through the second year (Table 1, Fig. 2i).

Aboveground interactions

For *Phacelia* in its first year, we found that competition at low elevations gave way to facilitation at high elevations (Table 2, Fig. 3a). There was no effect of aspect and no interaction between aspect and elevation (Table 2). For second year population success, which was very low, logRR was not

Table 1 The influence of elevation and aspect on the first and second year population success and overwinter survival of three species relocated to cooler topographic microclimates.

Species	Predictor variable	First year	Overwinter	Second year
<i>Horkelia</i>	Elevation	$F_{1,76} = 62.23, P < 0.01$	$F_{1,76} = 0.65, P = 0.45$	$F_{1,76} = 51.44, P < 0.01$
	Aspect	$F_{2,76} = 10.66, P < 0.01$	$F_{2,76} = 7.40, P < 0.01$	$F_{2,76} = 46.40, P < 0.01$
	Elevation \times aspect	$F_{2,76} = 8.68, P < 0.01$	$F_{2,76} = 3.70, P = 0.05$	$F_{2,76} = 30.75, P < 0.01$
	N.–S. Contrast	$F_{1,65} = 5.96, P = 0.02$	$F_{1,65} = 0.06, P = 0.80$	$F_{1,65} = 2.23, P = 0.14$
<i>Arabis</i>	Elevation	$F_{1,44} = 4.16, P = 0.01$	$F_{1,44} = 0.06, P = 0.81$	No survival
	Aspect	$F_{2,44} = 0.16, P = 0.70$	$F_{2,44} = 0.18, P = 0.84$	No survival
	Elevation \times aspect	$F_{2,44} = 0.01, P = 0.98$	$F_{2,44} = 0.59, P = 0.56$	No survival
	N.–S. Contrast	No effect of aspect	No effect of aspect	No survival
<i>Phacelia</i>	Elevation	$F_{1,49} = 16.59, P < 0.01$	$F_{1,49} = 0.37, P = 0.54$	$F_{1,49} = 0.52, P = 0.48$
	Aspect	$F_{2,49} = 5.39, P = 0.02$	$F_{2,49} = 0.97, P = 0.39$	$F_{2,49} = 0.72, P = 0.50$
	Elevation \times aspect	$F_{2,49} = 4.74, P = 0.02$	$F_{2,49} = 2.01, P = 0.14$	$F_{2,49} = 0.89, P = 0.68$
	N.–S. Contrast	$F_{1,45} = 6.84, P = 0.01$	No effect of aspect	No effect of aspect

F -statistics and P -values are from a GLMM with site as a random factor. Using this approach we first tested how population success was influenced by aspect, elevation and the interaction between aspect and elevation. If a significant effect of aspect was found, we then tested for a significant difference between north- and south-facing aspects using contrasts. Bold values $P < 0.05$.

significantly influenced by elevation, aspect, or their interaction (Table 2, Fig. 3d, g).

For *Horkelia* we again found a significant positive relationship between logRR and elevation, indicating that competition at low elevations gave way to facilitation at high elevations (Table 2 Fig. 3b). There was a significant interaction between aspect and elevation (Table 2). Overwinter survival was little influenced by neighbour interactions with only one site having logRR different than zero and logRR was not significantly influenced by elevation, aspect, or their interaction (Table 2, Fig. 3e). For second year population success we again found evidence for facilitation at high elevations, although only on north-facing and non-aspect sites (Table 2, Fig. 3h).

For *Arabis*, there was no consistent pattern of competition or facilitation (logRR) associated with elevation or aspect (Table 2, Figs. 3c, f, i).

Belowground feedbacks

First year population success for *Phacelia* was significantly higher at higher OM ($F_{1,42} = 27.95, P < 0.001$) and there was a significant interaction between aspect and OM ($F_{2,42} = 16.03, P < 0.001$), although no significant interaction between elevation and OM ($F_{1,42} = 2.63, P = 0.16$). The residuals of the OM population success model (Fig. 4) showed a significant influence of aspect ($F_{2,42} = 6.72, P = 0.006$), elevation ($F_{1,42} = 15.24, P = 0.009$) and their interaction ($F_{1,45} = 8.46, P = 0.006$) suggesting that microclimate is important independently of its effects on soil OM. Overwinter survival and second year population success were not influenced by OM ($F_{1,42} = 0.28, P = 0.60$ and $F_{1,42} = 0.22, P = 0.64$ respectively) and there was no significant interaction between aspect and OM ($F_{2,42} = 0.90, P = 0.41$ and $F_{2,42} = 0.58, P = 0.56$ respectively) or between elevation and OM ($F_{1,42} = 0.44, P = 0.41$ and $F_{1,42} = 0.01, P = 0.91$ respectively).

