

Portfolio effects, climate change, and the persistence of small populations: analyses on the rare plant *Saussurea weberi*

RONALD E. ABBOTT,¹ DANIEL F. DOAK,² AND MEGAN L. DEMARCHE^{2,3}

¹Independent Researcher, P. O. Box 1431, Greeley, Colorado 80632 USA

²Environmental Studies Program, University of Colorado Boulder, 4001 Discovery Drive, Boulder, Colorado 80309 USA

Abstract. The mechanisms that stabilize small populations in the face of environmental variation are crucial to their long-term persistence. Building from diversity–stability concepts in community ecology, within-population diversity is gaining attention as an important component of population stability. Genetic and microhabitat variation within populations can generate diverse responses to common environmental fluctuations, dampening temporal variability across the population as a whole through portfolio effects. Yet, the potential for portfolio effects to operate at small scales within populations or to change with systematic environmental shifts, such as climate change, remain largely unexplored. We tracked the abundance of a rare alpine perennial plant, *Saussurea weberi*, in 49 1-m² plots within a single population over 20 yr. We estimated among-plot correlations in log annual growth rate to test for population-level synchrony and quantify portfolio effects across the 20-yr study period and also in 5-yr subsets based on June temperature quartiles. Asynchrony among plots, due to different plot-level responses to June temperature, reduced overall fluctuations in abundance and the probability of decline in population models, even when accounting for the effects of density dependence on dynamics. However, plots became more synchronous and portfolio effects decreased during the warmest years of the study, suggesting that future climate warming may erode stabilizing mechanisms in populations of this rare plant.

Key words: climate; diversity–stability relationship; extinction; persistence; population model; portfolio effect; response diversity; synchrony.

INTRODUCTION

Small, isolated populations are a major component of biodiversity (Preston 1948, Ehrlich and Daily 1993). Small population size characterizes not only rare species, but also ecologically or geographically marginal populations of many common species (Brown 1984, Lawton 1993). Further, processes within small, isolated populations contribute disproportionately to the speciation and extinction rates that shape biodiversity (Brown 1984, Stanley 1986, Gavrilets et al. 2000, Matthies et al. 2004, Anacker and Strauss 2014). Yet small populations face a suite of demographic and genetic challenges (Lande 1988, Lynch et al. 1995, Leimu et al. 2006, O’Grady et al. 2006, Willi et al. 2006), and their ability to persist over long periods of time is a long-standing mystery. Understanding the drivers of population persistence has become increasingly relevant to conservation in this era of fragmentation and environmental change (Fahrig and Merriam 1994, Earn et al. 2000). In particular, the ability of species to expand their ranges in response to climate change will depend on the persistence of small populations at the leading edges of species’ ranges (Opdam and Wascher 2004), while ranges may be stabilized by the viability of small populations at trailing edges.

Temporal variation in abundance, due to both environmental and demographic stochasticity, is thought to be a major cause of population extinction (Lewontin and Cohen 1969, Tuljapurkar and Orzack 1980, Inchausti and Halley 2003, Drake and Lodge 2004). In particular, population stability relies on mechanisms that reduce the influence of environmental stochasticity on local abundance. Explanations for population stability include compensatory density dependence (Ginzburg et al. 1990, Sinclair and Pech 1996, Reed et al. 2013), migration within metapopulations (Stacey and Taper 1992, Engen et al. 2002), and buffering of critical life history stages (Pfister 1998, Morris and Doak 2004).

Another potentially powerful mechanism that may stabilize populations is within-population diversity in responses to environmental variation; such diversity has the potential to dampen population-level responses to environmental fluctuations. The importance of this same mechanism, but operating at the community level, has been increasingly recognized by ecologists, who have developed theory and analysis methods to explain the stabilizing effects of species diversity on community-level responses (Doak et al. 1998, Tilman et al. 1998, Elmquist et al. 2003, Loreau and de Mazancourt 2008, Thibaut and Connolly 2013). More recently, population ecologists have begun to apply these ideas to understand how spatial or genotypic diversity within populations may promote population persistence (Schindler et al. 2010,

Manuscript received 15 July 2016; revised 21 November 2016; accepted 6 January 2017. Corresponding Editor: Elizabeth E. Crone.

³Corresponding author. E-mail: megan.peterson@colorado.edu

2015, Acker et al. 2014). The strength of this stabilizing effect depends on individuals or sub-populations exhibiting diverse responses to common environmental drivers due to genotype-by-environment or spatiotemporal interactions. These differences generate weakened or negative correlations in abundance among sub-groups; in turn, this asynchrony among sub-groups dampens variation in total population abundance in a phenomenon commonly known as the portfolio effect (Doak et al. 1998, Schindler et al. 2010, Anderson et al. 2013). Density dependence within sub-groups can also act to amplify or weaken correlations in abundance, and may thus interact with environmental responses in the creation of portfolio effects.

Previously, investigations of this stabilizing mechanism have focused on response diversity at larger scales, such as ensembles of populations or obvious habitat or life history variation. Most notably, stabilizing effects at the scale of entire fisheries have been demonstrated through asynchrony among populations, life history cohorts, or habitats (Moore et al. 2010, 2014, Schindler et al. 2010, Thorson et al. 2014). However, even in the absence of obvious sub-groups, smaller-scale heterogeneity through microhabitat or genotypic variation could also provide important stabilizing effects, particularly in sessile organisms. For example, Acker et al. (2014) found that individual variation in the age of reproduction stabilizes semelparous plant populations. Yet there has been relatively little consideration of the effects of fine-scale spatial variation on population dynamics (Crone 2016), and the potential for such small-scale heterogeneity to promote population persistence remains largely unexplored.

Accurate forecasts of population persistence also require linking the mean and variance in population growth rate to directional changes in environmental drivers, such as temperature or precipitation (Boyce et al. 2006). While response diversity may stabilize current population dynamics, these effects could grow markedly weaker or stronger with changes in the mean or variance of environmental conditions. A particular concern is that genotypes or sub-populations that respond asynchronously to historical patterns of environmental variation may show increasingly synchronous responses (e.g., correlated declines in performance) in extreme environmental conditions. At the community level, synchrony among species has been shown to increase with warming and oligotrophic conditions in plankton communities (Jochimsen et al. 2013, Thompson et al. 2015) and reduced or more variable precipitation in grasslands (Hallett et al. 2014). At the population level, increased synchrony among sub-populations of salmon has been correlated with greater hatchery production, dam construction, and dramatic declines in overall abundance (Isaak et al. 2003, Moore et al. 2010, Satterthwaite and Carlson 2015). Yet no study, to our knowledge, has examined the potential for response diversity within populations to change with climate or the impact of these changes on population persistence, especially applied to

the highly local scales relevant to the persistence of small and isolated populations.

