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The demography of native and non-native plant species in mountain systems: examples in the Greater Yellowstone Ecosystem

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Abstract In mountainous areas, native and non-native plants will be exposed to climate change and increased disturbance in the future. Non-native plants may be more successful than natives in disturbed areas and thus be able to respond quicker to shifting climatic zones. In 2009, monitoring plots were established for populations of a non-native species (*Linaria dalmatica*) and a closely related native species (*Castilleja miniata*) on an elevation gradient in the Greater Yellowstone Ecosystem, USA. Population data were collected twice during the growing season for 3 years and used to calculate population vital rates for both species, and to construct population dynamics models for *L. dalmatica*. *Linaria dalmatica* vital rates were more associated with climatic/environmental factors than those of *C. miniata*. Population dynamics models for *L. dalmatica* showed no trend in population growth rate (λ) vs. elevation. The highest λ corresponded with the lowest vegetation and litter cover, and the highest bare ground cover. All populations with $\lambda < 1$ corresponded with the lowest measured winter minimum temperature. There was a negative association between λ and number of weeks of adequate soil moisture, and a weak positive association between λ and mean winter minimum temperature. Variance in vital rates and λ of *L. dalmatica* suggest broad adaptation within its current range, with the potential to spread further with or without future changes in climate. There is evidence that λ is negatively affected by persistent soil moisture which promotes the growth of other plant species, suggesting that it might expand further if other species were removed by disturbance.

Keywords Climate change · Elevation gradient · Invasive species · *Linaria dalmatica* · Population model · Vital rates

Introduction

Plant communities in mountainous areas of the world are facing an uncertain future. Climate change has the potential to alter both native (Crimmins et al. 2009; Engler et al. 2009) and non-native (Becker et al. 2005; McDougall et al. 2005; Marini et al. 2009; Pauchard et al. 2009) plant species ranges. The broad geographic ranges and climatic tolerances of non-native plant species, as well as characteristics that may facilitate rapid range shifts in the face of climate change (Hellmann et al. 2008), could result in increased success of non-native plants at higher elevations (McDougall et al. 2005; Crimmins et al. 2009). In addition, increased and altered human land use in mountainous areas could result in more opportunities for non-native plant species establishment due to both an increase in dispersal vectors and in suitable habitat (McDougall et al. 2009; Pauchard et al. 2009).

In general, non-native plant species richness tends to decrease at higher elevations in most geographical contexts (Pauchard et al. 2009; Alexander et al. 2011; Seipel et al. 2012). This response has been observed in some cases to be

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linear (Becker et al. 2005; McDougall et al. 2005), and to be hump shaped in others (Tassin and Riviere 2003; Arevalo et al. 2005). One recent exception to this generality was found by Paiaro et al. (2011), who observed that non-native species richness increased at both ends of an elevation gradient in central Argentina. When considering individual non-native species, several studies have noted decreases in occurrence and population size and/or vital rates with elevation (Liang et al. 2008; Alexander et al. 2009; Monty and Mahy 2009; Trtikova et al. 2010; Pollnac et al. 2012) and at least one has noted increased success at higher elevations (Ansari and Daehler 2010).

The presence of some exceptions to the general trends suggests that elevation is not the only explanatory factor related to non-native plant species distributions in mountain systems, and it is clear that there are several other factors besides elevation (i.e., climatic and environmental characteristics) which influence non-native plant species in these areas. Furthermore, the effects of these factors on any given species could manifest themselves in subtle ways. For example, imagine that seed viability is the only variable negatively affected by climatic and/or environmental factors for a particular species at high elevations, and all other variables (such as stem density) remain constant at high elevations. If seed viability is not measured, an important relationship could go unnoticed and some incorrect conclusions could be drawn based only on measurements of stem density. Thus, if questions related to the future of a non-native species in a mountainous area are to be addressed, population level demographic details of the species must be collected throughout its current range. However, we know of no demographic studies for individual non-native species which incorporate site-specific measurements of climate and environmental factors.

The differences in the population growth rate (λ) of a plant species between its range limits and its interior range have been hypothesized to vary based on whether or not that species has reached the limits of its potential range (Gaston 2003; Angert 2006; Eckhart et al. 2011). For example, if a species has filled its potential range, λ at the margins should be lower than λ for the interior populations because the marginal populations have theoretically encountered some limiting factor which suppresses growth and prevents them from expanding further (Gaston 2003, and references therein). Alternatively, for a species that has not yet reached the limits of its potential range, marginal populations may exhibit higher λ values because the species is in suitable habitat where limiting intraspecific density dependence is absent (Gaston 2003, and references therein). Eckhart et al. (2011) take this concept a step further, stating that: (1) covariation of λ with environmental factors known to influence λ across a species range suggests lack of adaptation as the primary limit to a species' current range and, (2) lack of association between λ and range position, and increases in λ at range limits both implicate dispersal as the primary factor defining range limits. Therefore, comparisons of λ for interior and range limit populations could provide insight into whether or not a non-native species has reached the limits of its potential range within an area, and what the barriers to expansion may be. In a mountainous area, evaluation of λ for a species throughout its current range allows for an assessment of the potential for the species to become established in upslope or down slope habitats under current climate conditions. Adding site-specific climatic and environmental data further allows one to hypothesize about possible changes in range due to changing climatic and environmental conditions.

The first objective of this study was to examine the relationships between specific population vital rates and site-specific environmental and climatic factors for a short lived perennial non-native plant species, *Linaria dalmatica* (L.) Mill, along an elevation gradient in the Greater Yellowstone Ecosystem (GYE). Using this species gave us the opportunity to test some of the aforementioned assumptions about λ in relation to range limits in the context of a mountain system using a non-native species with a known date and location of introduction (1957, in the town of Mammoth, B. Maxwell, personal communication). We hypothesized that vital rates of *L. dalmatica* would vary along the studied gradient in relation to climatic and environmental predictor variables, indicating the potential for climate induced changes in population dynamics. Our second objective was to compare the trends in vital rates for *L. dalmatica* to those of a closely related perennial native species, *Castilleja miniata* (Douglas ex Hook.), found along a similar elevation gradient. We hypothesized that vital rates of *C. miniata* would not vary throughout its distribution as much as those of *L. dalmatica* since it has been present in the area for a much longer period of time. This hypothesis relied on two assumptions. The first was that the residence time of *L. dalmatica* on the landscape has not been sufficient for this species to go through enough colonization/extinction events to have a distribution pattern which is matched with its ideal habitat (e.g., it is still found in areas where it might not be able to persist in the long term). The second was that the environment of the study was not subject to any recent abrupt and heterogeneous disturbances which could result in variable success of either species regardless of the historical suitability of the environment. To the best of our knowledge, both of these assumptions are valid. We do not believe that recent/ongoing climate change violates the second assumption because it is imposed on a broad scale compared to the ranges of these two species within the study area. Our third objective was to model population growth of *L. dalmatica*

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throughout its current range in our study area. We hypothesized that population growth rates would be lower at the upper elevation range limit of this species, indicating a potential climatic barrier.

Methods

Study area and site selection

This study was conducted along an elevation gradient within the GYE in the vicinity of Gardiner, MT, 45°01′60″N, 110°42′33″W, 1,598 m elevation. Three roads were chosen as elevation transects in the area. Each of these transects proceeded from elevations of approximately 1,700 m near the bottom of the Yellowstone River Valley in Gardiner, MT for variable distances to elevations just short of the highest elevation extent for the specific transect, but represented the highest point of road access (58 km–2,900 m for transect 1, 18 km–2,400 m for transect 2, and 15 km–2,200 m for transect 3). Transect 1 was within Yellowstone National Park, and the other two were just north of the park boundary on United States Forest Service roads.

