Popul Ecol
DOI 10.1007/s10144-014-0442-5

THE SOCIETY OF POPULATION ECOLOGY

ORIGINAL ARTICLE

Demographic effects of warming, elevated soil nitrogen and thinning on the colonization of a perennial plant

Elise Sylvie Gornish

Received: 18 September 2013 / Accepted: 27 April 2014

Abstract Global change is causing significant modifications to native plant communities. These effects can be direct through changes in productivity, or indirect through the spread of invading species. Identifying vital traits important for individual species' response to environmental variation could be useful for making predictions about how entire communities may respond to global change. I studied the effects of factors associated with global change on the demography of an experimentally introduced species, *Pityopsis aspera*. In a Florida old-field, I investigated how warming, increased soil nitrogen and thinning of the extant plant community affected survival, growth and reproduction of *P. aspera* using a life table response experiment. The estimated population growth rate (λ) of *P. aspera* was reduced by nitrogen addition, as a result of decreased fecundity. However, λ increased in response to the warming treatment, as a result of increased fecundity. In the presence of thinning, both warming and nitrogen served to increase λ as a result of an increase in the growth of young individuals. This experiment illustrates how different vital rates contribute to the population level responses of an experimentally introduced plant to warming, and nitrogen deposition. Results also show how these demographic responses may occur via indirect effects through established species. This work highlights the importance of studying interactions among temperature, soil nitrogen and demography across the entire life cycle in order to capture the complex and, often, non-additive relationships mediating global change effects.

Keywords Climate change · Indirect effects · Invasion · LTRE · *Pityopsis aspera* · Range shift

Introduction

Of the many factors associated with global change, studies suggest that atmospheric warming and increases in soil nitrogen deposition can be some of the most detrimental to natural systems (MEA 2005; IPCC 2007). The effects of recent increases in temperature and soil nitrogen have been documented in a variety of habitats and include shifts in timing of reproduction (e.g., Moller 2008), variation in species richness (e.g., Hansen et al. 2001) and changes in species abundance (e.g., Gilbert et al. 2008). One of the most pressing consequences of global warming is that many species are currently colonizing new areas, both in unoccupied pockets within their range, as well as outside range edges (Parmesan et al. 2000) to track their ideal environment. This worldwide reshuffling of species will lead to novel species assemblages, affecting native species (Verlinden and Nijs 2010), and ecosystem function (Parmesan and Matthews 2006). Due to the considerable ramifications of these invading species; understanding the effects of climate change will require the consideration of species colonizing new habitat.

Research has highlighted several factors that have utility for predicting species response to a changing environment. These include the magnitude and timing of

Electronic supplementary material The online version of this article (doi:10.1007/s10144-014-0442-5) contains supplementary material, which is available to authorized users.

E. S. Gornish (✉)
Florida State University, Tallahassee, FL 32306, USA
e-mail: egornish@ucdavis.edu

Present Address:
E. S. Gornish
University of California, Davis, Davis, CA 95618, USA

Published online: 18 May 2014

climate change, the initial location of an organism (Currie 2001), and niche breadth (Boulangeat et al. 2012). Demographic traits have also been shown to be particularly important for regulating population responses to environmental changes (Wisdom et al. 2000; Hoving et al. 2013), because life history traits can determine fitness-environment relationships (e.g., Buckley et al. 2010). Clearly, an understanding of how vital rates respond to environmental changes could facilitate the development of a predictive framework for overall species' responses to global change (e.g., Nicole et al. 2011). However, studies that explicitly link vital rates and increasing temperature and nitrogen deposition are still relatively uncommon, especially for newly introduced species.

Vital rate responses to the environment can be idiosyncratic. Research has documented how a species' vital rates can respond in dissimilar ways to modifications in density (e.g., Goldberg et al. 2001), stress (e.g., Martinez-Ramos et al. 2009), location (e.g., Shea et al. 2010), and to multiple disturbances (e.g., Mandle and Ticktin 2012). Responses to global change can also occur through differential effects across life stages (e.g., Lloret et al. 2009; Sousa et al. 2012) or by inducing life history trade-offs (e.g., Woodhams et al. 2008). For example, the duration of time spent in early life stages has been shown to be particularly vulnerable to warming, compared with the relatively unaffected phenology of later life stages for alpine chickweed (Post et al. 2008).

Elevated soil nitrogen and temperature can affect the vital rates of a newly introduced species both directly and indirectly, through changes to the extant community (Theoharides and Dukes 2007). For example, increased nitrogen may enhance the growth of an invading species, but may also enhance the growth of native competitors (Dunnett and Grime 1999; Gaston 2003). Understanding the underlying processes driving demographic changes within a population clearly requires an investigation of how the native community might interact with warming and nitrogen deposition to modify vital rates of potential invaders.

I investigated both the separate and combined effects of warming, elevated soil nitrogen, and change in the extant plant community, through thinning of biomass, on the vital rates of an experimentally introduced plant species. I colonized field plots with a plant species that was previously absent from an experimental site in which I simulated environmental changes expected to occur with global change to address the following questions: (1) Do changes in temperature, and nitrogen differentially affect vital rates of an experimentally introduced species to ultimately affect population growth rate? (2) How do changes in the extant community modify effects of warming and nitrogen deposition on the vital rates of this newly introduced species?

Methods

The site

This study was conducted across 3 years in a 1.6 hectare early successional field (last used for agriculture ca. 150 years ago), dominated by grasses and legumes, surrounded by a mixed loblolly-shortleaf pine forest at Tall Timbers Research Station, just south of the Florida-Georgia border. The soil type is a slightly acidic sandy loam (pH ranges from 5.2 to 6.0); prior to the start of the experiments, the field had been disked annually. Precipitation at the site averages 100.0 cm per year, and the average annual daytime temperature is 20.0 °C.

Treatments

The experiment was a randomized block design. There were three main factors simulating global change: nitrogen (two levels: nitrogen addition, and no nitrogen addition), warming (two levels: warming, and no warming), and thinning (two levels: natural plant cover, and thinned plant cover). To assess demographic effects of these treatments, I experimentally introduced a plant species into plots in different life stages (three levels: seeds; first-year plants; and adult plants). To minimize leaching of nitrogen between plots, the plots were arranged in a split-plot design, with nitrogen addition treatments arranged together within blocks. Each block of treatments was replicated 5 times in 2010 and 5 times in 2011 (Fig. 1). Each plot was 2.0 m^2, but measurements were only collected from the center 1.0 m^2 as a precaution against edge effects. Plots were separated by 1.0 m, and rows between plots were mowed annually.