Here, we use 20 years of census data for a rare alpine perennial plant, *Saussurea weberi* (Asteraceae), taken on the same 49 study plots, to test whether small-scale variation in abundance through time can substantially stabilize a population and to explore the future of such stability in a shifting climate regime. In particular, we test whether small-scale spatial asynchrony can contribute to population stability in the absence of obvious habitat heterogeneity. Further, we develop and test a general methodology to compare the strength of population stability with changing climate. We address four specific questions: (1) How is spatial asynchrony among plots related to other types of plot heterogeneity, such as spatial variation in abundance or growth rate? (2) Does spatial asynchrony among plots substantially contribute to population stability and persistence? (3) How is population growth and persistence affected by climatic variation? (4) How is population stability impacted by changes in climate?

METHODS

Study species

Saussurea weberi Hultén (Asteraceae) is a globally rare alpine perennial plant (Colorado Natural Heritage Program 2001). It is restricted to limestone- or dolomite-derived soils and is mostly known from only three disjunct regions in the Rocky Mountains: the Anaconda Range of southwest Montana, the Wind River Range in central Wyoming, and the Mosquito Range in Colorado (Abbott 1998, Spackman et al. 2001, Schorr 2013). Plants of *S. weberi* produce clustered heads of purple disk flowers, are self-incompatible, and are pollinated by bees and flies (Abbott 1998, Spackman et al. 2001). *Saussurea weberi* can also spread clonally, with rhizomes producing dispersed shoots. In our work, shoots were the unit of study, as it is not possible to identify connections between shoots without extensive disturbance.

Census plots

In 1996, 50 circular 1-m² plots were established around focal inflorescences of *S. weberi* that had previously been permanently marked as part of a pollination study (Abbott 1998). All plots were located within a 5-ha area at Horseshoe Cirque, Colorado (39.19227° N, 106.16904° W, 3,750 m above sea level). Each year from 1996 to 2015, we counted the total number of vegetative and floral shoots of *S. weberi* within each plot. *Saussurea weberi* was locally extirpated from one plot in 1999 and never recolonized, so this plot was removed from further analysis resulting in a total of 49 plots censused for 20 yr. On four other occasions, there were years in which we did not find any *S. weberi* shoots within a plot, usually due to extensive disturbance by gophers causing plots to be

buried in overturned soil. In these cases, shoots were recorded in the following year, so we retained these plots in the analyses. We used the total number of shoots within a plot each year as our measure of abundance (hereafter N), but used $N + 1$ for calculations of growth rates, density-dependent models, or log abundance to accommodate zeros in the data set. Analyses that excluded zeros to use N yielded very similar results. These plots are located on limestone-derived soils within alpine tundra and span an area that appears relatively homogeneous in terms of the local abiotic and biotic conditions (Appendix S1: Figs. S1, S2).

Types of spatial heterogeneity

We tested whether heterogeneity among plots contributes to population stability and persistence. First, we examined three metrics of plot performance: mean abundance over the 20-yr study period (\bar{N}), mean yearly log growth rate ($\log \lambda$), and mean correlation in log λ with other plots ($\bar{\rho}$). For each plot, we calculated the annual log(population growth rate) as $\log \lambda_t = \log[(1 + N_{t+1}) / (1 + N_t)]$ (hereafter $\log \lambda$) and estimated the mean annual log λ (hereafter $\overline{\log \lambda}$). We calculated Pearson correlation coefficients of log λ for all pairs of plots and used the mean correlation coefficient per plot ($\bar{\rho}$) as an indication of plot-level synchrony with other parts of the population. We examined the distribution of each of these metrics across all plots and tested for relationships between each pair of performance metrics using univariate linear regressions. All analyses were conducted in R v. 3.2.3 (R Core Development Team 2015).

Population synchrony and the portfolio effect

There is no single agreed-upon method to quantify the strength of portfolio effects or synchrony. We used two straightforward empirical approaches to quantify mean synchrony across the entire population and the strength of population stability. First, we calculated the population-level synchrony index (ϕ) following Loreau and de Mazancourt (2008) and Thibaut and Connolly (2013) as

$$\phi = \frac{\text{Var}(N_{\text{total}})}{(\sum_i \sqrt{\text{Var}(N_i)})^2} \quad (1)$$

where the numerator is the observed variance of the total population abundance and the denominator is maximal variance in abundance if all plots are perfectly synchronous but have differing temporal variation. The denominator is the squared sum of the standard deviations in abundance within each plot i . This index ranges from 0 if all plots are perfectly asynchronous or abundance is constant to 1 if all plots are perfectly synchronous. If all plots have equal variances, the synchrony index increases linearly with the mean correlation coefficient and decreases asymptotically with the number of

plots (Thibaut and Connolly 2013). In reality, the synchrony index also depends on the relationships between mean and variance in plot abundances and plot-specific mean correlation coefficients (Thibaut and Connolly 2013).

Second, we estimated the strength of the portfolio effect (PE) following Anderson et al. (2013) as

$$\text{PE} = \frac{\text{Var}_{\text{pred}}}{\text{Var}(N_{\text{total}})} \quad (2)$$

where the numerator is the predicted variance of the total population abundance from a linear regression of log variance on log abundance across all plots and the denominator is the observed variance of the total population abundance. This method for estimating portfolio effects takes into account the empirical mean–variance scaling relationship for a given study system, which is known to differ among taxonomic groups (Anderson et al. 2013). Values greater than one indicate stabilizing effects.

Population modeling

We tested the effects of spatial asynchrony and climate on population persistence using stochastic multi-site count-based population models. In these stochastic simulations, population growth was simultaneously projected in all plots over 100 yr, with the results used to characterize abundance and the probability of population decline over 10,000 replicates.

To more accurately characterize stabilizing diversity in population dynamics, we tested for evidence of density dependence (Appendix S1: Fig. S3) and autocorrelation in log λ within plots. We compared Ricker and density-independent models of log λ by fitting Poisson generalized linear mixed models (glmm) with the lme4 package (Bates et al. 2011). Briefly, we modelled the abundance in each plot at time $t + 1$ as a Poisson glmm with a log link function and an offset for log(N_t). We compared models including a fixed effect of abundance at time t (Ricker) to models with only an intercept (density-independent). In all models, we allowed the intercept to vary randomly with each observation to account for observation errors and overdispersion (Elston et al. 2001, Harrison 2014), and we compared models with random variation in the intercept and/or slope among years and/or plots using AIC_c. The best-supported model was a Ricker model with random variation in the intercept among years (Appendix S1: Table S1). We found no support for variation in either the intercept or slope among plots ($\Delta\text{AIC}_c = 1.90\text{--}49.37$), and when estimated, random coefficients in these models were extremely small. We used $N + 1$ as our measure of abundance in these models; using N and excluding zeros from the analysis yielded the same best-supported model in model comparisons and only trivial differences in the estimated coefficients and random effects.

We incorporated density dependence into our simulations by estimating an expected log λ for each plot in each

time step based on its abundance and the intercept and slope from the best-supported Ricker model. To this mean $\log \lambda$ value we added a plot specific correlated random value. These correlated random values were estimated by first taking the difference between the best supported model predictions (including fixed effects and observation random effects, but not year effects) and observed $\log \lambda$ values, and then obtaining the covariance matrix for these residual values. These residual values implicitly include year effects to allow for the observed covariances between plots and year effects (Appendix S1: Fig. S4), but estimate covariance values while accounting for observation errors and density effects. We used this covariance matrix to draw plot-specific random values from a multivariate normal distribution with all means centered on zero.