During July and August of 2008, the three elevation transects were surveyed for the presence of *L. dalmatica* and *C. miniata,* both hereafter referred to collectively as the test species. During initial surveys, an effort was made to identify every distinct population of the test species present within 5 to approximately 200 m of the elevation transects (roads) from their lowest elevations up to the highest extent that was navigable in a vehicle. *Linaria dalmatica* and *C. miniata* occurred from 1,700 to 2,300 m and from 2,100 to 2,800 m along the elevation gradient, respectively. During early spring 2009, three study sites were established for each species on each one of the three elevation transects (Fig. 1). Sites were selected from the pool of surveyed sites to represent a relatively even spread of elevations along each elevation transect. The sites essentially represented the low, medium, and high ranges for *L. dalmatica* and *C. miniata* in their respective local elevation distributions. Four 1 m^2 monitoring plots were established randomly at each one of these sites by throwing quadrats in areas where the test species was present. For *L. dalmatica*, it was not possible to select sites which had a uniform population size across the elevation gradient, and quadrats were thus distributed across a variable number of populations (distinct patches of the species separated by $>$10 m) within the spatial extent of each site (2,000–4,000 m^2). Populations ranged in size from 5 to 530 m^2 for five out of the nine sites, with the remaining four sites containing larger populations of 1,000–3,000 m^2. All *C. miniata* sites contained populations of the species which were $<$200 m^2 in size.

Measurement of climate and environmental variables

Temperature was measured every hour at each site using one Lascar EL-USB 1 temperature data logger (temperature logger) placed $\sim$0.5 m off the ground during the growing seasons (June to early September) of 2010 and 2011, and the winters of 2009/10 and 2010/11. Soil moisture was measured weekly at each site during the growing seasons of 2010 and 2011 using three Delmhorst gypsum blocks installed at random locations throughout each site at a depth of 15 cm in the ground following the procedure described in Aho and Weaver (2008). Throughout the growing seasons of 2010 and 2011, precipitation was measured weekly at each site using one rain gauge per site (Taylor Pro gauge).

Biotic environmental variables (canopy cover, percent of bare ground, litter, and vegetation cover) were estimated by the same observer at all sites during the growing season of 2011 from six random locations within the site for each variable except canopy cover, which was estimated at 4 random locations. Soil samples were taken to a depth of 10 cm (approximately 285 cm^3) from ten random locations at each site during the growing season of 2010 and analyzed for abiotic environmental variables (pH, organic matter, total nitrogen, potassium, and plant available phosphorous content).

Estimation of vital rates

Vital rates were collected for the purposes of: (1) determining the influences of climate and environmental factors on the vital rates for each species, (2) comparing the degree of association between vital rates and climatic/environmental variables among the test species, and (3) building demographic population models for *L. dalmatica*. Plots were monitored during early June and late August of each field season from 2009 to 2011. During each session, a 1 m^2 frame divided into 16 parts was placed over each plot. The location of each stem in the grid was then drawn on a piece of tracing paper, denoting seedlings, vegetative stems, or flowering stems with distinct symbols. Stems which were obviously arising from a common root crown were drawn to be touching on the mapping data sheet, such that individuals could be counted more precisely.

To estimate vital rates from early spring to late summer, sheets from subsequent monitoring sessions were overlaid (for example August 2009 was placed over June 2009) for each plot, and the number of stems which had: (1) transitioned from vegetative to flowering, (2) stayed vegetative, (3) died, or (4) appeared since the previous period were counted, as were the number of individuals which had survived, died, or appeared since the previous period. Similarly, looking at the time period from August to the

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Fig. 1 Map of study area showing plot locations

following June, the number of individuals that survived, perished, or appeared since the previous period was recorded. This yielded information on stem production, spring individual survival, transition to flowering stem, estimated vegetative ramet production (for *L. dalmatica* only), and fall individual survival rates. So few seedlings were observed that seedling survival could not be estimated from these data.

Linaria dalmatica seed production was estimated by counting the number of seed capsules present within each plot at each site during late August of each field season. Seed production per seed capsule was estimated by sampling forty-five capsules from plants outside of the monitoring plots at each site. Fifteen seed capsules were collected from each of the lowest, middle, and highest regions of the stems, with no more than one capsule being collected from a given stem. Capsules were then dried at constant temperature (43 °C) and seeds within were counted. To evaluate germination rates, four batches of 50 seeds were collected per site and placed in a germination chamber at 15 °C alternating 12 h light/12 h dark and monitored weekly for 5 weeks. To evaluate seedling survival, 5 pots of 5 seedlings at the cotyledon stage and 5 pots containing ten seeds (both using seed from the location of placement) were randomly placed at each site in late May/early June of 2011 and then monitored until mid-September. Pots were placed so that they were level with the ground surface and were not given any supplemental irrigation or fertilization.

Seed predation data were also collected at each site using four randomly located 8 cm × 8 cm plastic trays. Each tray had 2 holes drilled in the bottom, one for drainage and one for securing the tray to the ground using a nail. Trays were placed such that they were flush with the ground surface. They were filled with sand, and 50 *L. dalmatica* seeds were scattered on the surface of the sand. After 10 days, the remaining seeds were collected and counted. These data were used to refine seed production rates for each site in the population model.

Seed production, germination, longevity, predation, and seedling survival were used in conjunction with the vital rates described above to model the population dynamics of *L. dalmatica*. The only rate used in the models which was not based on field measurements was seedling competitive ability. Since seedlings of *L. dalmatica* are weak competitors with established vegetation (Gates and Robocker 1960; Robocker 1970), germinable seed crop was further reduced in the model by multiplying by the mean proportion of bare ground measured at each site, assuming random dispersal and random seed decay. That is, if a seed landed on existing vegetation, it was expected to die, but if it landed on bare soil, it was subject to germination. This assumption is supported by previous work (F.W. Pollnac and L.J. Rew, unpublished data), in which the presence and cover of *L. dalmatica* was found to be positively associated with increased bare ground, suggesting that establishment of this species is linked to increased bare ground. It is quite possible that seed decay and predation could also be related to the environment in which a seed lands, but we did not have data to test this.

For *C. miniata,* an estimate of seed production was achieved by randomly harvesting 10 flowering heads from outside of the monitoring plots at each of the *C. miniata* sites in the late summer of 2009. These flowering heads were dried at constant temperature (43 °C) for several weeks and then dissected such that for each seed capsule, the number of seeds could be counted. Seed germination and seed decay rates for this species were not measured.

Data analysis

Variance in vital rates along elevation gradients

All analyses were performed using R 2.14.1 (R-Development-Core-Team 2011). Before producing any population dynamics models, we wished to see if vital rates varied from site to site for each test species, and to see if there was any difference between species in the degree to which vital rates were associated with climatic/environmental variables. To address these objectives, vital rate data collected directly from study plots [spring and fall individual survival, stem production, transition to flowering stem, vegetative ramet production (for *L. dalmatica* only), and seed production] from different years were averaged for each 1 m^2 plot, such that in the analysis, each plot at each site had one vital rate value, yielding a sample size of 4 per site for each vital rate for each species. Climate data collected in successive years (Table 1) were averaged for each site because the overarching interest was in how the trajectory of population growth might be affected by changes in vital rates as influenced by climatic factors over time. Although yearly fluctuations in climatic variables likely produce fluctuations in vital rates, the time lag between the two is unknown, and population growth over time is a product of the averages of such fluctuations.