Nitrogen

I applied sodium nitrate ($NaNO_3$) at the soil surface of treatment plots in the amount of 4.0 g/m^2 per year (approximately 4× greater than background fertility), based on projected dry + wet nitrogen deposition rates for northern Florida in the next 50–100 years (Galloway et al. 2004; Holland et al. 2005). $NaNO_3$ can increase soil and foliar nitrogen (Fig. S1 in Electronic Supplementary Material (ESM)) without increasing the availability of other mineral nutrients and without significantly modifying soil pH. Six applications of equal amounts of $NaNO_3$ were applied during the growing season (May–October) per year. Each application was followed by the addition of

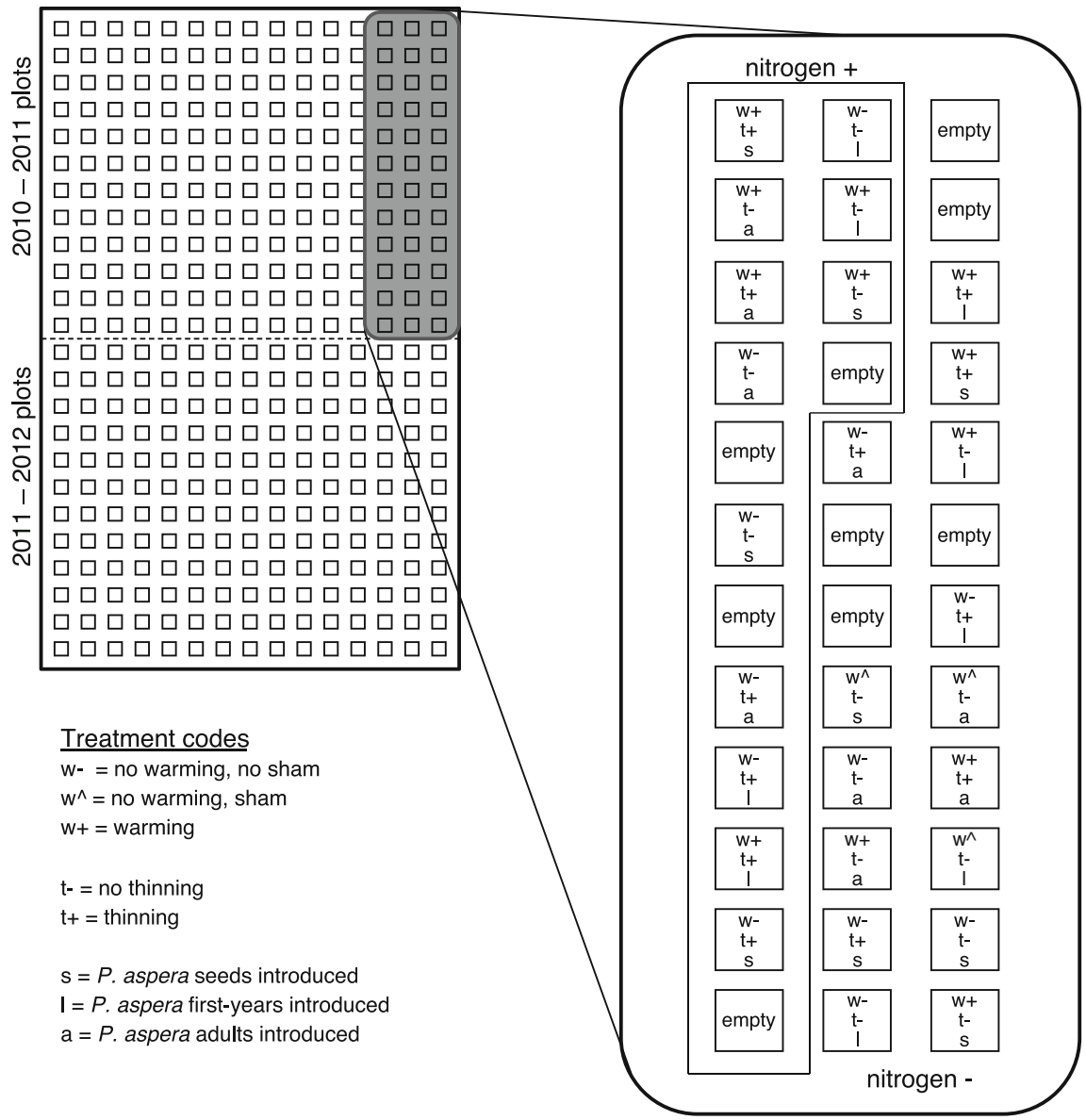

Fig. 1 Experimental setup illustrating split plot design and an example of random placement of treatments within a single replicate. Each block consists of 27 plots: 2 nitrogen levels × 2 warming levels × 2 thinning levels × 3 life stage levels + 3 extra sham plots (see text). Each *square* represents a 2.0 m^2 plot

800.0 mL of water to flush the nitrogen below the soil surface. The same amount of water was added to nitrogen control plots.

Warming

Warming was applied to experimental plots using open-top hexagonal chambers constructed of a pressure treated wood frame (2.5 × 5.0 cm) wrapped with 4.0 mil clear polyethylene plastic sheeting (Marion et al. 1997) to simulate projected average temperature increases in northern Florida in the next 50–100 years. The chambers acted as solar traps and increased the average ambient temperature by 2.5 °C (Fig. S2 in ESM) without significantly modifying soil moisture (Fig. S3 in ESM). The base of the chamber was 2.4 × 2.0 m, and each panel was 0.6 m tall. Due to uneven microtopography, the chambers sat approximately 3.0 cm above the ground, allowing for air circulation through the base of the greenhouses (Havstrom et al. 1993). The plastic was replaced annually due to weathering.

In total warming control plots (no nitrogen added, no thinning), sham greenhouse chambers were installed with a 72.6 × 48.3 cm square cut out of each plastic panel, which reduced the cover of the sheeting by 85 %. The temperature in sham plots did not differ significantly from complementary control plots, without sham greenhouses.

Thinning

In the thinned cover treatment plots, half of the above-ground biomass of all extant plants was removed. Plants to be removed were chosen by dividing the plot into 20 equal sections and randomly selecting 10 sections from which all above-ground plant parts (excluding experimentally introduced individuals, see below) were hand-cut at the soil surface and removed from the plot. Plants were thinned twice (in April and August) during 2011, and 2012 to maintain reduced biomass during the growing season. Plants in the natural cover plots were untouched.

Life stage

The most critical portion of this experiment was to quantify direct and indirect effects of elevated soil nitrogen and temperature on vital rates of an experimentally introduced species. *Pityopsis aspera* (Asteraceae Shuttle. ex. Small), a native species commonly known as pineland silkgrass, was used to colonize plots at different life stages in order to estimate appropriate vital rates. This herbaceous dicot is common in xeric sandhill habitats (Myers and Ewel 1990) in northern Florida and South Georgia. *Pityopsis aspera* is visited by (and therefore, presumably pollinated by) a variety of insects, including bees (Halictidae), butterflies (*Agraulis vanilla* and *Pyrgus communis*), flies (Tephritidae), and beetles. *Pityopsis aspera* is self-incompatible (Bowers 1972), and it reproduces both vegetatively and sexually. *Pityopsis aspera* was used as an experimental invader because it typically occurs in the understory of long-leaf pine forests and, therefore, could be reasonably expected to colonize the old-field through range filling as a response to a changing climate (e.g., Dullinger et al. 2012).