This simulation approach assumes no autocorrelation in $\log \lambda$ within a plot. Although $\log \lambda_t$ values between subsequent years tended to be negatively correlated within plots (Appendix S1: Fig. S5), Durbin-Watson tests for autocorrelation were only significant in 2 out of 49 plots after a Bonferroni correction for multiple testing. Incorporating June temperature (see *Climatic drivers of plot synchrony and population persistence*) as a predictor of annual $\log \lambda$ did not alter this result (Appendix S1: Fig. S5); residuals from these models were not significantly autocorrelated in any plots. In each simulation, each plot was initiated at its observed abundance in 2015 plus one.

In all simulations, we assumed zero dispersal among plots, based on two lines of evidence. First, annual plot-level population growth is independent of the total number of inflorescences, across all plots, in either the previous 1 or 2 yr (1 yr, $\beta = 0.00023$, $t = 1.623$, $P = 0.105$; 2 yr, $\beta = -0.00024$, $t = -1.704$, $P = 0.089$), suggesting that most population growth is achieved through within-plot recruitment and clonal reproduction. Second, the plot that became extinct in 1999 was not recolonized by *S. weberi* in the subsequent 16 yr of the study period. Thus, we assumed that, on the timescales of our simulations, it is extremely rare for individuals of *S. weberi* to disperse among plots and thus that extinct plots are not recolonized with any significant probability. To quantify population performance, we used mean numbers over each simulation, and also the probability of falling below a minimum number. Rather than choosing a single quasi-extinction threshold, we estimated the probability that the total population, summed across all plots, would decline below a percentage (varied from 0.01 to 0.99) of the observed minimum abundance ($N = 1,247$) within 100 yr.

We compared several alternative models to our base models to test the effects of spatial asynchrony and plot heterogeneity on population persistence. First, we ran simulations that assumed perfectly synchronous growth rates across plots. In these simulations, we preserved the total annual variance in $\log \lambda$ within each plot but altered the covariances among plots to produce perfect correlations (i.e., we set the covariance between two plots to the product of their standard deviations). We compared the probability of decline between these simulations and our

base models to test the importance of among-plot asynchrony for population persistence. Second, we used a simulation approach to compare the relative importance of heterogeneity in abundance and asynchrony among plots. We repeated the base population simulations after removing either (1) the five plots with the highest mean abundance (\bar{N}), (2) the five plots with the lowest mean Pearson correlation coefficient (with all other 48 plots; $\bar{\rho}$), or (3) five randomly selected plots (without replacement and resampled 500 times). We compared the mean abundance and probability of decline among these scenarios.

Climatic drivers of plot synchrony and population persistence

We downloaded monthly temperature and precipitation data from 1996 to 2015 for the 4 km² grid encompassing the study plots from the PRISM Climate Group (Oregon State University, data *available online*).⁴ Based on research in other alpine plant populations (e.g., Doak and Morris 2010), we initially expected temperature or precipitation in June or July to most strongly influence yearly variation in growth rates and abundance, and univariate regressions of abundance on each of these four variables identified June temperature as the best potential driver. We confirmed the importance of June temperature relative to other climatic variables through a formal model selection process that considered temperature and precipitation across several time periods. We fit linear and quadratic models of total *S. weberi* abundance (summed across all plots) in each year using annual, summer (June–August) and monthly (May–September) temperature means and precipitation sums, standardized to z scores with mean 0 and SD 1, as potential predictor variables. We fit all possible models using the dredge package (Barton 2014), with the constraints that models included four or fewer terms and that quadratic terms were only considered in conjunction with the respective linear terms. We compared model fit using AIC_c . As we predicted, June temperature had very high explanatory power across a wide range of models (AIC_c weight = 0.96, relative to 0.57 for the next highest variable, August precipitation). June temperature was the only climate variable that was present in every model in the 95% candidate set (Appendix S1: Table S2), and more complex models had only marginally better predictive power, so we chose June temperature as the best single variable predictor of *S. weberi* abundance.

We used several analyses to explore whether mean June temperature influences among-plot synchrony and population stability. First, we tested whether plots differed in their responses to mean June temperature. We considered annual \log abundance, $\log \lambda$, and residuals in $\log \lambda$ from a Ricker model as response variables and fit models with linear and quadratic terms for June temperature, plot, and plot \times temperature interactions as fixed effects (Appendix S1: Table S3). We compared the

⁴<http://prism.oregonstate.edu>

responses of the most and least synchronous plots by refitting these models using only the five plots with the highest (synchronous) or lowest (asynchronous) mean Pearson correlation coefficients ($\bar{\rho}$). Second, we subset the 20-yr data set into four 5-yr groups based on mean June temperature quartiles. We compared the strength of synchrony and population stability across these temperature quartiles by reestimating the Pearson correlation coefficients in $\log \lambda$ among plots, the synchrony index, and the portfolio effect separately for each 5-yr subset. We generated confidence intervals for each estimate by resampling plots with replacement to create 2000 replicate bootstrap data sets and used the bias-corrected and accelerated confidence intervals with the bca option in the boot package in R (Canty and Ripley 2016). Finally, we regressed mean June temperature on year to test whether June temperature has increased over the 20-yr time series.

RESULTS

Types of spatial heterogeneity

We detected small-scale variation in mean abundance, growth rate, and synchrony among plots (Fig. 1). However, these different types of plot heterogeneity were not clearly correlated. Variation in mean growth rate and mean synchrony were not significantly related to variation in mean abundance across plots in univariate regressions ($\bar{\lambda}$, $\beta = 0.0002$, $t = 0.671$, $P = 0.506$; $\bar{\rho}$, $\beta = 0.0009$, $t = 1.122$, $P = 0.267$; Fig. 1B, C). There was a significant relationship between mean synchrony and mean growth rate ($\bar{\rho}$, $\beta = 0.6309$, $t = 2.109$, $P = 0.040$), but this relationship explained very little of the variance among plots (adjusted $R^2 = 0.067$; Fig. 1F). Annual growth rates of most plots were positively correlated with each other, indicating