We employed a bootstrapped stepwise model selection procedure for analyzing these data to avoid pseudo-replication imposed by the structure of our study. For each of 1,000 bootstrap replicates, a random dataset was generated from our data by selecting 9 sites with replacement from our pool of sites. An information criterion approach (Burnham and Anderson 2002) was then used to determine which set of environmental and climatic predictor variables best explained the variance in each of the vital rates analyzed for each iteration. Full models contained elevation and all of the environmental and climatic predictor variables (Table 1) and any second order polynomial terms deemed necessary by examination of diagnostic plots of each vital rate plotted against individual predictor variables. A stepwise model selection procedure with both backward and forward selection was applied to the full model, and the resulting best model (based on Akaike's Information Criterion, AIC) for each iteration was recorded. Bar graphs depicting the number of best models containing different numbers of environmental/climatic variables were then qualitatively examined to compare the degree of association between vital rates and environmental/climatic variables for each species. Cases in which models without environmental/climatic variables were selected as the best model in 75 % of iterations were treated as evidence that these variables had little influence on that particular vital rate.

Population growth rate of Linaria dalmatica along elevation gradients

Population dynamics were modeled for each site using a difference equation model (to accommodate the two

Table 1 Environmental and climate characteristics of the nine *L. dalmatica* study sites

Site	1_1	1_2	1_3	2_1	2_2	2_3	3_1	3_2	3_3
Bare ground (%)	54.5	25.3	67.0	32.2	47.3	37.5	80.7	38.3	38.0
Canopy closure (%)	0.0	8.0	3.0	0.0	23.8	30.9	0.0	0.0	18.7
Elevation (m)	1737	2002	2237	1876	2015	2318	1785	1875	2159
Growing degree (days)*	1117.1	572.3	888.5	NA	960.6	781.4	1224.1	NA	895.8
Gs. frost free (days)	91	74	89	89	91	86	91	90	87
Gs. mean min. temperature (°C)	7.30	2.76	6.46	6.05	7.07	5.21	8.16	6.16	5.23
Gs. min. temperature (°C)	−1.8	−4.8	−1.8	−3.0	−1.5	−3.0	−0.8	−2.5	−3.3
Litter cover (%)	16.7	19.8	8.0	30.5	12.7	6.2	3.0	24.0	20.2
Soil pH	7.1	6.5	6.9	7.1	7.2	6.6	7.1	6.7	6.7
Precipitation (cm)	6.1	7.0	5.1	6.1	7.4	10.5	3.7	6.2	7.5
Total soil nitrogen (ppm)	1.5	4.5	2.5	2.0	1.5	5.5	1.5	3.0	1.5
Soil organic matter (%)	3.6	9.3	4.3	4.9	2.4	4.2	3.2	7.7	5.3
Soil phosphorous (ppm)	13.0	29.0	27.0	19.0	10.0	27.0	13.0	29.0	26.0
Soil potassium (ppm)	534.0	560.0	323.0	553.0	419.0	442.0	478.0	533.0	340.0
Vegetation cover (%)	28.8	54.8	26.8	37.3	40.0	56.3	16.5	37.7	41.8
Weeks of ad. soil moist.	6.0	7.0	7.5	6.0	6.5	7.0	4.0	6.0	7.0
Wint. frost (days)	211.5	251.0	224.0	NA	217.5	168.5	206.0	NA	230.5
Wint. mean min. temperature (°C)	−5.1	−6.4	−6.4	NA	−4.3	−3.3	−4.4	NA	−4.0
Wint. min. temperature (°C)	−29.3	−29.3	−29.3	NA	−25.3	−20.3	−26.8	NA	−23.8

For site, the first number is the transect identifier, and the second number is the site identifier (*1* low elevation, *2* middle elevation, *3* high elevation)

Gs growing season, *Wint.* winter, *min. temperature* minimum temperature, *ad. soil moist* adequate soil moisture (≥ -1.5 MPa), *NA* not available due to failure of data logger

* Calculated with base 10 °C

transitions) which was based on the vital rate data collected from each of the four individual plots. At each site, λ was estimated from vital rates in each of 3 years for each of the four plots. We wished to compare λ among sites accounting as best we could for both temporal variation among years and spatial variation among plots. We characterized the overall λ at each site as the arithmetic mean over plots of the geometric mean λ for each plot over years. We assessed the uncertainty in this measure with a parametric bootstrap as follows. For each site, we fit a linear mixed model (function lmer in package lme4 in R) to the 12 log transformed λs with the overall mean as a fixed effect, and variance components for year, plot, and residual error. For each of 1,000 bootstrap replicates, we generated 12 observed log λs by combining the site mean with 3 years effects, 4 plot effects, and 12 residual errors each drawn from centered normal distributions using the appropriate variances. The log λs were back transformed to λs and the arithmetic mean of the geometric mean λs was calculated and stored.

Separate mixed effects models were used to quantify the trend in λ in response to the fixed effects of elevation and each individual climatic or environmental variable, using the λ values from the parametric bootstrap. Site was included as a random effect to account for the temporal pseudo-replication inherent in the simulation and the spatial pseudo-replication imposed by study design. In addition, median λ values were assessed qualitatively for differences based on site characteristics using box and whisker plots. Although this qualitative assessment cannot generate any statements of statistical significance, we believe it is of value for its potential to elucidate trends which may be biologically significant which will aid in generating new hypotheses to test more quantitatively in the future. We looked for obvious shifts from $\lambda > 1$ to $\lambda < 1$ based on environmental characteristics. Instances where the highest or lowest median value of λ was positioned at either end of the range of the climatic or environmental variable being examined were viewed as indications that extreme values of λ may be related to extreme levels of the variable.

Results

Linaria dalmatica and *Castilleja miniata* vital rates

Linaria dalmatica sites were found to be variable in terms of both climate and environmental conditions (Table 1).

Vital rates also qualitatively appeared to vary from site to site (Fig. 2). *Castilleja miniata* sites also showed variability in climate and environmental conditions (Table 2), but vital rates appeared to be less variable in relation to both climate and environmental conditions than those of *L. dalmatica* (Fig. 3). For all of the measured *C. miniata* vital rates except seed production, the majority of best models from the boot-strapped analysis did not contain any climatic/environmental variables (Fig. 4). For *L. dalmatica,* the majority of best models included environmental or climatic variables for most vital rates, except the spring survival and seed production vital rates (Fig. 5). The frequency with which different climatic/environmental variables were included in best models for each species is displayed in Table 3.

Population growth rate of *Linaria dalmatica*

The mean projected population growth rate (λ) for *L. dalmatica* was found to be variable between sites (Fig. 6) but there was no clear trend in λ along the elevation gradient (Fig. 7). Based on the mixed effects models, there was a negative association between number of weeks of adequate soil moisture (≥ -1.5 Mpa) and λ ($P = 0.04$), and the suggestion of a positive association between winter mean minimum temperature and λ ($P = 0.07$). From the box plots, there were very few instances in which the distribution of λ showed any consistent pattern across levels of the climatic and environmental variables measured at each site. However, some weak patterns were noted. Lambda appeared to decrease as the number of weeks adequate soil moisture increased (Fig. 7), and to increase with increasing winter mean minimum temperature (Fig. 8). Winter minimum temperature appeared to have some influence on λ, in that the only sites where $\lambda < 1$ had the lowest measured minimum temperature (−29.5 °C, Fig. 8). Lambda did not show any notable relationships with any soil characteristics (Fig. 9). The highest value of λ was observed at the lowest value of vegetation cover (excluding *L. dalmatica*), the lowest value of percent litter cover, and the highest value of percent bare ground (Fig. 10).