The demography of *P. aspera* is investigated in detail elsewhere (Gornish 2013). Briefly, the life cycle of *P. aspera* can be divided into several broad stages (Fig. 2): first-years (individuals in their first year of life that might or might not produce flowers), and adults (larger individuals older than a year that might or might not produce flowers). Seeds produced by flowering individuals germinate into first-year individuals within a single year, hence the absence of a seed stage. First-year individuals have significantly lower survival than adult plants. First-year plants must become adults after 1 year (undergo growth). Every year, rosette adults must either remain in their stage class (undergo stasis) or become flowering adult individuals (undergo growth). Every year, flowering adult individuals can either remain in their stage class (undergo stasis) or become rosette adults (undergo retrogression). Both rosette and flowering adults can reproduce asexually through rhizomatous growth; although first-years cannot.

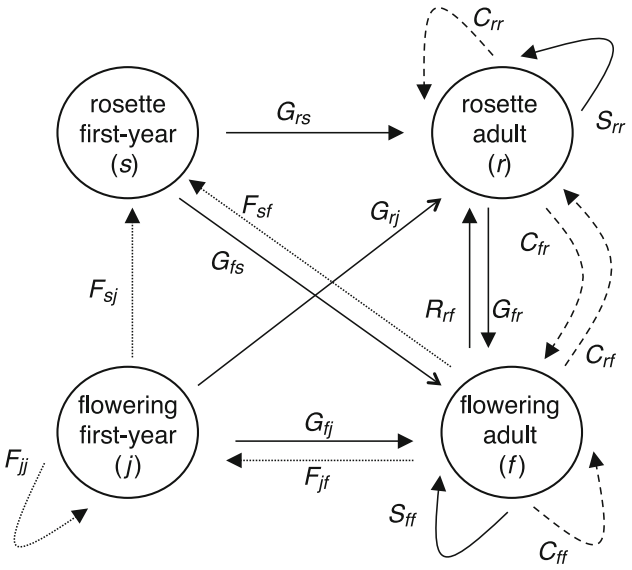

Fig. 2 Irreducible life cycle of *P. aspera,* with four stages (*s*, rosette first-year; *j*, flowering first-year; *r*, rosette adult, and *f*, flowering adult). Transitions between stages represent *G*, growth; *S*, stasis; and *R*, retrogression, all represented by *solid arrows*. *F*, sexual reproduction, is represented by a *dotted arrow*; *C*, clonal reproduction, is represented by a *dashed arrow*

Pityopsis aspera was experimentally introduced into plots in four different life stages (seed, first-year, adult, and none). This was done to isolate demographic stages most characteristic of each of the three stage process of colonization (introduction, establishment and persistence). For example, plants are introduced into areas in which they did not previously occur largely through seed dispersal. Since most of the plants in this stage are seeds, adding seeds simulated this part of the colonization process. In the establishment phase of colonization, populations often consist of mostly young, newly germinated individuals. To simulate this stage of colonization, I planted only seedlings. In the persistence stage, populations are generally more mature and can move into other areas through high seed production and dispersal. To simulate this stage of colonization, I planted only adults.

First-year individuals were generated by germinating *P. aspera* seeds collected from several natural populations in Tall Timbers in September 2009 and 2010. In January 2010 and 2011, seeds were germinated in petri dishes of sterilized coarse sand moistened with deionized water and kept in a growth chamber (14 h day at 30.0 °C and 10 h night at 21.0 °C). Seeds were checked every 2 days and transplanted once cotyledons were visible from petri dishes to square plastic pots (14.0 × 13.3 cm) filled with an equal mix of fine sand and soil (Farfad 52). These seedlings were briefly kept in a Florida State University greenhouse until planting in the field. Adults were also collected from four

natural populations (separated by a distance of at least half a kilometer to maximize genetic diversity) in Tall Timbers in September 2009 and 2010 and grown in the greenhouse (in the same soil mixture and pots as first-years) until planting. First-year plants and adults were planted in the field in mid April 2010 and 2011 at a density of 20 individuals per plot, 10 individuals in the center 1.0 m^2 of the plot and 10 in the interior periphery of the 2.0 m^2 plot. This density was chosen to match average densities of individuals in natural populations within Tall Timbers. Plastic sticks were inserted into the soil at the base of each planted individual and a unique numbered metal tag was attached to each stick to facilitate re-identification through time. Twenty holes were excavated and refilled in all plots in which plants were not installed, to simulate disturbance due to planting. Nitrogen and temperature treatments were applied 1 month (mid May 2010 and 2011) after planting to allow individuals to acclimate stress associated with planting activities. Plants censused as first-years in year t were censused as adults in year $t + 1$.

Plots treated with *P. aspera* seeds received 100 seeds, broadcasted evenly over the plot by hand 30.0 cm above the soil. Seeds were added in late October, when this species naturally disperses. Germination was assessed only throughout the following 2 months because *P. aspera* does not support a seed bank (E. Gornish, unpublished data). Although the achenes of the plant have two pappi to facilitate wind dispersal, seed dispersal into the experimental site from natural populations of *P. aspera* was unlikely as these populations were found at a minimum distance of 3.0 km from the experimental plots.

Data collection

Eighteen vital rates (Table 1) were estimated for *P. aspera* (Gornish 2013) using the experimental plots to parameterize stage-based transition matrices (**A**) for all plants exposed to each global change treatment. Because the planted 'populations' of *P. aspera* used for this experiment were likely not at equilibrium, deterministic matrix models were created from transition estimates because these types of models generally outperform stochastic matrices when only a limited number of years of data are available (Doak et al. 2005).

Vital rate data were aggregated among the replicate plots for each treatment within transition periods to generate a summary matrix of transition probabilities under each treatment. The stage-based matrix model for all analyses is:

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$$

where $\mathbf{n}(t)$ is a vector of all the individuals in the population at time t, classified by stage, $\mathbf{n}(t+1)$ is the vector for the population at the next time interval, and **A** is the matrix that shows how individuals in each stage class at one time may become or contribute to each stage class by one time unit (1 year) later. For these populations, **A** is a 4×4 matrix of demographic parameters in which nonzero entries describe transitions observed at least once during the study:

$$\mathbf{A} = \begin{pmatrix} 0 & F_{sj} & 0 & F_{sf} \\ 0 & F_{jj} & 0 & F_{jf} \\ G_{rs} & G_{rj} & S_{rr} + C_{rr} & R_{rf} + C_{rf} \\ G_{fs} & G_{fj} & G_{fr} + C_{fr} & S_{ff} + C_{ff} \end{pmatrix}$$

Demographic parameters included: F_{ij} average number of propagules produced that survived to the next census; $G_{ik} = \sigma_i \times \gamma_{ik}$ (probability of surviving and growing to a different stage); $S_{ik} = \sigma_i \times (1 - \sum_{i \neq k} \gamma_{ik})$ (probability of surviving and remaining in the same stage); $R_{i-1,i} = \sigma_i \times \alpha_{i-1,i}$ (probability of surviving and regressing to the previous stage); and C_{ik} asexual reproductive output. Vital rates included: $\sigma_i = P$(survival of an individual in stage i); $\gamma_{i+1,i} = P$(growth from i to $i+1$| survival); and $\alpha_{i-1,i} = P$(regression from i to i–1|survival). One transition matrix for *P. aspera* was created for each treatment combination of nitrogen addition, warming and thinning, per transition period (2010–2011 and 2011–2012), for a total of eight matrices for the each transition period: one each for nitrogen addition and no nitrogen addition treatments, with and without thinning, and warming and no warming treatments, with and without thinning.