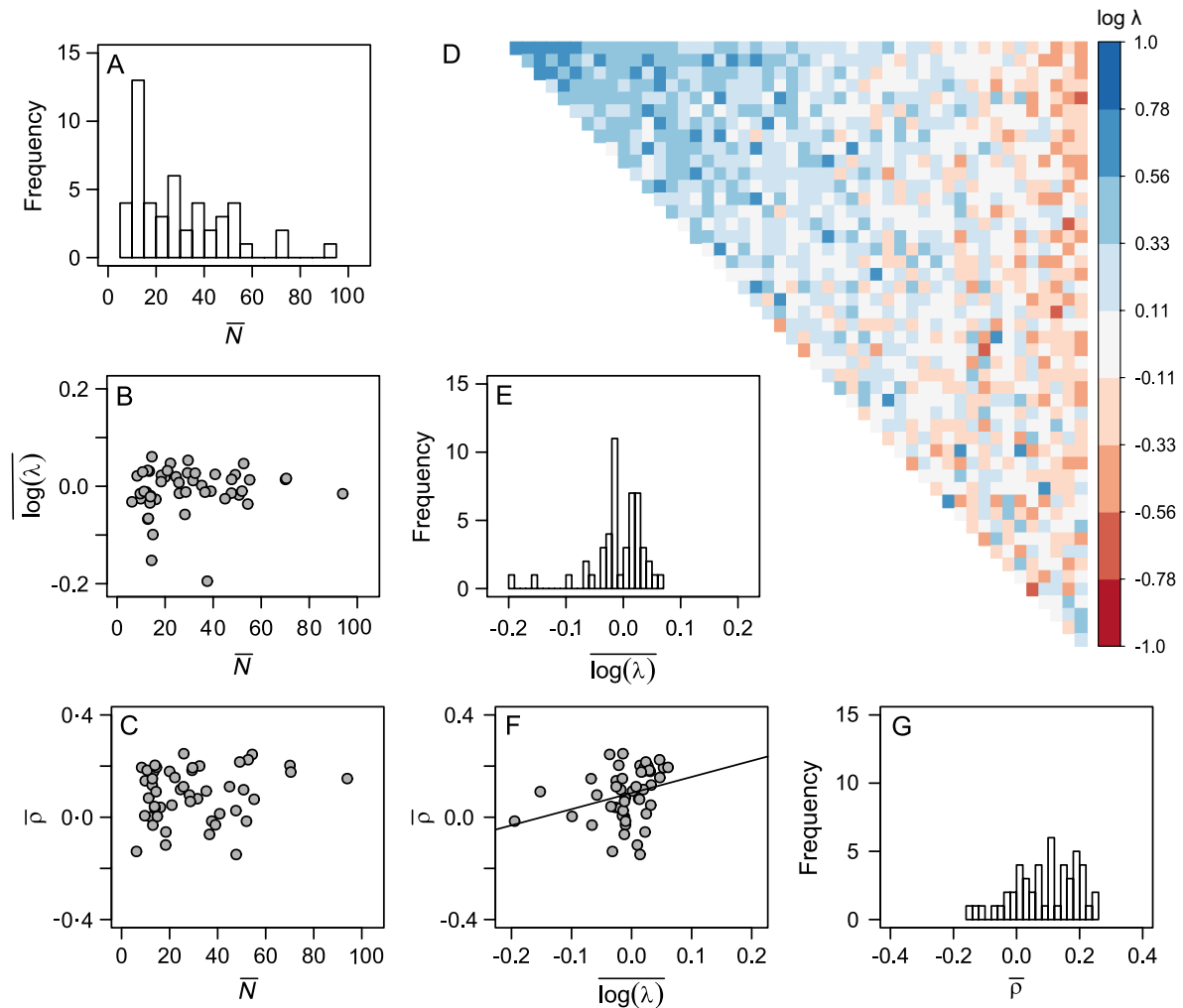


FIG. 1. Different types of plot heterogeneity: mean abundance (\bar{N}), mean annual growth rate $\overline{\log(\lambda)}$, and mean correlation in $\log \lambda$ with other plots ($\bar{\rho}$). (A, E, G) Histograms of each metric across all 49 plots. (B, C, F) Pairwise relationships between each of the metrics. (D) Correlation matrix of $\log \lambda$ between all pairs of plots. Darker shades indicate larger correlations (blue, positive; red, negative), and plots are ordered to group by strength and direction of correlations. [Colour figure can be viewed at wileyonlinelibrary.com]

similar temporal responses in abundance; however, a few asynchronous plots were weakly or negatively correlated with most other plots in the population (Fig. 1D). Correlations among plots were similar when using residuals in $\log \lambda$ from a Ricker model (Appendix S1: Fig. S6).

Population synchrony and the portfolio effect

The population-level synchrony index was 0.055. This value corresponds to a mean correlation coefficient of 0.035 if all plots had equal variances (Thibaut and Connolly 2013), indicating that plot fluctuations are close to independent. This low value reflects the influence of a few asynchronous plots as well as the negligible correlations between many other plots (Fig. 1D). Correspondingly, the population portfolio effect was 2.92; observed variance in total numbers was nearly three times lower than would be predicted by the mean to variance ratio expected from individual plots, showing that spatial asynchrony strongly reduces the variation in total abundance through time (Fig. 2A).

Population analyses

The risk of decline was markedly lower in simulations using the observed correlations in $\log \lambda$ among plots relative to simulations that assumed perfect synchrony (Fig. 2B). The lower risk of decline in observed simulations reflects the stabilizing influence of low synchrony among plots, since these simulations did not differ in their mean abundance (perfect synchrony simulations, mean = 1,724, SD = 587; observed simulations, mean = 1,728, SD = 208). The best-supported model of population growth estimated an intrinsic maximum growth rate (intercept) as 0.0508 (SE = 0.0197) and a density-dependent slope with N_t as -0.0013 (SE = 0.0003). The observation-level variance

was estimated as 0.0118 and the temporal variance was 0.0033.

Different types of plot heterogeneity had differing effects on population abundance and the relative risk of decline. Removal of the five plots with the highest abundance, representing 23% of the total population in 2015, increased the risk of small declines by immediately reducing the starting population size in simulations (Fig. 3). However, removal of the five plots with the lowest correlation coefficients, representing less than 10% of the total population in 2015, had the greatest effect on the risk of a dramatic decline (<75% of observed minimum abundance; Fig. 3). The mean population abundance was most sensitive to removal of plots with the highest mean abundance (Fig. 3). Random plot removal had the smallest effects on the probability of decline or the mean abundance. Removing the most abundant or least synchronous plots reduced the mean abundance to the 0.6th and 26th percentiles observed under random plot removal, respectively. Population simulations produced higher mean abundances relative to observations, but observed total abundances were well within the distribution of total abundances across simulations, and simulated abundances within plots were correlated with observed plot mean abundances (Appendix S1: Fig. S7).