Discussion

Associations between vital rates and the environment

Several of the vital rates for *L. dalmatica* were influenced by climate and environmental predictors, as has been

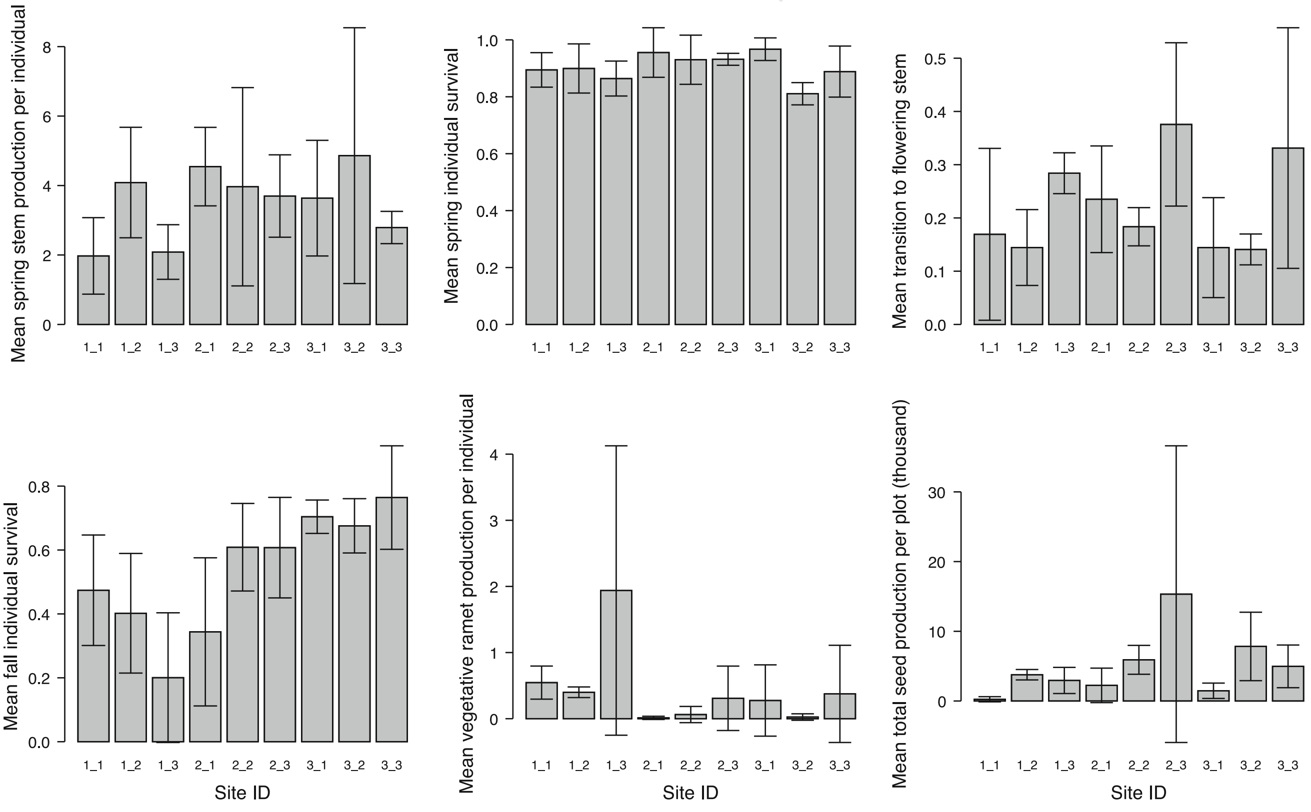

Fig. 2 Mean transition rates for each *L. dalmatica* site. *Error bars* represent 95 % confidence interval for the mean. For site ID, the first number is the elevation transect identifier, and the second number is the site identifier (*1* low elevation, *2* mid elevation, *3* high elevation). $n = 36$

Table 2 Environmental and climate characteristics of the nine *C. miniata* study sites

Site	1_1	1_2	1_3	2_1	2_2	2_3	3_1	3_2	3_3
Bare ground (%)	0.0	21.5	29.8	1.5	2.3	5.0	0.3	0.0	3.5
Canopy closure (%)	39.4	26.3	33.2	47.6	35.4	12.0	43.8	77.4	60.5
Elevation (m)	2096	2683	2812	2151	2303	2368	2159	2183	2239
Growing degree (days)*	NA	432.3	337.0	667.8	769.9	507.5	913.0	723.4	NA
Gs. frost free (days)	NA	76	63	85	83	81	88	86	NA
Gs. mean min. temperature (°C)	NA	4.7	4.1	4.3	4.8	3.9	5.5	4.2	NA
Gs. min. temperature (°C)	NA	−3.5	−2.5	−3.5	−3.5	−3.3	−2.8	−2.5	NA
Litter cover (%)	27.2	29.2	46.0	16.8	23.2	21.2	21.8	32.5	26.8
pH	6.3	6.0	6.0	6.9	6.2	6.4	6.3	6.4	5.8
Precipitation (cm)	NA	NA	NA	9.3	11.3	15.7	7.7	6.6	10.2
Soil nitrogen (ppm)	1.0	3.5	4.5	2.5	7.5	5.0	9.5	0.5	1.5
Soil organic matter (%)	9.3	6.6	4.0	6.2	9.0	7.3	11.4	7.2	27.2
Soil phosphorous (ppm)	16.0	52.0	30.0	4.0	17.0	33.0	29.0	40.0	18.0
Soil potassium (ppm)	258.0	603.0	316.0	238.0	400.0	358.0	471.0	371.0	372.0
Vegetation cover (%)	95.4	51.8	25.8	89.6	84.1	85.1	86.2	77.1	72.3
Weeks of ad. soil moist.	8.0	9.0	9.5	9.5	8.5	12.0	9.5	11.0	12.0
Wint. frost (days)	256.5	246.0	243.5	242.0	238.5	245.0	227.0	206.0	226.0
Wint. mean min. temperature (°C)	−8.6	−4.2	−3.0	−7.5	−3.8	−6.8	−1.4	−3.2	−1.8
Wint. min. temperature (°C)	−33.5	−29.0	−21.3	−30.0	−22.0	−30.0	−22.0	−19.0	−17.5

For site, the first number is the transect identifier, and the second number is the site identifier (*1* low elevation, *2* middle elevation, *3* high elevation)

Gs growing season, *Wint.* winter, *min. temperature* minimum temperature, *ad. soil moist* adequate soil moisture (≥−1.5 MPa), *NA* not available due to failure of data logger

