

Individual variation and ecotypic niches in simulations of the impact of climatic volatility

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ABSTRACT

Expectations of the impacts of climatic variation on species can depend on whether and how intraspecific variability is incorporated in models. Coefficients of variation from tree-ring records of *Pinus albicaulis* through time and across space were used to parameterize volatility and individuality, respectively. The records across sites were used to differentiate the average modes on an environmental gradient for Gaussian fitness of ecotypic niches, and to add further individual variation in mode and standard deviation of these functions in individual-based Monte Carlo simulations of reproduction and mortality with inheritance of individual variability. Ecotypic gamma and Shannon diversity decreased with volatility included, however, the decreases were mitigated by niche differentiation, but not individual-level variability. Increasing climatic volatility may threaten biodiversity, but less so if a species has ecotypes as represented by ecotypic niches in the model. The results illustrate the usefulness of these parameterizations and of simulations versus analytical solutions.

1. Introduction

1.1. Background

Ongoing global climate changes will likely include change in climate variability and extremes (Easterling et al., 2000; Rahmstorf and Coumou, 2011; hereafter climatic volatility, because climate scientists use variability for any type of change). This type of change could have ecological consequences at least as great as changes in mean climate (e.g., Vasseur et al., 2014). Of primary concern is whether climatic volatility will cause extinctions and lower biodiversity (Urban, 2015; Malanson et al., 2017). However, the consequences will likely be buffered by both interspecific and intraspecific variability in fitness relative to environment, such as through phenotypic plasticity (e.g., Valladares et al., 2014; Ashander et al., 2016). Our objective is to assess how tree rings can indicate climatic volatility and intraspecific variability in fitness and how these factors might affect the intraspecific diversity of populations.

The potential for increasing climatic volatility, is important (e.g., IPCC, 2012) and contentious (Alexander and Perkins, 2013). Observations and model results are inconsistent. Increases in variance over the past century have been reported (Easterling et al., 2000; Meehl et al., 2000; Rahmstorf and Coumou, 2011), including some based on

biological indicators (Millar et al., 2007; Li et al., 2011, 2013; Fowler, 2012). Geographically specific studies based on ice core (Huntingford et al., 2013) and arctic temperature data (Screen, 2014) do not show trends, however, and methodologies for projecting extremes are uncertain (Sippel et al., 2015).

Interspecific and intraspecific variability in fitness in relation to climatic gradients could affect species abundance and survival in periods of climate change. Adler et al. (2006) found that climatic variability resulted in coexistence through the temporal storage effect, and concluded that future increases in climatic volatility could strengthen this effect. Newer work has indicated that intraspecific variability may interact with environmental variability in maintaining coexistence (e.g., Violle et al., 2012; Han et al., 2016; Turcotte and Levine, 2016; Martinez-Garcia and Tarnita, 2017). Clark (2010) showed that populations were able to coexist based on the variation in demographic traits among the individuals within them. Other work, however, indicated that intraspecific variation could reduce coexistence. Barabas and D'Andrea (2016) reported that intraspecific variation reduced coexistence in a 2-species model unless the variation differed so that a specialist and a generalist with the same mean traits coexisted. Hart et al. (2016) modeled nonlinear averaging, trait variation, and stochastic demography and found that the three, in combination, decreased coexistence. In their model the potential for individual

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variation to reduce niche differentiation was a key explanation. Hausch et al. (2018) found some resolution to this apparent contrast in experiments in which whether intraspecific variability decreased or maintained coexistence depended on mis- or evenly-matched competition in a stable environment.

Efforts to include intraspecific variation in simulations follow a number of directions, of which individual-based models have been important. Brown et al. (2007) used measures of plant parts to parameterize a spatially explicit simulation using resource distribution as the base for population processes that resulted in differences in genotype diversity. Kautz et al. (2014) incorporated variability among bark beetles in a spatially explicit simulation to examine system-level infestation. Laughlin and Joshi (2015) examined interactions of traits and environmental gradients to relate intraspecific variability and niche dimension. Malanson (2018) reported on simulations that showed increasing climatic volatility might not be mitigated by interspecific and individual variability because some effects of negative climatic anomalies, such as extinctions, could not be balanced by positive ones. Individual-based models allow representation of intraspecific variability, but their ability to separate species, subspecies or ecotypes, and individual levels has not been fully exploited.