Climatic drivers of population persistence

Total *S. weberi* abundance during the census period was negatively correlated with annual variation in mean June temperature ($\beta = -65.68$, $t = -4.987$, $P < 0.001$; Fig. 4). Differences in plot-level synchrony, quantified as the mean correlation coefficient, reflect in part the differences among plots in their responses to June temperature. There was a significant plot \times temperature interaction for \log abundance, but not $\log \lambda$ ($\log N$, $F = 1.87$, $df = 48, 833$, $P < 0.01$;

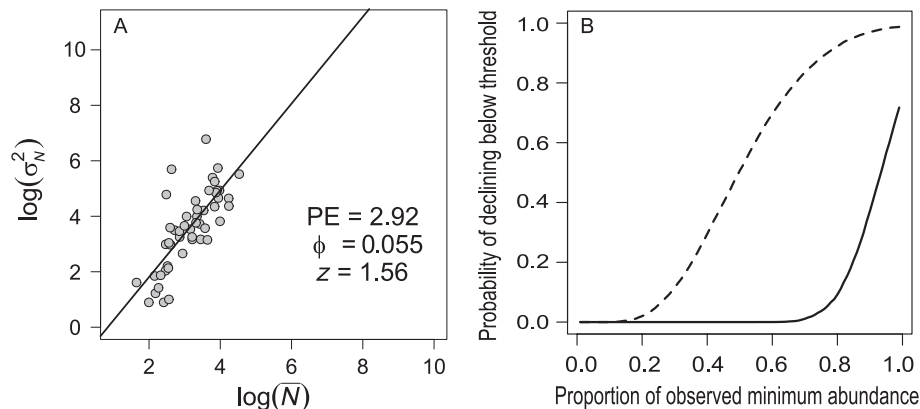


FIG. 2. Portfolio effects and population persistence in *Saussurea weberi*. (A) Shows $\log(\text{variance})$ vs. $\log(\text{mean abundance})$ for all 49 plots (gray circles) and across the whole population (gray triangle). Portfolio effect (PE) is the ratio of the predicted to the observed variance for the whole population. Synchrony index (ϕ) is the ratio of observed variance to the squared sum of the plot standard deviations. Taylor's law z is the slope of the regression of $\log(\text{variance in abundance})$ on $\log(\text{mean abundance within plots})$. (B) Probability of declining below a threshold within 100 yr based on simulations using either the observed $\log \lambda$ correlations (solid line) or assuming perfect synchrony (dashed line).

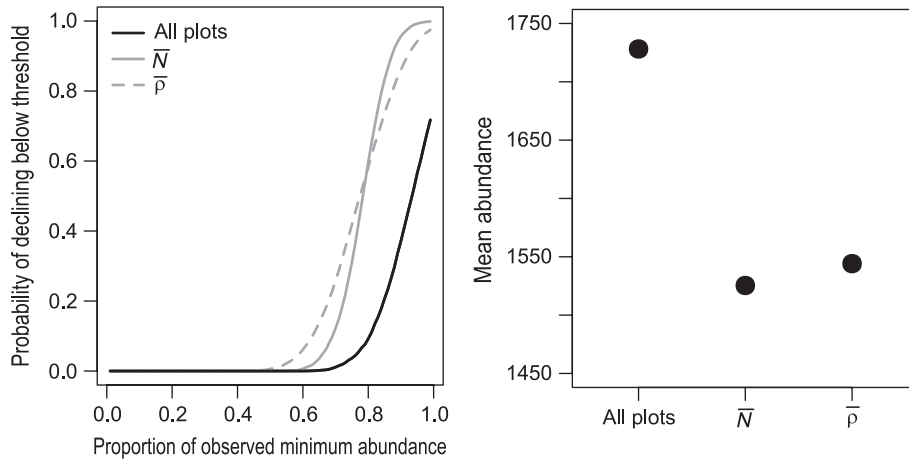


FIG. 3. Relative importance of different types of plot heterogeneity. Comparison of simulations including all plots (solid black line) with simulations removing the five plots with either the highest abundance (\bar{N} , solid gray line) or lowest mean correlation coefficient ($\bar{\rho}$, dashed gray line) for mean population abundance (right) and risk of declining below the observed minimum abundance within 100 yr (left).

log λ : $F = 0.56$, $df = 48, 784$, $P = 0.99$; Appendix S1: Table S3). Further, the most synchronous plots exhibited declines in both log abundance and log λ with the highest June temperatures (Appendix S1: Table S3; Fig. 5). Conversely, annual variation in log abundance and log λ were not significantly related to June temperature in asynchronous plots (Appendix S1: Table S3; Fig. 5). Repeating these analyses with residuals in log λ from a Ricker model did not alter these results (Appendix S1: Table S3).

June temperature also influences the overall strength and pattern of synchrony and population stability. Because of the effect of June temperature in driving synchrony among more synchronous plots (Fig. 5), using 5-yr subsets of the data with similar temperatures resulted in lower estimates of synchrony and higher estimates of the portfolio effect, relative to estimates across the entire

20-yr time series. However, by comparing among temperature quartiles, we found a reduction in population stability in warmer years. Population-level synchrony is stronger in warmer years (Fig. 6A), due to a shift toward more positive correlation coefficients in log λ among plots (Fig. 6B). Similarly, portfolio effects were weakest in the warmest quarter of years (Fig. 6C). Stronger portfolio effects occurred for all three of the other quartiles, with the strongest portfolio effects occurring for years close to median temperatures. Confidence intervals for these estimates, obtained by resampling plots with replacement, were very large (Fig. 6), indicating the importance of a few asynchronous plots in driving these patterns. When plots were resampled with replacement, portfolio effects were weaker and synchrony was stronger in the warmest quartile, relative to the second quartile, in

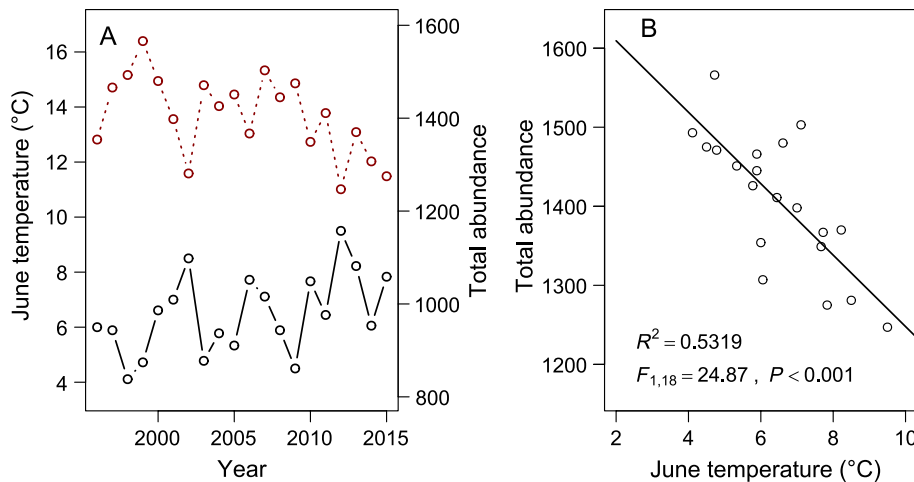


FIG. 4. Annual variation in *Saussurea weberi* abundance in relation to mean June temperature. (A) Annual variation in mean June temperature (solid line) and total abundance of *S. weberi* (dashed line). (B) Annual abundance declines with increasing June temperatures. [*Colour figure can be viewed at wileyonlinelibrary.com*]