Table 1 Vital rates estimated for *P. aspera*

Parameter
Rosette first-year survival (σ_s)
Rosette first-year growth to rosette adult (γ_{rs})
Rosette first-year growth to flowering adult (γ_{fs})
Flowering first-year sexual reproduction of rosette first-year (F_{sj})
Flowering first-year sexual reproduction of flowering first-year (F_{jj})
Flowering first-year survival (σ_j)
Flowering first-year growth to rosette adult (γ_{rj})
Flowering first-year growth to flowering adult (γ_{fj})
Rosette adult survival (σ_r)
Rosette adult growth to flowering adult (γ_{fr})
Rosette adult asexual reproduction to rosette adult (C_{rr})
Rosette adult asexual reproduction to flowering adult (C_{fr})
Flowering adult sexual reproduction of rosette first-year (F_{sf})
Flowering adult sexual reproduction of flowering first-year (F_{jf})
Flowering adult survival (σ_f)
Flowering adult regression to rosette adult (α_{rf})
Flowering adult asexual reproduction to rosette adult (C_{rf})
Flowering adult asexual reproduction to flowering adult (C_{ff})

Flower number was counted for all flowering individuals per plot. Five pollinated flower heads (visually identified by color, petal turgor and flower angle) were also collected, per plot, and seed number in each head was counted (across treatments, mean = 34.0, SD = 4.0). The average seed number of each group of flower heads was used as an estimate of average number of seeds produced per individual flower head for each plot. Seeds collected from each treatment were also germinated in a growth chamber to determine average percent germination. After demographic data were collected, all pollinated flowers were collected by hand from all individuals of *P. aspera* residing in experimental plots to remove seed rain. This ensured that any new individuals of *P. aspera* that appeared in the plots were the result of asexual reproduction.

Numbers of asexually produced individuals were calculated for each stage class through the identification of new individuals (first-years produced by vegetative growth) in each plot and the assumption that these new individuals were produced by the nearest *P. aspera* present in the previous year. Each year, these new individuals were marked with a plastic stick and given a unique numbered metal tag. ANOVA results show an absence of an effect of history (planted vs. asexually reproduced) on adult survival and fecundity. Therefore, the models did not distinguish between asexually reproduced adults and planted adults in the analysis.

Transition matrices of *P. aspera* from experimental control plots were compared to matrices developed with data from a natural (non-experimental) population approximately 5.0 km away from the study site (Gornish 2013). A mantel test demonstrated no difference in matrix elements between the experimental control population and the non-experimental natural population.

Analysis

Although two transition periods were available from the 3 years of data collection, analyses were only conducted on data from the final transition period (2011–2012). This was done because competition experienced by *P. aspera* from the extant plant community was likely much lower (and more contrived) in the first year of the experiment due to the annual disking of the field prior to the initiation of the experiment.

The asymptotic population growth rate (λ) was derived from each matrix. To compare λ across treatments, non-parametric randomization tests were conducted, based on random permutations (Caswell 2001), which have been shown to be more powerful than comparing bootstrapped confidence intervals (Manly 1991). To understand how λ varies as a result of the experimental treatments, a test statistic was used:

$$\theta = |\lambda^{(t)} - \lambda^{(c)}|$$

Under the null hypothesis, no difference exists between the λ of a treatment matrix ($\lambda^{(t)}$) and the λ of a control matrix ($\lambda^{(c)}$), and $\theta = 0.0$. The distribution of θ was calculated by pooling transition data from each individual (with their demographic histories) in each treatment. From this data set, individuals were randomly permuted, while maintaining sample sizes obtained for each treatment. To derive estimates of fecundity for the model, the flower number of each randomly chosen individual was multiplied by a seed number (per fruit) that was drawn from a probability distribution of seed numbers, derived from the mean seed number per fruit calculated from each treatment plot (e.g., Angert 2006). To estimate contributions of fruits to first-year rosettes and flowering individuals for the model, flower numbers of randomly chosen individuals were multiplied by a ratio of new rosette first-years and flowering first-years that was drawn from a distribution of ratios, derived from the mean ratio of new rosette first-years to flowering first-years calculated for each treatment plot. For each permutation, a projection matrix and an associated λ was calculated for the treatment and control. θ was calculated for each of 10,000 permuted data sets. The significance level of my observed θ was established by determining how much greater my observed values was, compared to the calculated θ distribution.

Life table response experiments (LTRE) on the stage-structured matrix models (Caswell 2001) were also conducted to estimate treatment effects on λ. The retrospective LTRE analysis can identify the parameters that most influence differences in λ between control plots and plots exposed to nitrogen addition warming and thinning, on the basis of sensitivities of each vital rate and the difference of each parameter between control and treatment plots. For the LTRE, the sensitivity of λ to all vital rates ($\boldsymbol{x}$) at a matrix $\bar{\mathbf{A}}$ evaluated at the mean of vital rates between control ($\mathbf{A}^{(c)} = \mathbf{A}[\boldsymbol{x}^{(c)}]$) and treatment ($\mathbf{A}^{(t)} = \mathbf{A}[\boldsymbol{x}^{(t)}]$) matrices was computed:

$$\frac{d\lambda}{dx_k} = \sum_{i,j} \frac{\partial \lambda}{\partial a_{i,j}} \frac{\partial a_{i,j}}{\partial x_k} \Bigg|_{\bar{\mathbf{A}}}$$

where the partial derivatives of λ with respect to each of the elements of $\boldsymbol{x}$ (vector of vital rates) is found using $\boldsymbol{a}_{ij}$ = element in matrix $\bar{\mathbf{A}}$. The LTRE decomposition was then calculated using:

$$\lambda^{(t)} - \lambda^{(c)} \approx \sum_k \left(x_k^{(t)} - x_k^{(c)}\right) \frac{d\lambda}{dx_k} \Bigg|_{\bar{\mathbf{A}}}$$

Confidence intervals were computed for all LTRE contributions using bootstrap resampling (Caswell 2001).