* Calculated with base 10 °C

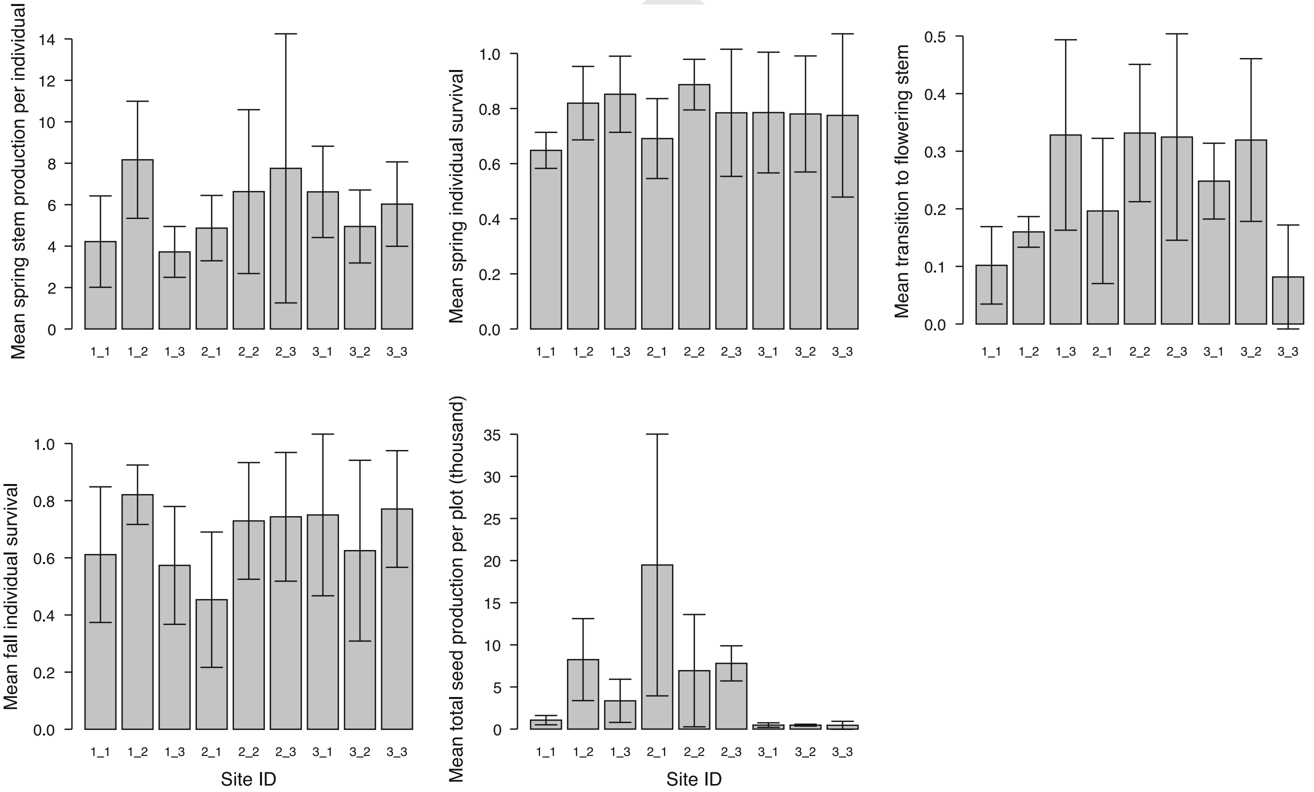

Fig. 3 Mean vital rates for each *C. miniata* site. *Error bars* represent 95 % confidence interval for the mean. For site ID, the first number is the transect identifier, and the second number is the site identifier (*1* low elevation, *2* mid elevation, *3* high elevation). $n = 36$

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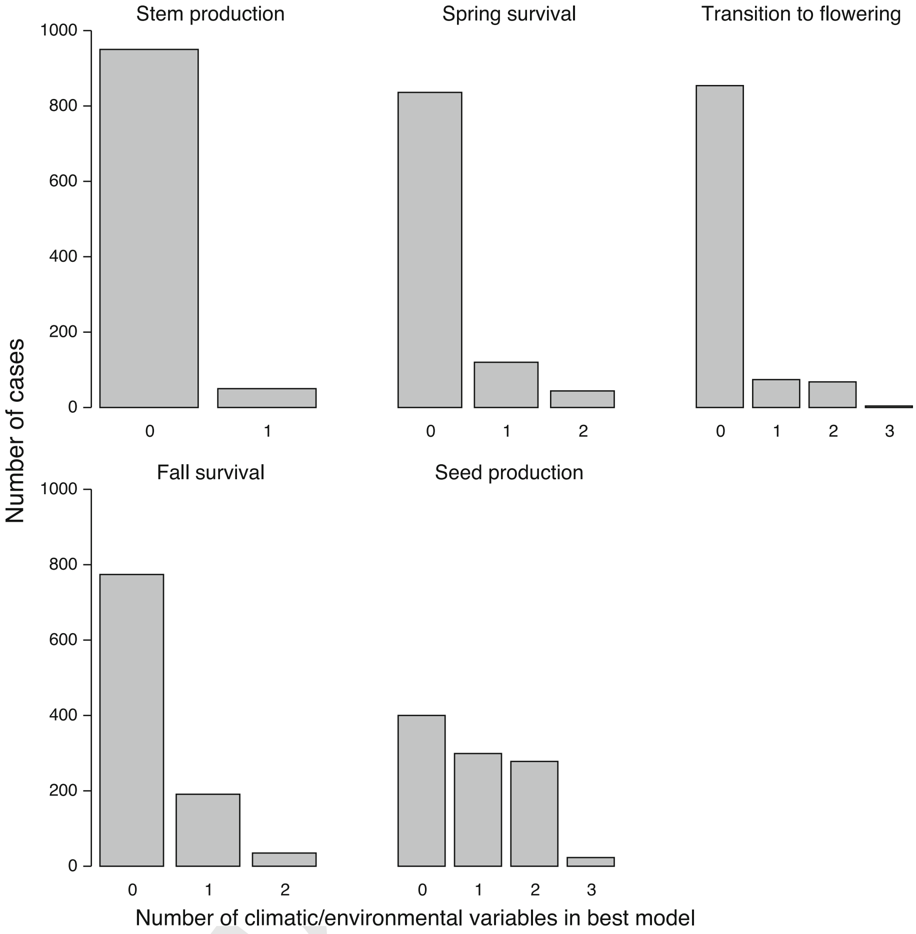

Fig. 4 Number of cases from a 1000 iteration boot-strap procedure where vital rate best models from stepwise AIC model selection contained different numbers of environmental and climatic variables for *Castilleja miniata*

shown for other plant species along environmental gradients (Mack and Pyke 1984; Carlsson and Callaghan 1994; Chambers et al. 2007; Purves 2009; Eckhart et al. 2011; Gimenez-Benavides et al. 2011). As we had hypothesized, *L. dalmatica* vital rates were associated with variation in climatic and environmental conditions to a greater extent than those of the closely related native species *C. miniata.* This is most likely due to the difference in the level of adaptation of each species to its environment (Eckhart et al. 2011 and references therein) based on the length of time that each species has had to adapt to conditions within its current range.

The fact that the vital rates for *C. miniata* did not seem to be as influenced by climatic or environmental variables is not surprising. Climatic conditions varied less during the study within *C. miniata*'s current range than in the range of *L. dalmatica* (F.W. Pollnac and L.J. Rew, unpublished data). Notably, winter minimum temperatures were stable within *C. miniata*'s range (F.W. Pollnac and L.J. Rew, unpublished data). Thus, perhaps the lack of variability in vital rates based on climate and environmental conditions is due in part to the fact that these conditions were less variable over the surveyed range for *C. miniata* than they were for *L. dalmatica*. This would suggest that *C. miniata,* having had more time to equilibrate within its range by going through colonization and extinction events, has occupied a geographic range where its vital rates are relatively stable due to more constant climatic conditions. It is also possible that *C. miniata* has had time to adapt to the variability present within its current range such that its vital rates can remain stable in spite of climatic variation, as has been hypothesized by Eckhart et al. (2011). Although we cannot formally test either of these hypotheses, our data suggest that it is a combination of both, given that there was less variability in most (but not all) of the climatic conditions along this species' elevation range (F.W. Pollnac and L.J. Rew, unpublished data), and that whatever variability there was did not seem to affect the vital rates of the species to any great extent. In contrast, *L. dalmatica* is a relative newcomer to the area, and therefore its vital rates may be more susceptible to climatic/environmental variations because it has not had time to either adapt or go extinct in marginal environments where its vital rates may be adversely affected. This generally reflects the concept of the taxon cycle which states that species with longer residence times tend to exhibit contracted ranges in interior