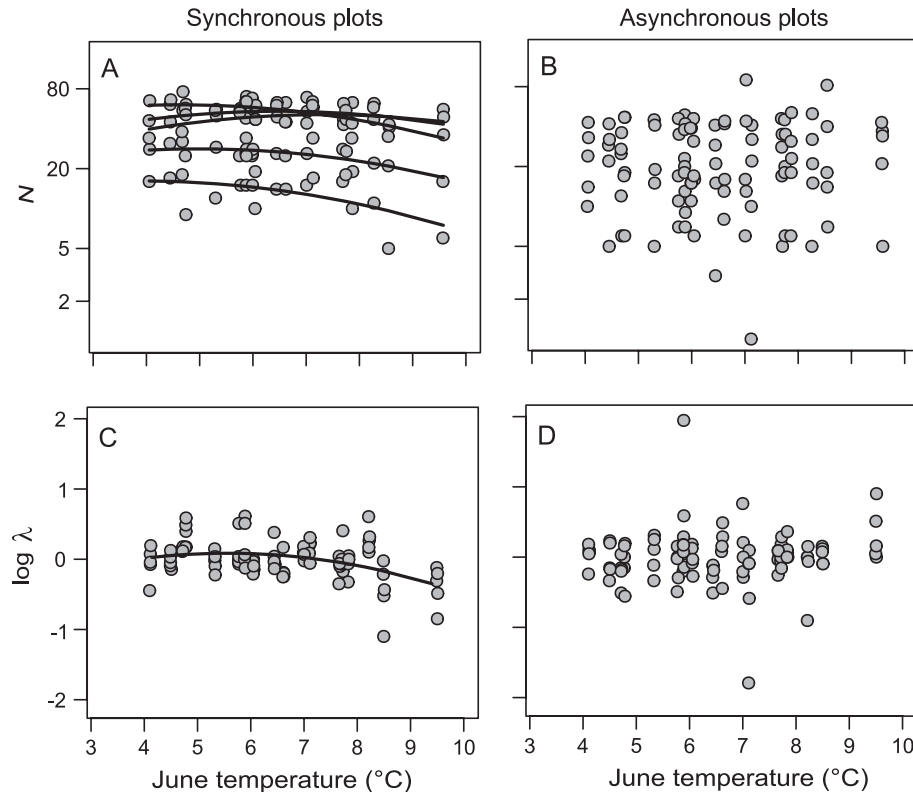


FIG. 5. Synchrony among plots is partially driven by similar responses to June temperature. Regression lines from the best-fit models for each group and response variable (Appendix S1: Table S3). (A and B) Annual abundance and (C and D) annual $\log \lambda$ within plots as a function of June temperature for the five plots with the highest (A and C; synchronous) and lowest (B and D; asynchronous) mean correlation coefficients. Note that the y -axis in panels A and B is on a log scale.

81% and 55% of the bootstrapped data sets, respectively. Finally, mean June temperature has increased during the 20-yr study period (Fig. 6D; year, $\beta = 0.112$, $t = 2.184$, $P = 0.042$).

DISCUSSION

The mechanisms that stabilize small populations in the face of environmental variability are crucial to their conservation (Boyce et al. 2006). Here, we show that weakly or negatively correlated responses across small spatial scales play an important role in stabilizing a population of a rare alpine perennial plant, *S. weberi*. Yet stabilizing mechanisms may themselves change with environmental shifts, potentially leading to rapid declines in abundance (Doak and Morris 2010, Lawson et al. 2015). For *Saussurea*, plot-level dynamics become more synchronous and population stability is reduced as June temperature increases, as it has over the last 20 yr at this population's location.

Small-scale spatial heterogeneity and population persistence

Diversity–stability relationships have been demonstrated at ecosystem and community scales (Loreau et al.

2001, Tilman et al. 2006, Cardinale et al. 2007, Thibaut et al. 2012), and more recently among habitats or life history strategies within populations (Schindler et al. 2010, Anderson et al. 2013, Thorson et al. 2014). We examined temporal variation in abundance of *S. weberi* across 1-m² plots and found diverse responses to June temperature at even this small spatial scale. Accounting for this diversity in population models reduced the probability of decline relative to a model where all plots are strongly synchronous. Although less-studied, such small-scale diversity in dynamics, either among genotypes or microhabitats, may be an important stabilizing mechanism within populations, particularly in sessile organisms. Critically, this implies that data from small sub-samples of a population may overestimate the temporal variability, and thus the risk of decline, of the entire population. Additional simulations could address how the degree of response diversity and potential for dispersal among sub-groups affects the magnitude of portfolio effects and the potential for bias in population models.

In this study, we cannot distinguish whether asynchrony among plots is due to genotypic or micro-environmental interactions with June temperature. These plots are located in alpine tundra on limestone-derived soils and do not span any obvious habitat boundaries. However, several

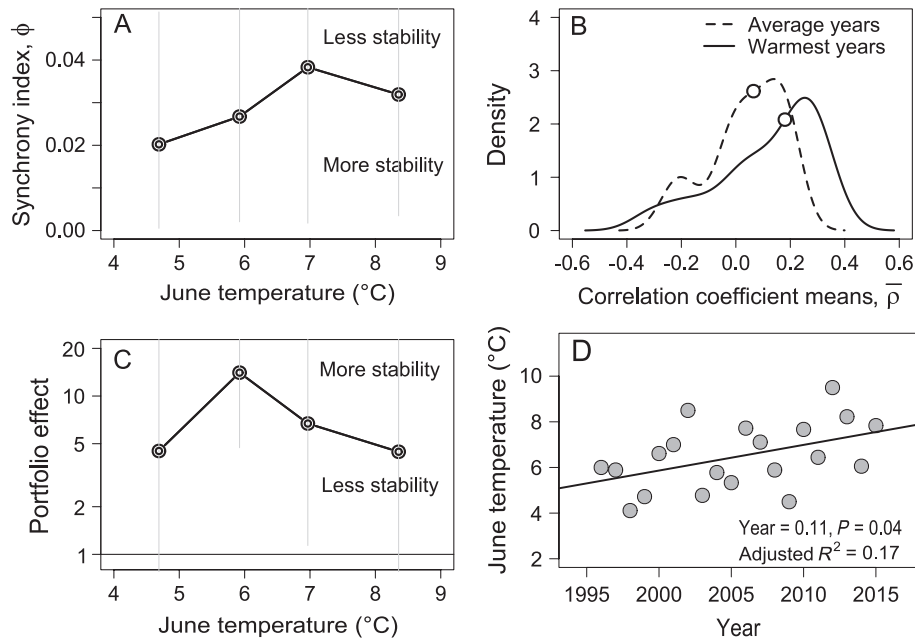


FIG. 6. Among-plot synchrony and portfolio effects are influenced by mean June temperature. (A) Population-level synchrony index and (C) portfolio effect estimates for 5-yr subsets of the 20-yr time series based on June temperature quartiles. The x -axis gives the mean June temperature within each subset. Gray lines in panels A and C give the bias-corrected and accelerated confidence intervals (BCa) from 2,000 bootstrap replicates; upper confidence limits exceed the scale of these plots. Note: the y -axis in panel C is on a log scale. (B) The frequency distribution of correlation coefficient plot means in the second quartile (dashed line) and the fourth and warmest quartile (solid line) created using the density function in R. Circles give the medians of each distribution. (D) June temperature has increased across the 20-yr time series (slope, P value, and adjusted R^2 are given for a regression of temperature on year).

environmental variables are likely to differ among plots, including local nutrient availability, micro-topography, the intensity of grazing or competition, and the frequency of soil disturbance. Although we did not detect any environmental features separating asynchronous plots from the rest of the population, it is probable that multiple unobserved or even unobservable aspects of the local environment influence the effects of June temperature within these plots. Alternatively, genotype-by-environment interactions could drive plot asynchrony. *Saussurea weberi* can produce new shoots clonally, and plots at this small spatial scale could represent different genets with similar or divergent temperature responses. Importantly, accounting for density dependence using Ricker models did not alter the magnitude of correlations among plots. This suggests that density dependence within plots is not driving these asynchronous responses in *S. weberi*. However, in other systems, density dependence at fine spatial scales could act to either increase or decrease synchrony and its population effects.