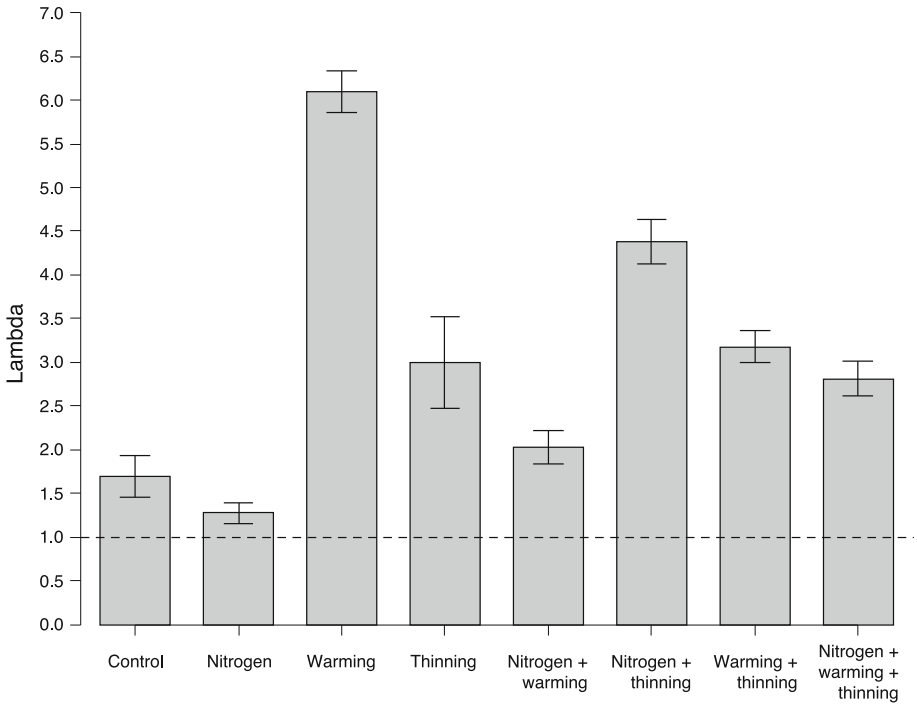

Fig. 3 Lambda (λ) across treatments during the transition period 2011–2012. *Broken line* indicates λ at which population growth is at a level of self replacement. *Error bars* are means ± CI

Individuals, along with their transition histories, were randomly selected with replacement, maintaining treatment sample sizes. A population projection matrix was then created for each treatment and control population and a LTRE analysis was conducted. This process was iterated 10,000 times, and 95 % confidence intervals were determined from the distributions of LTRE contribution values. Non-overlap of confidence intervals was used as an approximate indication of significant differences among contribution values. All analyses were conducted in R version 2.15 (R Development Core Team 2012) using the popbio package.

Results

Population growth rates

In 2012, *P. aspera* had population growth rates (λ) >1.0 across all treatments (Fig. 3; see Table S1 in ESM for matrices), showing the lowest λ in the control (1.7) and nitrogen addition (1.28) plots and the highest λ in the warming only (6.1) and nitrogen addition + thinning (4.4) plots. Permutation tests show that, compared to controls, λ values were significantly higher in populations exposed to the warming treatment, the nitrogen addition + warming treatment, the warming + thinning treatment, and the nitrogen addition + warming + thinning treatment ($P < 0.001$).

Combinations of main effects were generally not additive. Nitrogen addition + warming, warming + thinning, and nitrogen addition + warming + thinning all resulted in much lower growth rates than would be expected from the main effects, while nitrogen addition + thinning resulted in a much larger effect than expected (Fig. 3).

Life table response experiment

Nitrogen

The slight reduction in λ in nitrogen addition plots was a result of negative contributions from rosette first-year survival (σ_s) and the fecundity of both flowering first-years (F_j) and flowering adults (F_f). Because λ was relatively insensitive to these parameters ($\sigma_s = 0.33$; $F_f = 0.06$; $F_j = 0.38$), nitrogen addition likely reduced σ_s in addition to adult fecundity, resulting in a lower population growth rate (Fig. 4a).

Warming

Overwhelmingly, fecundity of both flowering first-years and adults were responsible for the significantly larger λ of populations exposed to warming, compared to control (Fig. 4b). However, because the sensitivity of λ to contributions of new flowering first-years from flowering first-years (F_{jj}) is large (0.60), it is likely that warming resulted in increased reproduction (both F_f and F_j).

Thinning

Contributions of changes in vital rates due to thinning were very similar to those documented for warming (Fig. 4c).