1.2. Rationale

The aim of this paper is to further explore the effects of climatic volatility on populations with and without intraspecific variability in fitness on an environmental gradient. We ask: with climatic volatility, would a population with the fitness of individuals distributed along an environmental gradient differ in diversity metrics from one where the individuals were identical? Gause (1934) and Chesson (2000) would lead us to expect that volatility, which increases mortality and extinctions, could also slow competitive exclusion so diversity could persist longer. Therefore, the effect of volatility is not certain. As a result, our expectations become:

- Greater volatility leads to greater intraspecific diversity unless it increases extinction.
- Intraspecific variability supports greater diversity at levels of volatility that increase extinction.

To examine these propositions, we used a novel parameterization of a gridded individual-based model to examine the effects of different aspects of variability on diversity (Fig. 1). We used coefficients of variation from measurements of tree-ring-width data through time and across space to parameterize volatility and individuality, respectively. Two summaries of the latter were used to differentiate two levels of intraspecific variation: niche (different average modes on an environmental gradient for Gaussian fitness functions) and individual variability (individual variation in mode and standard deviation of these functions). Reproduction and mortality were simulated, and composite metrics of diversity were calculated.

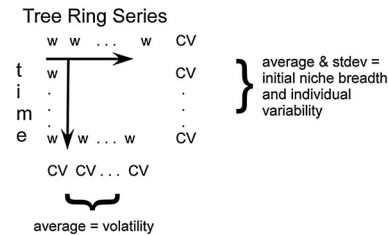
2. Material and methods

2.1. Tree-ring data

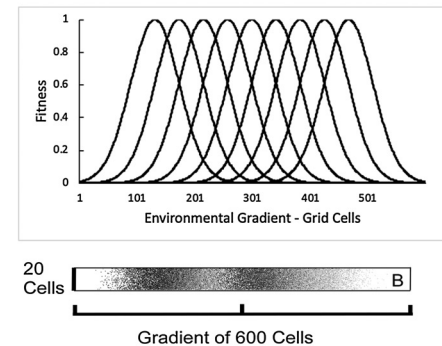
We used tree-ring data to guide selection of parameters for the initial niche breadths and separation of the Gaussian distributions of fitness on an environmental gradient (Fig. 1), its variation among individuals, and for climatic volatility. The stages were:

- 1 Calculate the standard deviation, σ , of niche breadth from the average coefficient of variation (CV) of site chronologies of tree-ring widths across trees in the same year (Fig. 1, upper, across rows), which is also used to parameterize differences among ecotypes.
- 2 Calculate the CV through years for all trees, not site chronologies,

A. First, parameters:



B. Then, initialization and simulation:



C. Followed by analysis:

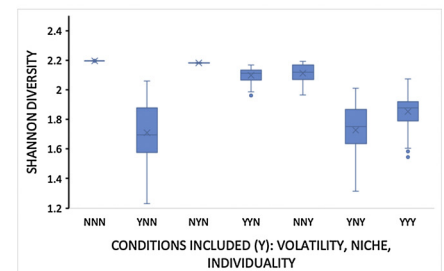


Fig. 1. Conceptual diagram of the major steps of the modeling project. First, the variability among individuals and populations and the volatility of the climate are based on the coefficient of variation (CV) of tree rings (w are widths): in the same year (across rows) and through time (down columns), respectively (panel A). Then, these population values were used to parameterize nine virtual ecotypes using Gaussian niche functions (panel B, top) to simulate processes on grids of cells (panel B, bottom). The simulations created output in diversity metrics for differences among initial conditions with and without (Y or N) volatility, niche, and individuality (example result for Shannon diversity shown in panel C).

the average of which is used to parameterize individual variability.

3 Calculate the volatility from the average CV of tree-ring widths through years (Fig. 1, upper, down columns).

We used 14 site chronologies with 940 individual tree-ring series for *Pinus albicaulis* from the International Tree-Ring Data Bank (ITRDB; www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring). These were chronologies from the northern Rocky Mountains that had at least 400 years of record within the past 500 years. Tree-ring data provided an internally consistent indication of both environmental variation (here volatility, down the columns of standardized increments) and biological variability (here individual variability, across the columns of individual trees) as measures contained within the same data (year x tree tables; Fig. 1, upper) where referral to human-defined data (i.e., measures of climate) were unnecessary. The tree-ring data were cross-dated in ITRDB, to ensure calendar year resolution, and we standardized to remove the biological growth trend of decreasing

widths with age, but without variance stabilization or autoregressive modeling, using ARSTAN (Cook and Krusic, 2005)

First, to set equal niche breadth of ecotypes we calculated the coefficient of variation (CV) of the chronologies of 14 sites for each year in which all had a record and then took the average CV. Although the variation captured by this CV includes that caused by spatial environmental differences across sites in addition to tree growth in a single year (as well as sample error), we used it to represent the niche differentiation of ecotypes.