First year population success, overwinter survival and second year population success of *Horkelia* were not significantly influenced by OM ($F_{1,74} = 2.15, P = 0.15$; $F_{1,74} = 0.13, P = 0.71$ and $F_{1,74} = 0.39, P = 0.53$ respectively) and there was no signif-

icant interaction between aspect and OM ($F_{2,74} = 1.71, P = 0.19$; $F_{2,74} = 0.07, P = 0.93$ and $F_{2,74} = 1.34, P = 0.26$ respectively) or elevation and OM ($F_{1,74} = 0.67, P = 0.42$; $F_{1,74} = 0.03, P = 0.86$ and $F_{1,74} = 1.21, P = 0.27$ respectively).

For *Arabis*, first year population success and overwinter survival were not significantly influenced by OM ($F_{1,42} = 1.78, P = 0.19$ and $F_{1,42} = 0.44, P = 0.51$ respectively) with no significant interaction between aspect and OM ($F_{2,42} = 0.44, P = 0.64$ and $F_{2,42} = 0.65, P = 0.53$ respectively) or elevation and OM ($F_{1,42} = 0.15, P = 0.70$ and $F_{1,42} = 0.16, P = 0.69$ respectively).

Plot-scale environmental factors

For *Horkelia*, we found that population success was significantly higher in plots that had higher soil moisture, higher soil strength, lower canopy density and on steeper slopes. Overwinter survival was higher at higher soil moisture, higher soil strength and on steeper slopes (Table S1). Second year population success was higher at higher soil moisture and higher soil strength (Table S1). *Arabis* and *Phacelia* were not significantly influenced by these local environmental factors at any stage (Table S1).

Germination

Per cent germination was greater at higher elevations and on north-facing aspects for *Phacelia* and *Horkelia* (Fig. S3). Per cent germination of *Arabis* was negatively related to elevation, with the greatest germination and survival at lower elevations (Fig. S3). Neighbours had positive effects at higher elevations for % germination of *Phacelia* (Fig. S3). Neighbours had no effect on germination of *Horkelia* or *Arabis* (Fig. S3).

DISCUSSION

We found that cooler microclimates (higher elevations, north-facing aspects) were more favourable for two of our three study species, *Horkelia* and *Phacelia*, than the sites these species currently occupy within the study area, suggesting that