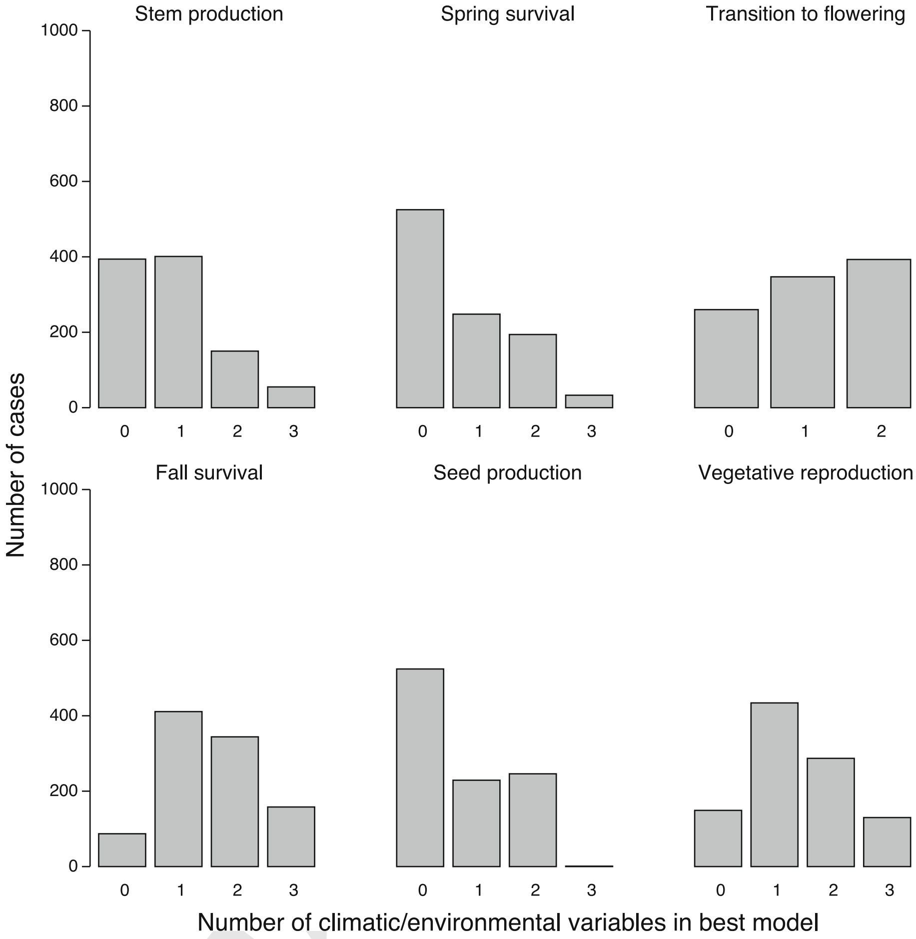

Fig. 5 Number of cases from a 1000 iteration boot-strap procedure where vital rate best models from stepwise AIC model selection contained different numbers of environmental and climatic variables for *Linaria dalmatica*

Table 3 Frequency with which the listed variables (*top row*) were included in best models for each dependent variable

	Dependent variable	Gs. mean min. temperature (°C)	Polynominal Gs. mean min. temperature (°C)	Wint. mean min. temperature (°C)	Gs. frost free (days)	Wint. frost (days)
L. dalmatica	Stem production	0.33	0.00	0.08	0.04	0.00
	Spring survival	0.42	0.00	0.23	0.09	0.00
	Fall survival	0.74	0.00	0.50	0.25	0.03
	Vegetative reproduction	0.71	0.00	0.45	0.27	0.03
	Seed production	0.40	0.03	0.11	0.00	0.00
	Transition to flowering	0.47	0.44	0.22	0.00	0.00
C. Miniata	Stem production	0.06	0.00	0.00	0.00	0.00
	Spring survival	0.07	0.00	0.06	0.04	0.00
	Fall survival	0.22	0.00	0.20	0.09	0.00
	Seed production	0.54	0.00	0.37	0.02	0.00
	Transition to flowering	0.08	0.00	0.10	0.07	0.00

Model selection was performed for 1000 bootstrapped replicates using a stepwise selection procedure with backward and forward selection based on AIC

Gs growing season, *Wint.* winter, *min. temperature* minimum temperature

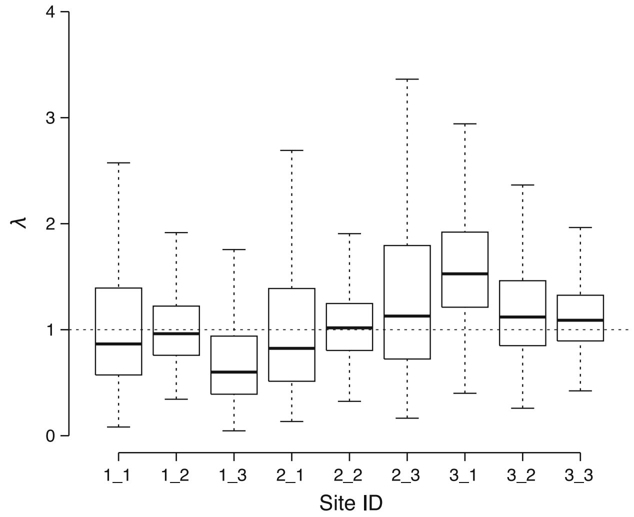

Fig. 6 Boxplots of the distribution of the projected growth rate (λ) values for *L. dalmatica* by site (site ID) from a parametrically bootstrapped matrix, based on estimated plot and year variance components. $n = 1000$ for each site. For site ID, the first number is the transect identifier, and the second number is the site identifier (*1* low elevation, *2* mid elevation, *3* high elevation)

habitats whereas colonizing/ruderal species exhibit expanded ranges in marginal habitats (Wilson 1959). It also suggests that if climate were to change in the future, *L. dalmatica*'s range would be less likely to shrink (with its comparably broader tolerance to a variety of climatic conditions, including temperature) than would *C. miniata*'s.

Population growth rate of *Linaria dalmatica* and its potential to spread to higher elevations

There was no decrease in λ with increased elevation as we had hypothesized. The lack of a decrease in λ at the current high elevation limit of this species suggests that it may not yet have reached the limits of its potential range (Gaston 2003). However, there was weak evidence that λ for this species was influenced by some of the measured climate or environmental variables. In addition, although overall seed production for *L. dalmatica* increases with elevation, germination rates decrease at the highest elevations (F.W. Pollnac and L.J. Rew, unpublished data). These results