Regardless of the mechanisms, response diversity has important consequences for population persistence and should be considered in conservation planning (Hilborn et al. 2003, Anderson et al. 2015). In our population models, loss of the five most asynchronous plots, representing only 10% of the *S. weberi* population, had a greater impact on the risk of a dramatic decline than loss of 23% of the population in the most abundant plots. Similarly, studies of

portfolio effects in salmon suggest that conserving diversity in life history, thermal tolerance, or other sub-population characteristics stabilizes overall fishery abundances (Moore et al. 2010, Thorson et al. 2014, Anderson et al. 2015). Thus, conservation of asynchronous groups, including those living in different microhabitats or different genotypes, will be more effective than conservation prioritization based on abundance alone (Earn et al. 2000).

Stabilizing mechanisms in a warming world

Populations are increasingly impacted by shifts in climate regime (Parmesan and Yohe 2003, Chen et al. 2011). Systematic changes in the mean and variability of local climate can have profound impacts on population growth rates (Lawson et al. 2015). Here, we demonstrate an additional consequence of climate change: the loss of population stability through portfolio effects. Although spatial asynchrony has stabilized the abundance of *S. weberi* over the past 20 yr, we find evidence that this stabilizing mechanism may be sharply reduced with future environmental change. Specifically, among-plot synchrony increased and population-level stability decreased in the warmest years of the study period. Growth rates and abundances within synchronous plots also declined with the warmest June temperatures. Further, June temperatures have steadily increased over the 20-yr census period. Decreased population growth rates combined

with greater synchrony among plots suggest that *S. weberi* could decline rapidly with continued warming.

We examined population synchrony and portfolio effects across temperature quartiles to explore the impact of changing climate on population persistence. One advantage of this approach is that it captures changes in stability during the most extreme climate conditions. However, these analyses also require long-term data to encompass sufficient climate variation and an understanding of the climatic variables that drive population dynamics; even a 20-yr study provides scant data for such explorations. Other studies have compared stability through time using sliding window analysis or by comparing early and late portions of the time series, then correlating changes in stability with temporal shifts in other environmental factors (Moore et al. 2010, Satterthwaite and Carlson 2015). Alternatively, experimental manipulations could potentially be used to quantify portfolio effects under current and future climate regimes (e.g., Thompson et al. 2015). By testing for environmental or temporal shifts in population stability, we can gain a broader understanding of the strength of portfolio effects within populations and the sensitivity of such effects to changing climate.

Taken together, our findings suggest that (1) portfolio effects can operate at small scales to stabilize populations even in the absence of obvious habitat or life history variation, and (2) such stabilizing mechanisms can weaken with directional environmental changes. The loss of stabilizing mechanisms could magnify and accelerate the negative impacts of climate change in small populations.

ACKNOWLEDGMENTS

With regard to the field work portion of this project, thanks to all agencies that contributed financial support; special thanks, also, to Barbara Siems for years of logistical support, to Mr. Will Ewing and Mr. Clifford Trentman for permission to access field sites, and to field assistants Barry, Obie, and Steiger for their invaluable help. Support for analysis and modeling came from NSF DEB-1242355 and DEB-1340024.

LITERATURE CITED

- Abbott, R. E. 1998. Aspects of the pollination biology of a rare alpine calciphile, *Saussurea weberi* Hult n (Asteraceae) (M.S. thesis). University of Northern Colorado, Greeley, Colorado, USA.
- Acker, P., A. Robert, R. Bourget, B. Colas, and M. Johnson. 2014. Heterogeneity of reproductive age increases the viability of semelparous populations. *Functional Ecology* 28:458–468.
- Anacker, B. L., and S. Y. Strauss. 2014. The geography and ecology of plant speciation: range overlap and niche divergence in sister species. *Proceedings of the Royal Society B* 281:20132980.
- Anderson, S. C., A. B. Cooper, N. K. Dulvy, and D. Hodgson. 2013. Ecological prophets: quantifying metapopulation portfolio effects. *Methods in Ecology and Evolution* 4:971–981.
- Anderson, S. C., J. W. Moore, M. M. McClure, N. K. Dulvy, and A. B. Cooper. 2015. Portfolio conservation of metapopulations under climate change. *Ecological Applications* 25:559–572.
- Barton, K. 2014. MuMIn: multi-model inference. R package version 1.10.0. <http://cran.r-project.org/package=MuMIn>
- Bates, D., M. Maechler, and B. Bolker. 2011. lme4: linear mixed-effects models using S4 classes. <http://CRAN.R-project.org/package=lme4>
- Boyce, M. S., C. V. Haridas, C. T. Lee, and The Nceas Stochastic Demography Working Group. 2006. Demography in an increasingly variable world. *Trends in Ecology & Evolution* 21:141–148.
- Brown, J. H. 1984. On the relationship between abundance and distribution of species. *American Naturalist* 124:255–279.
- Canty, A., and B. Ripley. 2016. boot: bootstrap R (S-Plus) functions. <https://cran.r-project.org/package=boot>
- Cardinale, B. J., J. P. Wright, M. W. Cadotte, I. T. Carroll, A. Hector, D. S. Srivastava, M. Loreau, and J. J. Weis. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences USA* 104:18123–18128.
- Chen, I.-C., J. K. Hill, R. Ohlem ller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026.
- Colorado Natural Heritage Program. 1997. Colorado rare plant guide. www.cnhp.colostate.edu
- Crone, E. E. 2016. Contrasting effects of spatial heterogeneity and environmental stochasticity on population dynamics of a perennial wildflower. *Journal of Ecology* 104:281–291.
- Doak, D. F., D. Bigger, E. K. Harding, M. A. Marvier, R. E. O'Malley, and D. Thomson. 1998. The statistical inevitability of stability–diversity relationships in community ecology. *American Naturalist* 151:264–276.
- Doak, D. F., and W. F. Morris. 2010. Demographic compensation and tipping points in climate-induced range shifts. *Nature* 467:959–962.
- Drake, J. M., and D. M. Lodge. 2004. Effects of environmental variation on extinction and establishment. *Ecology Letters* 7:26–30.
- Earn, D. J. D., S. A. Levin, and P. Rohani. 2000. Coherence and conservation. *Science* 290:1360–1364.
- Ehrlich, P. R., and G. C. Daily. 1993. Population extinction and saving biodiversity. *Ambio* 22:64–68.
- Elmqvist, T., C. Folke, M. Nystr m, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and Evolution* 1:488–494.
- Elston, D. A., R. Moss, T. Boulinier, C. Arrowsmith, and X. Lambin. 2001. Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. *Parasitology* 122:563–569.
- Engen, S., R. Lande, and B. E. Saether. 2002. The spatial scale of population fluctuations and quasi-extinction risk. *American Naturalist* 160:439–451.
- Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* 8:50–59.
- Gavrilets, S., H. Li, and M. D. Vose. 2000. Patterns of parapatric speciation. *Evolution* 54:1126–1134.
- Ginzburg, L. R., S. Ferson, and H. R. Ackakaya. 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. *Conservation Biology* 4:63–70.
- Hallett, L. M., et al. 2014. Biotic mechanisms of community stability shift along a precipitation gradient. *Ecology* 95:1693–1700.
- Harrison, X. A. 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ* 2:e616.
- Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences USA* 100:6564–6568.