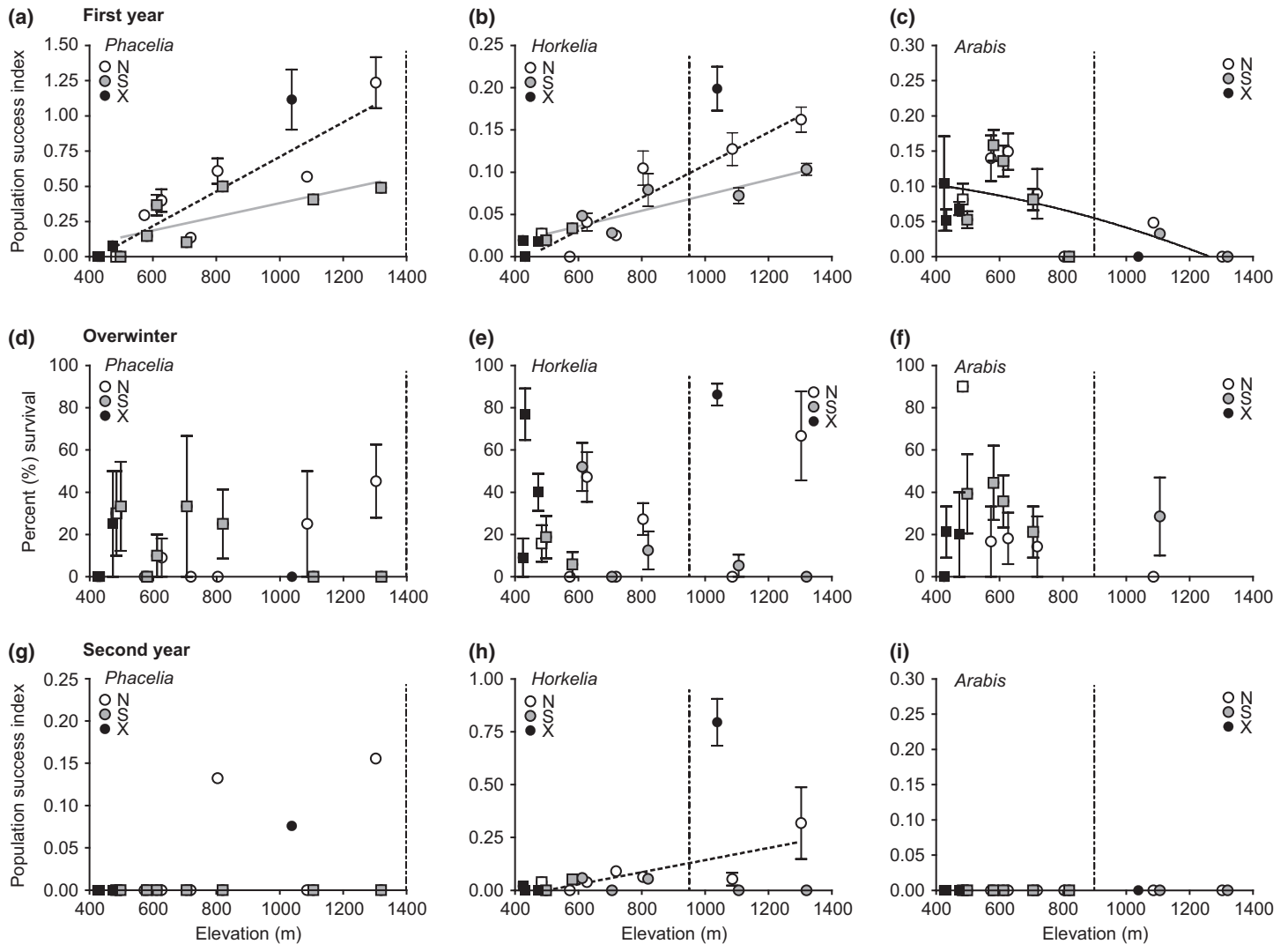


Figure 2 First year population success ((a–c) calculated as summed biomass of all individuals within a plot), per cent overwinter survival (d–f) and second year population success (g–i) in relation to aspect and elevation in control subplots. For graphing purposes we present site means to better illustrate patterns, but analyses were conducted on plot data. A significant positive relationship between population success and elevation and/or a significantly higher population success on north-facing aspects indicates that relocated species do better in cooler environments. Vertical dashed lines represent published upper elevation limit for the target species and square symbols represent sites where species were actually observed; North-facing aspects (N: white symbols, black dashed line), south-facing aspect (S: grey symbols, grey line) and non-aspect sites (X: black symbols); Black solid lines are regressions with all aspects (N, S, X) combined.

these species may be out of equilibrium with current climatic conditions and have not yet dispersed naturally to more favourable cooler microclimates. In addition, we found that the success of these two species in cooler microclimates was facilitated by aboveground interactions with neighbouring species, and for *Phacelia* also by variation in soil organic matter that is likely the effect of the neighbouring plant community. Thus, both of these species' survival in future warmer climates would likely be underestimated by models that did not include aboveground interactions and belowground feedbacks. Existing studies have successfully moved species to cooler latitudes (McLane & Aitken 2012) and cooler elevations (Liu *et al.* 2012), but have largely only focused on how macroclimatic variables influence species success. Our study represents one of the first studies to experimentally test the ability for species

to persist in rugged environments via short distance movements from south- to north-facing aspects, and to simultaneously test for the importance of plant–plant interactions and belowground feedbacks in such shifts. Moreover, ours is among the first studies to find that within a warming region, species actually succeeded better in microclimates cooler than their home locations, suggesting that the time when migration is critical for species survival may be relatively imminent.

We found that *Horkelia* and *Phacelia* experienced the greatest degree of competition in warmer sites (lower elevations) but that they benefited from facilitation at cooler sites (higher elevations), similar to patterns that have been observed along elevation gradients extending into the alpine zone (Callaway *et al.* 2002). The facilitative effects of neighbours at high elevations are often due to physical protection from wind and