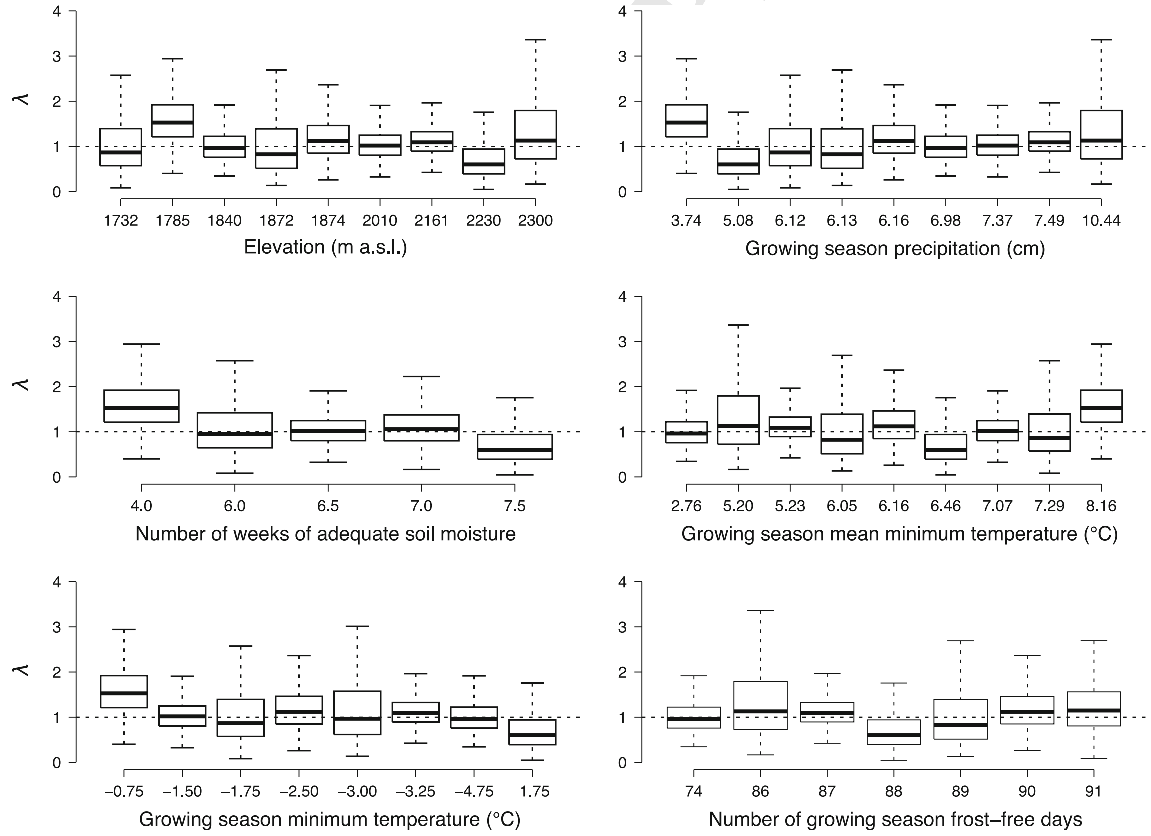

Fig. 7 Boxplots of distribution of growth rate (λ) values for *L. dalmatica* by elevation and growing season climate variables from a parametrically bootstrapped matrix, based on estimated plot and year variance components

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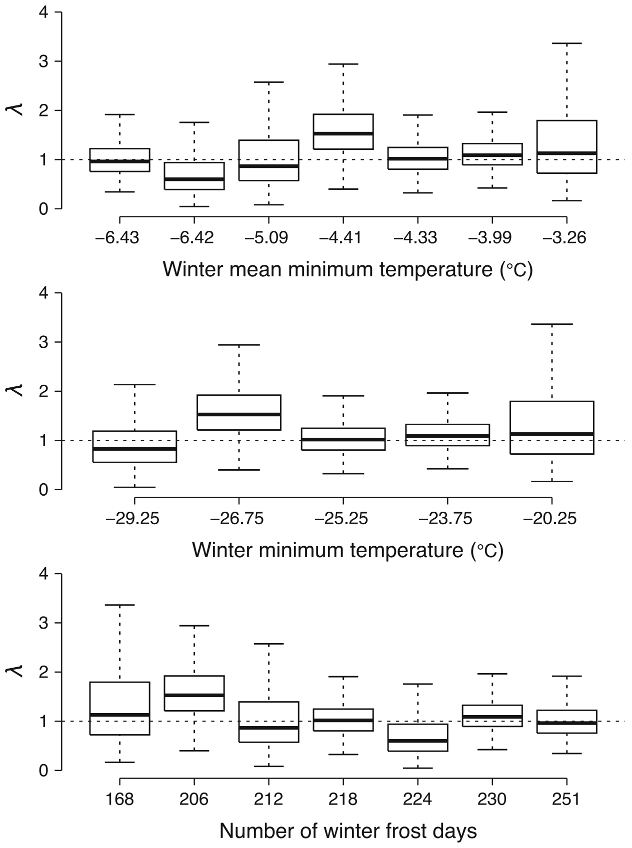

Fig. 8 Boxplots of distribution of growth rate (λ) values for *L. dalmatica* by winter climate variables from a parametrically bootstrapped matrix, based on estimated plot and year variance components

suggest that: (1) dispersal (Eckhart et al. 2011) and/or propagule pressure may not be the primary limit to this species' current range, and (2) there may still be some climatic limit which is preventing the seeds of this species from germinating and/or seedlings from establishing at higher elevations.

The general lack of strong relationships between λ and many of the measured climate variables suggests that *L. dalmatica* may be able to tolerate a broad range of climatic conditions. Other studies have suggested that non-native plants which successfully invade mountain systems must be broadly adapted to cope with the variable climatic conditions found along the elevation gradients in these areas (Alexander et al. 2011). However, winter minimum temperature had an interesting relationship with λ, in that the only sites where $\lambda < 1$ corresponded to the lowest measured winter minimum temperature. This suggests that this species may only be broadly adapted to a point, and that success of this species above its current elevation range may be limited by extremely low winter temperatures, as is common with plants in cold environments (Stocklin and Baumler 1996; Hobbie and Chapin 1998). Anything that would tend to increase winter temperatures, be it insulation due to increased snow pack or increased air temperatures under a warming climate, may favor the over winter survival of this species. Given the sensitivity of population levels to the over-winter survival rate (data not shown), this could result in large increases in population size. We have hypothesized that the location of this survival barrier could be shifted in the future based on increased snow pack prior to extremely cold temperature events and/or a warming climate. However, properties of the vegetative community also appear to be exerting influence on λ of *L. dalmatica* throughout its current elevation range.

Population growth appeared to increase with decreased number of weeks of adequate soil moisture. Those sites with more persistent soil moisture generally had higher levels of vegetative cover and lower levels of bare ground (Table 1). The fact that the highest value of λ for this species occurred where both vegetation and litter cover were the lowest and where percent bare ground was the highest suggests that the relationship between λ and weeks of adequate soil moisture is related to increased growth of other vegetation and consequent litter production. These patterns suggest that while the current range of establishment of this species may be limited by climate, established populations may be primarily limited by characteristics of the vegetative community. Robocker (1974) noted that this species has low competitive ability in established perennial communities. Other studies have also shown negative associations between single non-native species abundances and vegetative community characteristics such as native species richness (Knight and Reich 2005) or native species diversity (Ortega and Pearson 2005), and that increased plant litter can decrease establishment of non-native plants (Hager 2004; Bartuszevige et al. 2007). Our results follow the same pattern, which suggests that if areas within or just outside of *L. dalmatica*'s current range in the GYE were to become more disturbed, which increases bare ground, this species would be likely to expand its range and/or the extent of current populations as a result.