Second, to set the variability of the individuals, we calculated the CVs of all individual series across years for every year in which at least 100 trees had a record. We used the average of these CVs.

Third, to represent climatic volatility we calculated the CV of the standardized tree-ring series through all years for each tree (here, down columns in Fig. 1, whereas above it was across rows). The average of these CVs represented the volatility of the environment of this species across its range in the northern Rocky Mountains (V_v). *P. albicaulis* evolved to survive in a volatile environment, but its growth as indicated in tree rings is relatively complacent (Perkins and Swetnam, 1996; Luckman et al., 1997). The data used preceded the recent extensive die-back caused by blister rust.

2.2. Model design and initialization

The simulation was designed and implanted as outlined following a simplified ODD protocol (Grimm et al., 2010). The ODD protocol categories included:

2.2.1. Purpose

The model simulated population dynamics for a species on an environmental gradient for cases with and without intraspecific individual variation and with or without climatic volatility.

2.2.2. Design concepts

The mode and standard deviation of Gaussian fitness functions on an environmental gradient could differ among individuals. The terms of this variation were inherited by offspring. Individuals interacted indirectly by occupying space. Climatic volatility was examined by shifting the underlying environmental gradient relative to the individual fitness distributions. Processes were stochastically implemented via Monte Carlo routines with a uniform random number generator. Gamma and Shannon diversity over the grid were observed at each iteration.

2.2.3. Entities, state variables, scales

To address our questions, we needed to simulate ecotypes with initially identical niche breadth evenly distributed on an environmental gradient, represented by a grid of cells, and so we created an arbitrary nine ecotypes (so that some persist with eventual extinctions) ecotypes having Gaussian distributions of fitness on the gradient (Fig. 1, middle). The environmental gradient was represented by grid of 425 cells in breadth, which is arbitrary and simply long enough to encompass all species without spatial constraints. The height of the grid allows some redundancy and is wrapped into a cylinder to avoid edge effects; the height was set at 20 cells. Only one individual occupied a cell.

2.2.4. Initialization

Given that the initial distributions of fitness were identical, we used the tree-ring data from a single species to parameterize the niche breadth for the nine virtual ecotypes and their intraspecific variability as well as climatic volatility. While an arbitrary niche breadth and variability would suffice, we based ours on observations to limit unrealistic parameterization, but the simulation may not represent a particular species. The fitness distribution of each species was calculated as:

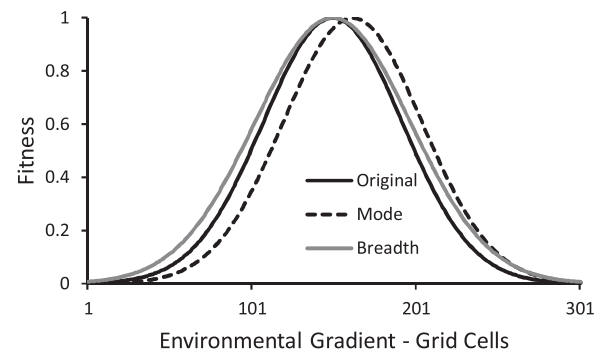


Fig. 2. For one of the subspecies in Fig. 1, middle, its mode and standard deviation changed to represent individual-level variability. The original mode was set at the middle of the environmental gradient and its standard deviation, 42 cells, was derived from tree ring data.

$$D_s = \exp(-((x-\mu_s)^2/2\sigma_s^2)) \quad (1)$$

with x the grid column of the cell, μ_s the modal grid column and σ_s^2 the variance of the fitness distribution of the ecotype, s .

For the first level of intraspecific variability the modes for the nine ecotypes were equally spaced along the gradient with the middle one at the 200th cell to represent ecotypic niche differentiation. The cases without niche were modeled by using the central mode, cell 300, for all nine ecotypes (only the central fitness function in Fig. 1, middle). We used the average of the first CV in the tree ring analyses as the standard deviation in number of cells on the gradient for the niche breadth of the initial distributions. Given this breadth, the distance between modes was set at σ of the Gaussian distributions so that competition would be high.

For the second level of intraspecific variability, individual-level variability, we used a multiplier from the CVs of the individual tree-ring series. The average of this CV was used as the standard deviation of a random-normal distribution, with a mean of 1, from which a multiplier was drawn for every individual. This multiplier for intraspecific variability, F_i , was used to alter the position of the mode and the variance of the fitness distribution from the ecotype standard (Fig. 2; as noted by Laughlin and Joshi, 2015); F_i was limited to a range of 0–2 given the weak connection between growth and the demographic processes simulated.