- Inchausti, P., and J. Halley. 2003. On the relation between temporal variability and persistence time in animal populations. *Journal of Animal Ecology* 72:899–908.
- Isaak, D. J., R. F. Thurow, B. E. Rieman, and J. B. Dunham. 2003. Temporal variation in synchrony among chinook salmon (*Oncorhynchus tshawytscha*) redd counts from a wilderness area in central Idaho. *Canadian Journal of Fisheries and Aquatic Sciences* 60:840–848.
- Jochimsen, M. C., R. Kummerlin, and D. Straile. 2013. Compensatory dynamics and the stability of phytoplankton biomass during four decades of eutrophication and oligotrophication. *Ecology Letters* 16:81–89.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241:1455–1460.
- Lawson, C. R., Y. Vindenes, L. Bailey, and M. van de Pol. 2015. Environmental variation and population responses to global change. *Ecology Letters* 18:724–736.
- Lawton, J. H. 1993. Range, population abundance and conservation. *Trends in Ecology & Evolution* 8:409–413.
- Leimu, R., P. I. A. Mutikainen, J. Koricheva, and M. Fischer. 2006. How general are positive relationships between plant population size, fitness and genetic variation? *Journal of Ecology* 94:942–952.
- Lewontin, R. C., and D. Cohen. 1969. On population growth in a randomly varying environment. *Proceedings of the National Academy of Sciences USA* 62:1056–1060.
- Loreau, M., and C. de Mazancourt. 2008. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *American Naturalist* 172:E48–E66.
- Loreau, M., et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–808.
- Lynch, M., J. Conery, and R. Burger. 1995. Mutational meltdowns in sexual populations. *Evolution* 49:1067–1080.
- Matthies, D., I. Brauer, W. Maibom, and T. Tschardt. 2004. Population size and the risk of local extinction: empirical evidence from rare plants. *Oikos* 105:481–488.
- Moore, J. W., M. McClure, L. A. Rogers, and D. E. Schindler. 2010. Synchronization and portfolio performance of threatened salmon. *Conservation Letters* 3:340–348.
- Moore, J. W., J. D. Yeakel, D. Peard, J. Lough, and M. Beere. 2014. Life-history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds. *Journal of Animal Ecology* 83:1035–1046.
- Morris, W. F., and D. F. Doak. 2004. Buffering of life histories against environmental stochasticity: accounting for a spurious correlation between the variabilities of vital rates and their contributions to fitness. *American Naturalist* 163:579–590.
- O'Grady, J. J., B. W. Brook, D. H. Reed, J. D. Ballou, D. W. Tonkyn, and R. Frankham. 2006. Realistic levels of inbreeding depression strongly affect extinction risk in wild populations. *Biological Conservation* 133:42–51.
- Opdam, P., and D. Wascher. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation* 117:285–297.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences USA* 95:213–218.
- Preston, F. W. 1948. The commonness, and rarity, of species. *Ecology* 29:254–283.
- R Core Development Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org>
- Reed, T. E., V. Grotan, S. Jenouvrier, B. E. Saether, and M. E. Visser. 2013. Population growth in a wild bird is buffered against phenological mismatch. *Science* 340:488–491.
- Satterthwaite, W. H., and S. M. Carlson. 2015. Weakening portfolio effect strength in a hatchery-supplemented Chinook salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences* 72:1860–1875.
- Schindler, D. E., J. B. Armstrong, and T. E. Reed. 2015. The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment* 13:257–263.
- Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465:609–612.
- Schorr, R. A. 2013. Using distance sampling to estimate density and abundance of *Saussurea Weberi* Hultén (Weber's Saw-Wort). *Southwestern Naturalist* 58:378–383.
- Sinclair, A. R. E., and R. P. Pech. 1996. Density dependence, stochasticity, compensation and predator regulation. *Oikos* 75:164–173.
- Spackman, S., G. Doyle, and D. G. Anderson. 2001. Visiting insect diversity and visitation rates for two globally-imperiled plant species in Colorado's Mosquito Range. Colorado Natural Heritage Program, Fort Collins, Colorado, USA.
- Stacey, P. B., and M. L. Taper. 1992. Environmental variation and the persistence of small populations. *Ecological Applications* 2:18–29.
- Stanley, S. M. 1986. Population size, extinction, and speciation: the fission effect in Neogene bivalvia. *Paleobiology* 12:89.
- Thibaut, L. M., and S. R. Connolly. 2013. Understanding diversity-stability relationships: towards a unified model of portfolio effects. *Ecology Letters* 16:140–150.
- Thibaut, L. M., S. R. Connolly, and H. P. A. Sweatman. 2012. Diversity and stability of herbivorous fishes on coral reefs. *Ecology* 93:891–901.
- Thompson, P. L., B. E. Beisner, and A. Gonzalez. 2015. Warming induces synchrony and destabilizes experimental pond zooplankton metacommunities. *Oikos* 124:1171–1180.
- Thorson, J. T., M. D. Scheuerell, E. R. Buhle, and T. Copeland. 2014. Spatial variation buffers temporal fluctuations in early juvenile survival for an endangered Pacific salmon. *Journal of Animal Ecology* 83:157–167.
- Tilman, D., C. L. Lehman, and C. E. Bristow. 1998. Diversity-stability relationships: statistical inevitability or ecological consequence? *American Naturalist* 151:277–282.
- Tilman, D., P. B. Reich, and J. M. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441:629–632.
- Tuljapurkar, S., and S. H. Orzack. 1980. Population dynamics in variable environments 1. Long-run growth rates and extinction. *Theoretical Population Biology* 18:314–342.
- Willi, Y., J. van Buskirk, and A. A. Hoffman. 2006. Limits to the adaptive potential of small populations. *Annual Review of Ecology, Evolution, and Systematics* 37:433–458.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.1738/supinfo>