In the absence of establishment limitations, the lack of any strong climate/environmentally induced trends in λ suggests that this species could potentially spread outside of its present range under current climatic conditions. The lack of a consistent decrease in λ at the upper elevation limits of this species is further evidence of this. Additionally, while germination of seeds from high elevation

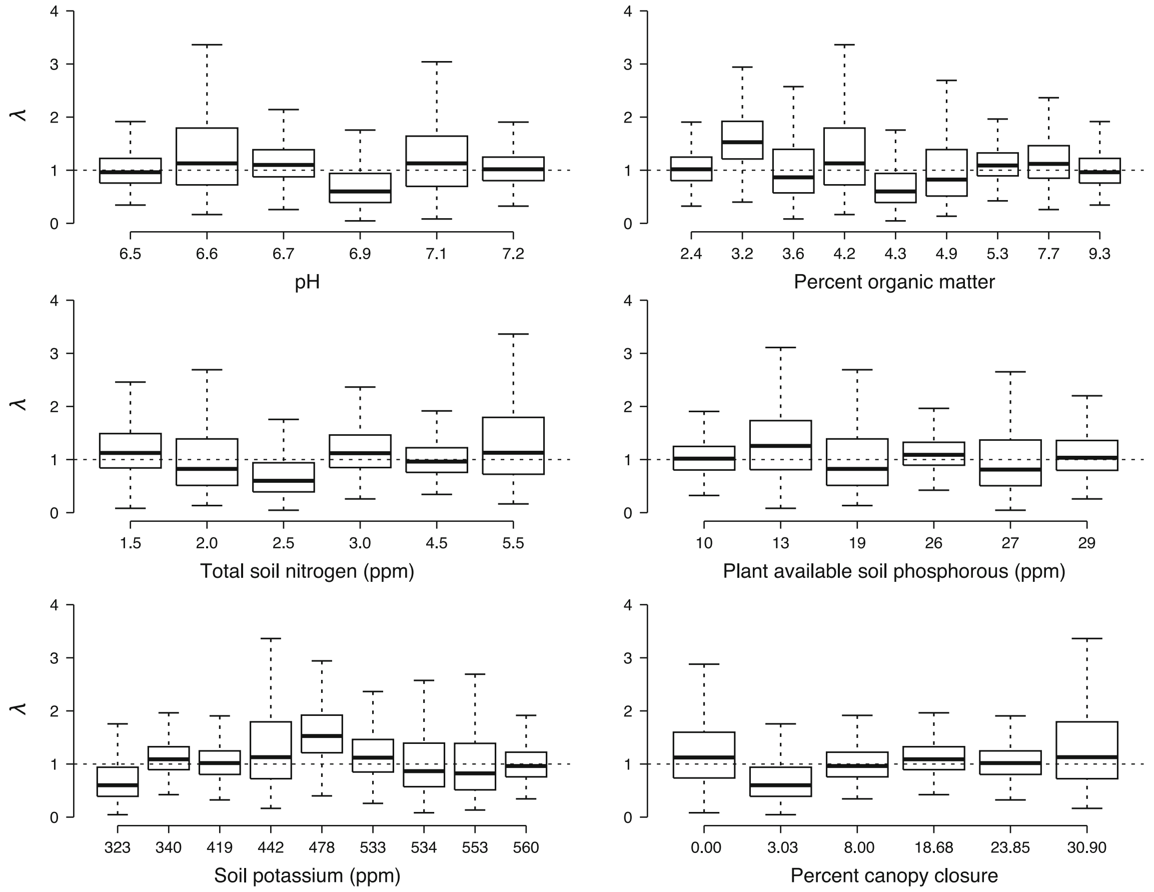

Fig. 9 Boxplots of distribution of growth rate (λ) values for *L. dalmatica* by environmental variables from a parametrically bootstrapped matrix, based on estimated plot and year variance components

sources was lower, the fact that propagule pressure for this species is not constrained at higher elevations suggests that it could successfully spread upward in the absence or reduction of climatic barriers (F.W. Pollnac and L.J. Rew, unpublished data). It is still possible that climate may be limiting the establishment of *L. dalmatica* above its current elevation limits, but our current data do not provide conclusive evidence of this. In the future, more specific tests of germination, establishment, and survival need to be conducted to test the hypothesis that this species is currently experiencing an establishment based climatic limit to further spread to higher elevations.

Although established *L. dalmatica* plants are viewed as competitive, in that increased *L. dalmatica* density has been shown to be associated with decreased density of other plants (Robocker 1974; Wilson et al. 2005), whether or not this species is capable of displacing other vegetation is still questionable. Seedlings were rare in this study, and are noted to not be particularly competitive with established vegetation (Gates and Robocker 1960; Robocker 1974) so this species may have difficulty establishing in heavily vegetated areas. However, the alpine zone is subject to frequent natural soil disturbances (e.g., frost heaving and animal burrowing), is relatively sparse in established vegetation, and is likely to experience increased anthropogenic disturbance in the future. Thus, in the absence of climate constraints, the alpine/subalpine zone would seem to be an ideal habitat for potential *L. dalmatica* establishment. Since *L. dalmatica* has been shown to be broadly adapted and we have not been able to provide any conclusive evidence of climatic limitation for this species, populations at its upper range limits should not be ignored in management efforts. In addition, areas above its current elevation range should be surveyed frequently for the presence of this species in order to prevent the spread of this species into higher elevation environments. Due to the sensitive nature of alpine habitats and the large proportion of plant diversity and endemic species contained therein (Körner et al. 2011), the impacts of non-native plant species in these areas could be particularly harsh. This, in

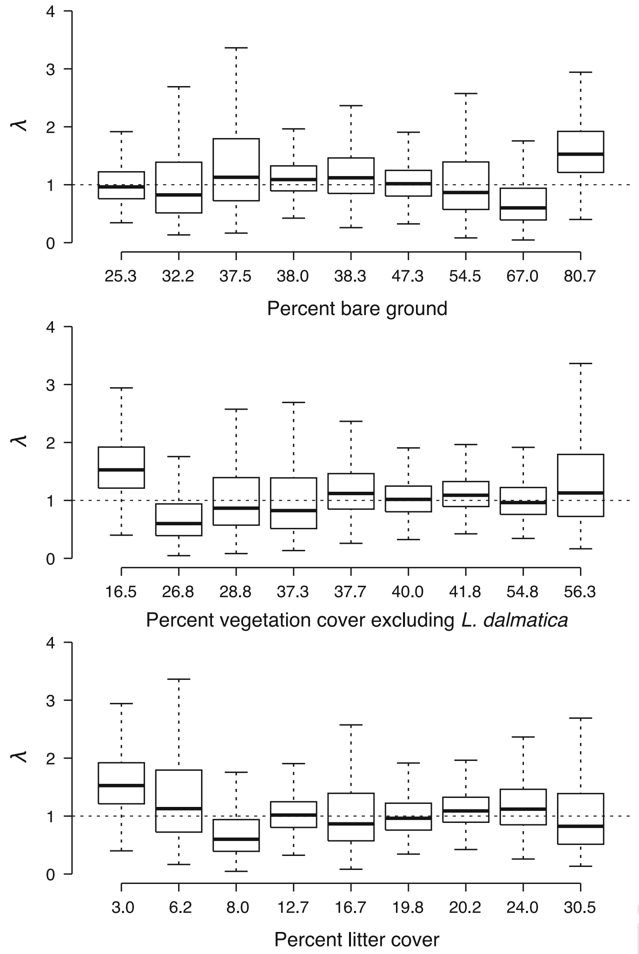

Fig. 10 Boxplots of distribution of growth rate (λ) values for *L. dalmatica* by environmental variables from a parametrically bootstrapped matrix, based on estimated plot and year variance components

itself, may be enough justification to increase efforts to limit invasions of non-native plant species, such as *L. dalmatica*, into these areas.

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