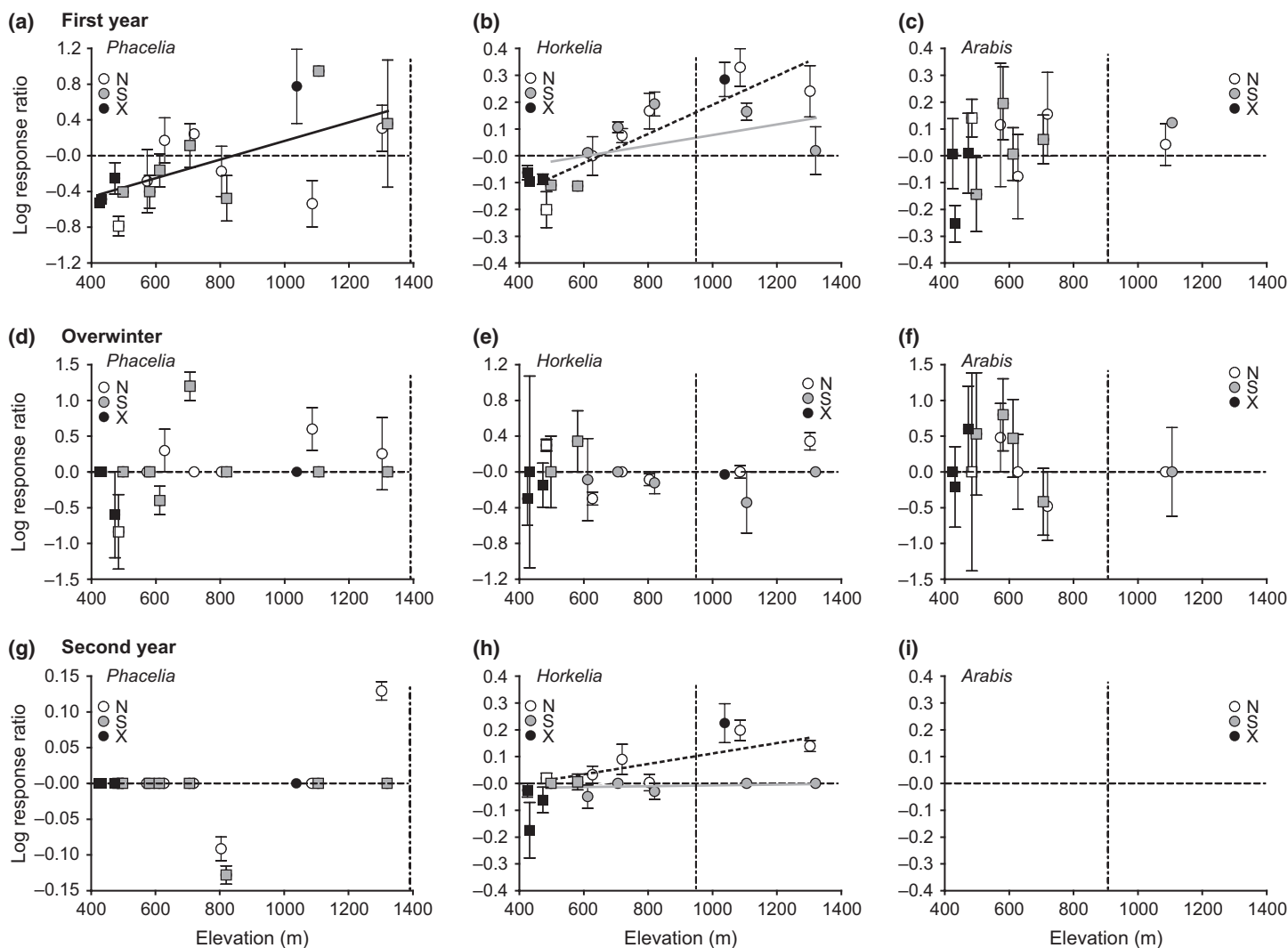


Figure 3 Biotic interactions in relation to aspect and elevation for our three target species for first year population success (a–c), per cent overwinter survival (d–f) and second year population success (g–i). We calculated biotic interactions for each variable as the log response ratio of control subplots divided by neighbour+litter removal subplots, where positive values indicate facilitation and negative values indicate competition (Goldberg *et al.* 1999). For graphing purposes, we present site means to better illustrate patterns, but analyses were conducted on plot data. Vertical dashed lines represent published upper elevation limit for the target species and square symbols represent sites where species were actually observed; North-facing aspects (N: white symbols, black dashed line), south-facing aspect (S: grey symbols, grey line) and non-aspect sites (X: black symbols); Black solid lines are regressions with all aspects (N, S, X) combined.

cold (Callaway *et al.* 2002; Brooker *et al.* 2008). In our study, while minimum temperatures did not differ between north- and south-facing aspects or along our elevation gradient (Fig. 1c), we did find that neighbours significantly increased minimum growing season temperatures by approximately 0.5°C, which may have been especially beneficial for seedling growth at our coldest sites. Our results demonstrate that for species moving into cooler locations, interactions with the background community may not necessarily be negative, but rather may be critical to survival.