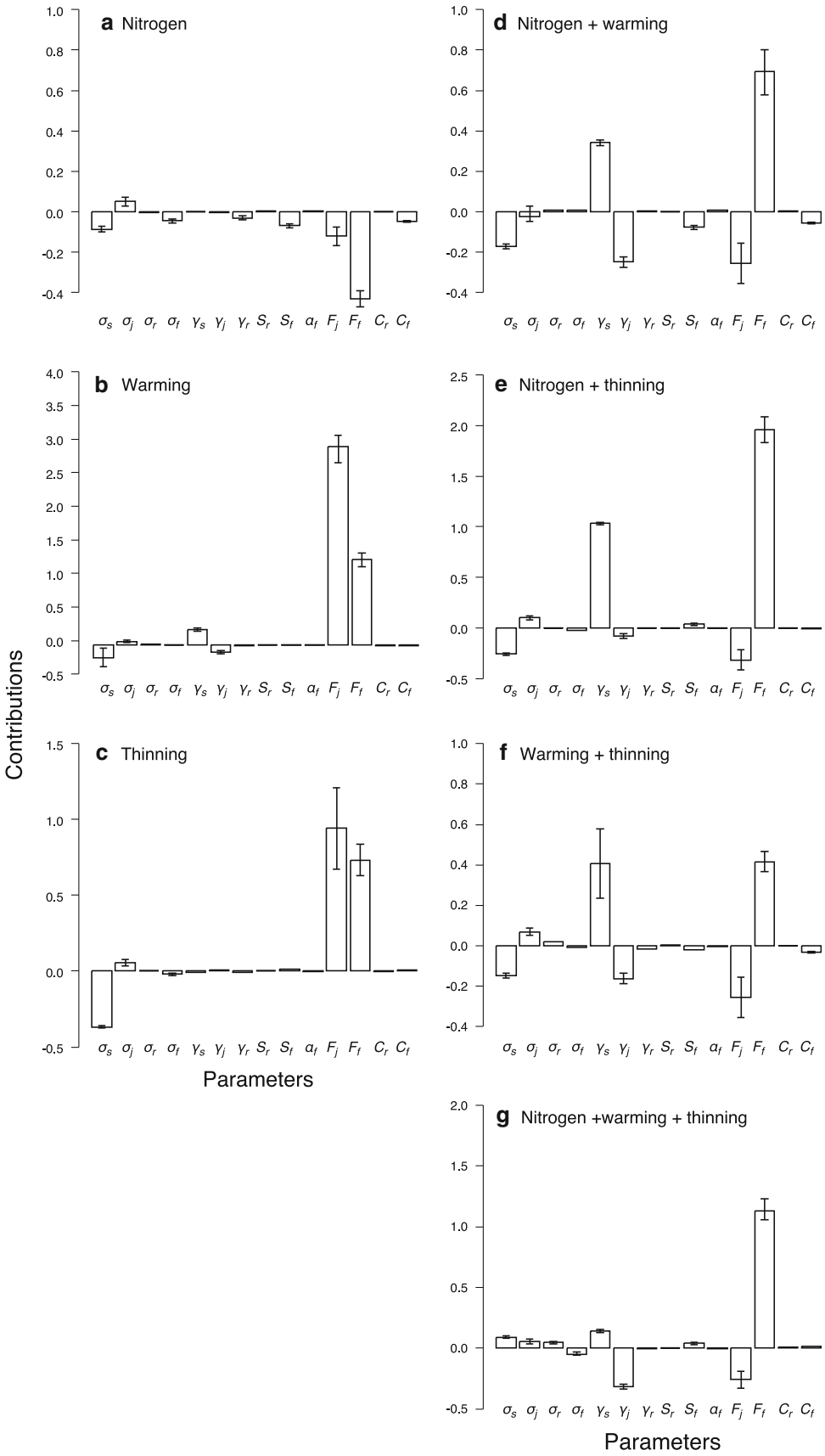

Fig. 4 LTRE contributions between 2011 and 2012. Parameters described in Table 1. S_r rosette adult survival, S_f flowering adult survival, α_f flowering adult regression to rosette adult, C_r rosette adult asexual reproduction, and C_f flowering adult asexual reproduction. In graphs, contributions of sexual (F_{ij}) and asexual reproduction (C_{ij}) were summed together by stage for clarity. The scales of the vertical axis differ among the panels. Error bars are means ± CI

Fecundity of both flowering first-years and adults had large, positive effects on λ. Because the sensitivities of the fecundity parameters were relatively small ($F_{sj} = 0.05$; $F_{jj} = 0.39$; $F_{sf} = 0.03$; $F_{jf} = 0.23$), it is likely that thinning increased fecundity of both life stages. Finally, σ_s had a negative contribution, likely resulting from the large sensitivity (0.89) of λ to this vital rate.

Nitrogen + warming

Many vital rates contributed either positively or negatively to the small difference in λ between control plots and nitrogen addition + warming plots (Fig. 4d). Rosette first-year growth (γ_s) and adult fecundity contributed positively to a higher treatment λ. Because the sensitivity of γ_{fs} is large (0.98), the lower sensitivity transitions, including γ_{rs} (sensitivity 0.08), F_{sf} (sensitivity 0.10), and F_{jf} (sensitivity 0.15) are likely enhanced by the interaction between nitrogen and warming treatments. The positive effects of the treatment, however, are counteracted by a variety of vital rates that demonstrated negative contributions. These include σ_s (with the large sensitivity of 0.75); γ_j (with small sensitivity elements; $\gamma_{rj} = 0.03$ and $\gamma_{fj} = 0.34$); adult flowering stasis (S_f) with a small sensitivity (0.33) and fecundity of flowering first years (also with small sensitivity elements; $F_{sj} = 0.95$ and $F_{jj} = 0.15$).

Nitrogen + thinning

The nitrogen and thinning treatment had a non-additive interaction, resulting in a much larger λ than expected from the effects of nitrogen and thinning individually. Although σ_s contributed negatively to this difference (with a very large sensitivity of 1.39), γ_s and F_j contributed positively (Fig. 4e). Because the sensitivity of γ_{fs} is large (1.48), differences in the transition probabilities γ_{rs} (sensitivity 0.06), F_{sf} (sensitivity 0.07), and F_{jf} (sensitivity 0.11) were responsible for the positive contributions, similar to what was documented for the nitrogen + warming treatment.

Warming + thinning

Patterns of vital rate contributions to a larger λ in the warming + thinning plots compared to control plots were similar to those documented for the nitrogen + thinning plots. Positive contributions from γ_s and F_j were overwhelmingly responsible for the difference in λ (Fig. 4f). However, because the sensitivity of γ_{fs} is large (1.20), the transition probabilities γ_{rs} (sensitivity 0.08), F_{sf} (sensitivity 0.08), and F_{jf} (sensitivity 0.15) most likely benefited from the treatment effects.

Nitrogen + warming + thinning

Different vital rates made opposing contributions to a larger λ in the nitrogen + warming + thinning plots compared to control plots (Fig. 4g). Parameters σ_s and F_f contributed positively to the difference in λ. The large sensitivity of σ_s (0.7), however, suggests that the fecundity of adult individuals (sensitivity of $F_{sf} = 0.73$ and sensitivity of $F_{jf} = 0.11$) is predominantly enhanced by the combination of the three treatments. Alternatively, the small sensitivities of F_j and γ_j suggest that the negative contributions of these parameters are a result of antagonistic treatment effects on these parameters.

Discussion

The vital rates that predominantly drive population level responses to nitrogen deposition and warming are largely understudied. This study documents how these two factors of global change can modify vital rates of an experimentally introduced species in different ways (Bonte et al. 2008). Between 2011 and 2012, the main effects of warming and thinning, and the interactive effects of warming + thinning, and warming + nitrogen addition significantly increased the asymptotic population growth rate (λ) of *P. aspera* in the experimentally invaded plots (Fig. 3). Alternatively, nitrogen addition decreased the growth rate. The vital rates that contributed to these differences were dissimilar across treatments, likely due to different environmental requirements of individuals at different life stages (e.g., Takenaka et al. 1996).

Nitrogen

The nitrogen addition treatment resulted in a smaller λ than was found for control populations. This could be a result of direct toxicity effects, which can increase the mortality of juveniles (Hahn and Dornbush 2012), because plant uptake of nitrogen is highest during early stages and declines with age (Simpson 1986). Fecundity was also found to contribute disproportionately to differences in λ (Garcia and Ehrlen 2002; Koop and Horvitz 2005). This was unexpected because nitrogen is known to increase fecundity by enhancing flower or seed production (Hartness 1993; Drenovsky and Richards 2005) through a release of nutrient limitation. Possibly, the negative contribution of adult fecundity to differences in λ was related to a negative effect of nitrogen on germination, which can be particularly vulnerable to environmental effects (Ehrenfeld 1990). The effects of nitrogen on germination are likely indirect. For example, the well-established decrease in light availability with nitrogen addition (e.g., Hautier et al. 2009)

could reduce the suitability of the soil for germination conditions. The absence of a negative nitrogen effect on adult fecundity in the presence of the reduced native treatment (Fig. 4e) further supports an indirect effect. In this case, the thinning treatment provided more light to the soil surface, even in the presence of nitrogen.