Soils contained more organic matter in the cooler environments of higher elevations and on north-facing aspects, and for *Phacelia* we found a significant positive relationship between soil OM and population success in the first year. In our moisture-limited, Mediterranean-climate study system, the

higher OM (as well as higher N and P) we observed in cooler sites may be due to slower decomposition (Silver & Miya 2001; Fierer *et al.* 2005) or a shift in the root to shoot ratio of the neighbour vegetation (Perez & Frangi 2000; Ma *et al.* 2010). We still observed strong positive effects of cooler locations on population success for *Phacelia* when soil variation was statistically controlled (Fig. 4), suggesting that soil OM enhanced, but was not primarily responsible for, higher success in cooler environments. Nonetheless, our result shows that the ability of species to colonise cooler sites may be helped, rather than impeded, by the belowground variation associated with cooler climates.

One of our study species, *Arabis*, did not benefit either from cooler sites or from the above- or belowground variation associated with these sites. The niche of *Arabis* may include

Table 2 The influence of elevation and aspect on the relative interaction intensity (logRR: log ratio of control subplots divided by neighbour+litter removal subplots for each variable) calculated for first and second year population success and overwinter survival of three species relocated to cooler topographic microclimates.

Species	Predictor variable	First year	Overwinter	Second year
<i>Horkelia</i>	Elevation	$F_{1,109} = 19.41, P < 0.01$	$F_{1,109} = 0.59, P = 0.45$	$F_{1,109} = 26.43, P < 0.01$
	Aspect	$F_{2,109} = 0.89, P = 0.43$	$F_{2,109} = 0.42, P = 0.66$	$F_{2,109} = 5.48, P < 0.01$
	Elevation x aspect	$F_{2,109} = 6.06, P = 0.01$	$F_{2,109} = 1.77, P = 0.18$	$F_{2,109} = 17.72, P < 0.01$
	N.–S. contrast	No effect of aspect	No effect of aspect	$F_{2,86} = 0.89, P = 0.35$
<i>Arabis</i>	Elevation	$F_{1,60} = 0.39, P = 0.54$	$F_{1,60} = 0.57, P = 0.45$	No survivors
	Aspect	$F_{2,60} = 0.09, P = 0.91$	$F_{2,60} = 0.51, P = 0.60$	No survivors
	Elevation x aspect	$F_{2,60} = 0.32, P = 0.73$	$F_{2,60} = 0.44, P = 0.65$	No survivors
	N.–S. Contrast	No effect of aspect	No effect of aspect	No survivors
<i>Phacelia</i>	Elevation	$F_{1,118} = 20.02, P < 0.01$	$F_{1,118} = 1.96, P = 0.21$	$F_{1,118} = 0.38, P = 0.56$
	Aspect	$F_{2,118} = 1.52, P = 0.24$	$F_{2,118} = 0.16, P = 0.84$	$F_{2,118} = 0.12, P = 0.88$
	Elevation x aspect	$F_{2,118} = 2.63, P = 0.09$	$F_{2,118} = 0.43, P = 0.65$	$F_{2,118} = 0.64, P = 0.53$
	N.–S. contrast	No effect of aspect	No effect of aspect	No effect of aspect

F-statistics and *P*-values are from a GLMM with site as a random factor. Using this approach we first tested how population success was influenced by aspect, elevation and the interaction between aspect and elevation. If a significant effect of aspect was found, we then tested for a significant difference between north- and south-facing aspects using contrasts. Bold values $P < 0.05$.

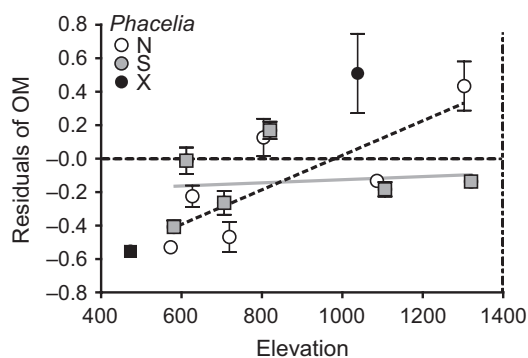


Figure 4 The interactions between OM and aspect and elevation on the first year population success of *Phacelia* in control plots. To graphically represent how OM interacts with aspect and elevation, we plot these residuals against aspect and elevation. The significant relationship with aspect or elevation found here suggests that microclimate is important independently of its effects on soil OM. For graphing purposes we present site means to better illustrate patterns, but analyses were conducted on plot data. Vertical dashed lines represent published upper elevation limit for the target species and square symbols represent sites where species were actually observed; North-facing aspects (N: white symbols, black dashed line), south-facing aspect (S: grey symbols, grey line) and non-aspect sites (X: black symbols); Black solid lines are regressions with all aspects (N, S, X) combined.

specialised requirements that we did not quantify, such as microbial symbionts (Wardle *et al.* 2004) or subtle microhabitat needs (fractured serpentine talus; M.J. Spasojevic & S. Harrison, personal observations). Moreover, *Arabis* flowers much earlier than *Horkelia*, *Phacelia*, and most other species in the community (April–May rather than June–July), and has higher specific leaf area than these two species (Harrison *et al.* 2010), suggesting that its functional strategy involves escaping in time both from the high temperatures of midsummer (hence the lack of benefit from cooler sites) and from peak community biomass (hence the lack of neighbour removal effects). In

any case, this result provides a cautionary note concerning generalisations about species movements into cooler environments.

For all three of our target species, overwinter survival was not lower in cooler sites. This was not surprising as we found little difference among sites in minimum annual temperature (Fig. 2a). That overwinter survival for all three of our species generally did not change with elevation or aspect may be due to the buffering effect of snowpack on minimum temperatures. Snowpack reaches its optimal isolating capacity at a depth of approximately 40 cm (Zhang 2005; Mellander *et al.* 2007; Lawrence & Slater 2010) and our temperature data show long periods where temperature did not change at our higher elevation sites, suggesting temperature buffering by snow. Of our three species, only *Horkelia* was significantly affected by aspect in terms of its overwinter survival; our results suggested that shallower slopes and stronger soils may interact to prevent snowmelt from washing *Horkelia* out of our plots.

Our study region has warmed 2°C in the last 55 years (Damschen *et al.* 2010; Harrison *et al.* 2010), and this trend is predicted to continue. Strikingly, mean and maximum temperatures (Fig. 1b) differed between high elevation north- and south-facing aspects in our study by about 7°C, suggesting that a broad range of species may be able to use these sites as refugia well into the future. Similar patterns of topographic thermal buffering have been found at both comparable spatial scales (Olson *et al.* 2012) and at smaller spatial scales (Scherrer & Korner 2011), adding to evidence suggesting that populations in rugged environments may persist in the face of changing climate (Luoto & Heikkinen 2008; Randin *et al.* 2009; Spasojevic *et al.* 2013). Over the coming century, precipitation is not predicted to change strongly, but seasonal water deficits are expected to intensify as temperatures increase (Thorne *et al.* 2012). This increase in water stress may exacerbate the importance to plants of the lower insolation and higher soil organic matter found on north-facing aspects.

Extreme climatic events are likely to play an important role in the long-term population success of our study species. Our second study year, 2013, was the most extreme drought year ever recorded in the study region, and the benefits of cooler microclimates appeared to be intensified in 2013 compared to the more normal conditions of 2012. However, it is possible that future extreme freezing events could undermine success in the cooler locations. Another possibility is that a shortage of pollination will constrain plant fitness in novel sites. Based on our observations, however, *Horkelia* and *Phacelia* are visited by insects of many orders, including bees that are common at high elevations. More generally, relocation efforts within topographically complex landscapes may have less risk of pollinator limitation than long-distance latitudinal relocations (Swarts & Dixon 2009; Menz *et al.* 2011).

In conclusion, our results suggest a great potential for high-elevation north-facing aspects to shelter species from climate change either via natural dispersal or assisted relocation. Furthermore, our results confirm conceptual work suggesting the importance of topography in buffering plant species against climate change (Randin *et al.* 2009; Scherrer & Korner 2011; Olson *et al.* 2012) and confirms the importance of including topography in models of future species distributions (Luoto & Heikkinen 2008). Finally, we show that the buffering capacity of topography can only be fully understood by considering how aboveground biotic interactions and belowground feedbacks may vary with topographic microclimates. Understanding the strength and directionality of these feedbacks is critical for accurate predictions of biotic response to global change (Van der Putten 2012).

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AUTHORSHIP

M.S., S.H., H.D., and R.S. designed the study. M.S. wrote the first draft of the manuscript and all authors contributed substantially to revisions. M.S. collected data and conducted analyses, with input and assistance from S.H. H.D. conducted lithological analyses and created geological map. R.S. assisted on soil analysis.

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