Warming

Large, positive contributions of fecundity to differences in λ between warming and control plots were also found. Warming can affect fecundity by increasing seed production (Chuine et al. 2012), and seed weight (Williams et al. 2007), due to a lengthening of the growing season (Sletvold et al. 2013), or an increase in moisture availability. For example, open top warming chambers can increase local humidity conditions, thereby increasing germination and fruit production in water limited systems (Escudero et al. 1999). Alternatively, when λ is large, transitions that require less time to complete (a single year, in the case of fecundity) contribute more to λ than transitions that require more time to complete (more than a single year, in the case of adult survival, which requires multiple transitions through germination, growth and survival over a span of several years; Caswell 1985).

Thinning

Population growth rates were significantly higher in the thinned plots compared to control plots, as expected from competition theory. However, in addition to demonstrating a demographic effect of the thinning treatment, this result also highlights a potential bias in the experiment. For example, the community imposing competitive pressure on *P. aspera* during the experiment was one that had been disked annually up until two years before data collection occurred. Therefore, this community was likely less mature than one that could be experienced by an invading *P. aspera* in a less contrived environment. It is possible that this younger community imposed an overall weaker competitive effect on *P. aspera*, leading to overestimation of λ across treatments.

Thinning of the extant plant community was expected to modify demographic response to nitrogen addition and warming for two reasons. First, productivity can be important in mediating indirect responses to global change (Fridley et al. 2011) because species interactions play a role in moderating response to the environmental (Gilman et al. 2010). Second, many studies have found that responses to multiple treatments simulating global change are significantly smaller in magnitude than additive responses of single factor treatments (Shaw et al. 2002; Reich 2009; Wu et al. 2011).

Rosette first-year growth (γ_s) provided a significant positive contribution (Fig. 4e, f) to differences in λ for *P. aspera* when thinning was crossed with nitrogen addition or warming; a dynamic that was notably absent in the single factor treatments. Earlier life stages likely benefited from the reduction in competition that occured in thinned plots (Goldberg and Barton 1992; Burke and Grime 1996), but could only exploit this competitive release when accompanied by additional resources, provided by the nitrogen and warming treatments. Like other studies that have identified the reactivity of reproductive traits to a reduction in competition (Humphrey and Pyke 1998; Dyer and Rice 1999), adult fecundity also found to contribute positively to differences in λ in the thinning + global change treatment plots compared to controls.

Because of correlations among traits that mediate population growth (Sakai et al. 2001), focusing research on a single life stage limits understanding of the mechanisms underlying persistence of a plant species in the face of a changing environment (sensu Harrington et al. 1999). Documenting multiple demographic characteristics in a single study highlights the importance of understanding the sensitivity of population growth rate, which can be differentially affected by changes in vital rates, to lower level demographic effects of climate change. Many factors, such as species traits, community interactions, and habitat characteristics, probably affect a species in different ways across life stages (Theoharides and Dukes 2007), therefore, future research attempting to understand demographic response to elevated soil nitrogen and warming should incorporate multiple life stages.

Acknowledgments Countless volunteers helped in the field under less than ideal conditions, and I cannot thank them enough. I also appreciate the help of R. Weidner for all aspects of greenhouse chamber design and construction, and my dissertation committee for guidance: T. E. Miller, A. A. Winn, N. Underwood, A. Mast, J. Chanton, and J. Hellmann. Portions of this research were funded by Florida State University.

References

Angert AL (2006) Demography of central and marginal populations of Monkeyflowers (*Mimulus cardinalis* and *M. lewisii*). Ecology 97:2014–2025

Bonte D, Travis JMJ, De Clercq N, Zwertvaegher I, Lens L (2008) Thermal conditions during juvenile development affect adult dispersal in a spider. Proc Natl Acad Sci USA 105:17000–17005

Boulangeat I, Lavergne S, Van Es J, Garraud L, Thuiller W (2012) Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients. J Biogeogr 39:204–214

Bowers FD (1972) A biosystematic study of Heterotheca Section Pityopsis. Ph.D. Dissertation. University of Tennessee, Knoxville, TN

Buckley LB, Urban MC, Angilletta MJ, Crozier LG, Rissler LJ, Sears MW (2010) Can mechanism inform species' distribution models? Ecol Lett 13:1041–1054

Burke MJW, Grime JP (1996) An experimental study of plant community invisibility. Ecology 77:776–790

Caswell H (1985) The evolutionary demography of clonal organisms. In: Buss LW, Cook RE, Jackson JBC (eds) Population biology and evolution of clonal organisms. Yale University Press, London, pp 187–225

Caswell H (2001) Matrix population models: construction, analysis and interpretation. Sinauer Associates, Sunderland

Chuine I, Morin X, Sonie L, Collin C, Fabrequettes J, Degueldre D, Salager J, Roy J (2012) Climate change might increase the invasion potential of the alien C4 grass *Setaria parviflora* (Poaceae) in the Mediterranean Basin. Diversi Distrib 18:661–672

Currie DJ (2001) Projected effects of climate change on patterns of vertebrate and tree species richness in the conterminous United States. Ecosystems 4:216–225

Doak DF, Gross K, Morris WF (2005) Understanding and predicting the effects of sparse data on demographic analyses. Ecology 86:1154–1163

Drenovsky RE, Richards JH (2005) Nitrogen addition increases fecundity in the desert shrub *Sarcobatus vermiculatus*. Oecologia 143:349–356

Dullinger S, Willner W, Plutzar C, Englisch T, Schratt-Ehrendorfer L, Moser D, Ertl S, Essl F, Niklfeld H (2012) Post-glacial migration lag restricts range filling of plants in the European Alps. Global Ecol Biogeogr 8:829–840

Dunnett NP, Grime JP (1999) Competition as an amplified of short-term vegetation responses to climate: an experimental test. Funct Ecol 13:388–395

Dyer AR, Rice KJ (1999) Effects of competition on resource availability and growth of a California bunchgrass. Ecology 80:2697–2710

Ehrenfeld JG (1990) Dynamics and processes of barrier island vegetation. Rev Aquat Sci 2:437–480

Escudero A, Somolinos RC, Olano JM, Rubio A (1999) Factors controlling the establishment of *Helianthemum squamatum*, an endemic gypsophyle of semi-arid Spain. J Ecol 87:290–302

Galloway JN, Dentener FJ, Capone DG, Boyer EW, Howarth RW, Seitzinger SP, Asner GP, Cleveland CC, Green PA, Holland EA, Karl DM, Michael AF, Porter JH, Townsend AR, Vorosmarty CJ (2004) Nitrogen cycles: past, present, and future. Biogeochemistry 70:153–226

Garcia MB, Ehrlen J (2002) Reproductive effort and herbivory timing in a perennial herb: fitness components at the individual and population levels. Am J Bot 89:1295–1302

Gaston KJ (2003) The structure and dynamics of geographic ranges. Oxford University Press, New York

Gilbert B, Dillon PJ, Somers KM, Reid RA, Scott L (2008) Response of benthic macroinvertebrate communities to El Nino related drought events in six upland streams in south-central Ontario. Can J Fish Aquat Sci 65:890–905

Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD (2010) A framework for community interactions under climate change. Trends Ecol Evol 25:325–331

Goldberg DE, Barton AM (1992) Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. Am Nat 139:771–801

Goldberg DE, Turkington R, Olsvig-Whittaker L, Dyer AR (2001) Density dependence in an annual plant community: variation among life history stages. Ecol Monog 71:423–446

Gornish ES (2013) Effects of density and fire on the vital rates and population growth of a perennial Goldenaster. AoB Plants 5:plt041

Hahn PG, Dornbush ME (2012) Exotic consumers interact with exotic plants to mediate native plant survival in a Midwestern forest herb layer. Biol Invasions 14:449–460

Hansen A, Neilson RP, Dale VH, Flather CH, Iverson LR, Currie DJ, Shafer S, Cook R, Bartlein PJ (2001) Global change in forests: responses of species, communities, and biomes. Bioscience 51:765–779

Harrington R, Woiwod I, Sparks T (1999) Climate change and trophic interactions. Trends Ecol Evol 14:146–150

Hartness DC (1993) Regulation of clonal growth and dynamics of *Panicum virgatum* (Poaceae) in tallgrass prairie: effects of neighbor removal and nutrient addition. Am J Bot 80:1114–1120

Hautier Y, Niklaus PA, Hector A (2009) Competition for light causes plant biodiversity loss after eutrophication. Science 324:636–638

Havstrom MT, Callaghan TV, Johasson S (1993) Differential growth responses of *Cassiope tetragona*, an arctic dwarf shrub, to environmental perturbations among three contrasting high-and sub-arctic sites. Oikos 66:389–402

Holland EA, Braswell BH, Sulzman J, Lamarque J (2005) Nitrogen deposition onto the United States and Western Europe: synthesis of observations and models. Ecol Appl 15:38–57

Hoving H, Gilly WF, Markaida U, Benoit-Bird KJ, Brown ZW, Daniel P, Field JC, Parassenti L, Liu B, Campos B (2013) Extreme plasticity in life-history strategy allows a migratory predator (Jumbo Squid) to cope with a changing climate. Global Change Biol 19:2089–2103

Humphrey LD, Pyke DA (1998) Demographic and growth responses of a guerrilla and a phalanx perennial grass in competitive mixtures. J Ecol 86:854–865

Intergovernmental Panel on Climate Change (IPCC), Working Group I (2007) Climate change 2007: impacts, adaptation and vulnerability. Cambridge University Press, Cambridge

Koop AL, Horvitz CC (2005) Projection matrix analysis of the demography of an invasive, nonnative shrub (*Ardisia elliptica*). Ecology 86:2661–2672

Lloret F, Penuelas J, Prieto P, Llorens L, Estiarte M (2009) Plant community changes induced by experimental climate change: seedling and adult species composition. Perspect Plant Ecol 11:53–63

Mandle L, Ticktin T (2012) Interactions among fire, grazing, harvest and abiotic conditions shape palm demographic responses to disturbance. J Ecol 100:997–1008

Manly BFJ (1991) Randomization and Monte Carlo methods in biology. Chapman & Hall, New York

Marion GM, Henry GHR, Frechman DW (1997) Open-top designs for manipulating field temperature in high-latitude ecosystems. Global Change Biol 3:20–32

Martinez-Ramos M, Anten NPR, Ackerly DD (2009) Defoliation and ENSO effects on vital rates of an understory tropical rain forest palm. J Ecol 97:1050–1061

Millennuium Ecosystem Assessment (MEA) (2005) Ecosystems and human well-being: synthesis of the millennium ecosystem assessment. Island Press, Washington DC

Moller AP (2008) Climate change and micro-geographic variation in laying date. Oecologia 155:845–857

Myers RL, Ewel JJ (1990) The ecosystems of Florida. University of Central Florida Press, Orlando

Nicole F, Dahlgren JP, Vivat A, Till-Bottraud I, Ehrlen J (2011) Interdependent effects of habitat quality and climate on population growth of an endangered plant. J Ecol 99:1211–1218

Parmesan C, Matthews J (2006) Biological impacts of climate change. In: Groom MJ, Meffe GK, Carroll CR (eds) Principles of conservation biology. Sinauer Associates, Sunderland, pp 333–360

Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on terrestrial biota. Bull Am Met Soc 81:443–450

Post ES, Pedersen C, Wilmers CC, Forchhammer MC (2008) Phenological sequences reveal aggregate life history response to climatic warming. Ecology 89:363–370

R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. url:http://www.R-project.org/ (ISBN 3-900051-07-0)

Reich PB (2009) Elevated CO_2 reduced losses of plant diversity caused by nitrogen deposition. Science 326:1399–1402

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. Annu Rev Ecol Syst 32:305–332

Shaw MR, Zavaleta ES, Chiariello NR, Cleland EE, Mooney HA, Field CB (2002) Grassland responses to global environmental changes suppressed by elevated CO_2. Science 298:1987–1990

Shea K, Jongejans E, Skarpaas O, Kelly D, Sheppard AW (2010) Optimal management strategies to control local population growth or population spread may not be the same. Ecol Appl 20:1148–1161

Simpson RJ (1986) Translocation and metabolism of nitrogen: whole plant aspects. In: Lambers H, Neeyeson JJ, Stulen I (eds) Fundamental, ecological and agricultural aspects of nitrogen metabolism in higher plants. Martinus Nijhoff, Dordrecht, pp 71–96

Sletvold N, Dahlgren JP, Oien D, Moen A, Ehrlen J (2013) Climate warming alters effects of management on population viability of threatened species: results from a 30-year experimental study on a rare orchid. Global Change Biol 19:2729–2738

Sousa LL, Seabra R, Wethey DS, Xavier R, Queiroz N, Zenboudji S, Lima F (2012) Fate of a climate-driven colonization: demography of newly established populations of the limpet *Patella rustica* Linnaeus, 1758, in northern Portugal. J Exp Mar Biol Ecol 438:68–75

Takenaka A, Washitani I, Kuramoto N, Inoue K (1996) Life history and demographic features of *Aster kantoensis,* an endangered local endemic of floodplains. Biol Conserv 78:345–352

Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytol 176:256–273

Verlinden M, Nijs I (2010) Alien plant species favoured over congeneric natives under experimental climate warming in temperate Belgian climate. Biol Invasions 12:2777–2787

Williams AL, Wills KE, Janes JK, Schoor JKV, Newton PCD, Hovenden MJ (2007) Warming and free-air CO_2 enrichment alter demographics in four co-occuring grassland species. New Phytol 176:365–374

Wisdom MJ, Mills LS, Doak DF (2000) Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. Ecology 81:628–641

Woodhams DC, Akford RA, Briggs CJ, Johnson M, Rollins-Smith LA (2008) Life history trade offs include disease in changing climates: strategies of an amphibian pathogen. Ecology 89:1627–1639

Wu ZT, Dijkstra P, Koch GW, Penuelas J, Hungate BA (2011) Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Global Change Biol 17:927–942