To initialize the populations, 50,000 trials were run in which a random species and a random grid cell was chosen, and whether it established or not was determined as a function of the ecotype fitness at that cell. Initialization resulted in the nine ecotypes being evenly mixed on the gradient in the cases without variability and separated, but with considerable overlap, in the cases with intraspecific variability (Fig. 1, middle).

2.2.5. Process overview and scheduling

At each iteration the gradient shifted back and forth to represent climatic volatility; the number of cells offset from the original gradient at each iteration was derived from tree-ring data. The CV from the third tree-ring step, above, was used to determine a random number of grid cells (V_v) on the gradient, offset from the individuals' initial mode (fractions were rounded to an integer number of cells). This value was drawn once every iteration and applied to all reproduction and mortality chances; i.e., the climate in each year varies so the calculation of volatility can be visualized as having the environmental gradient shift back and forth under the simulated individuals.

To combine volatility and individual variability in the reproduction and mortality of individuals at each iteration, the mode and niche breadth of fitness were included in functions of the Monte Carlo simulation. Reproduction (R_{xti}) was varied for individuals with an addition for volatility (V_v) and a multiplier for intraspecific variability (F_i).

The multiplier was applied to both the modal position of the niche and to its variance, and so we used its square root, $\sqrt{F_i}$, twice:

$$R_{x_{ti}} = \exp(-(x + V_i) - \mu\sqrt{F_i})^2 / 2\sigma^2\sqrt{F_i} \quad (2)$$

where V_i is the volatility in number of cells to be added to shift the environment on the gradient in a given iteration, and F_i is the multiplier that moves the mode and changes the niche breadth of the individual. Volatility was computed at each iteration with a random-normal number with a mean of zero and a standard deviation derived from tree-ring data indicative of climatic volatility. Intraspecific variability was similarly computed (mean = 1, standard deviation derived from tree-ring data indicative of intraspecific variability). For mortality, the rate was halved because while reproduction should be as sensitive as growth to environmental variation, mortality is not (the trees survived the variability indicated), and so:

$$M_{x_{ti}} = 2e^{-(x + V_i/2) - \mu\sqrt{F_i})^2 / 2\sigma^2\sqrt{F_i}} \quad (3)$$

The rates for reproduction ($R_{x_{ti}}$) and mortality ($M_{x_{ti}}$) of each individual at its cell on the environmental gradient was used in the Monte Carlo calculations. Each produced a propagule at probability $R_{x_{ti}}$. Given unknowns for parameterizing dispersal kernels, the propagule was dispersed to a random cell on the grid, which it occupied if empty (ubiquitous dispersal decreased alpha diversity by 8% or less relative to a Gaussian kernel with a standard deviation (σ) of 42 cells in limited trials). Then all individuals experienced mortality at probability $1 - M_{x_{ti}}$.

We ran combinations without and with volatility, niche differentiation (single mode and different modes), and individual variability, each for 500 iterations, after which most values were close to equilibrium, and for 50 replications, of which averages are reported. We implemented the simulation on the Netlogo platform (Wilensky and NetLogo, 1999). The model is available at ir.uiowa.edu attached to a link to this paper.

2.3. Diversity metrics

We report two metrics of diversity: gamma diversity (the number of extant ecotypes) and Shannon diversity (which captures evenness more than richness). We used a General Linear Model for ANOVA with Tukey post hoc tests for comparisons to determine differences among the cases.

3. Results

Across the chronologies of *P. albicaulis* in a given year, the average CV was 0.24. This value was used to set the same niche width for all ecotypes. This and the CV of the individuals (0.52) were used in determining the multiplier, F_i . The average of the CVs for the temporal records was 0.21 which was used to set the volatility (V_i).

The diversity metrics differed dramatically with volatility, and given no variance for gamma diversity we did not test this factor further (Table 1; except to note that ANOVA and Tukey without volatility both niche and individual variability lowered Shannon diversity slightly but significantly). The proportional changes in Table 1 showed that volatility without any niche differentiation or individual variability lowered gamma diversity by 11% and Shannon diversity by 25%. Niche differentiation mitigated these losses, which indicated that extinctions occurred in fewer simulation replications, and ecotype populations were more even (Table 1). The loss of gamma diversity was minimal, however. The significant differences in ANOVA were confirmed by the Tukey tests.

With volatility, the effect of niche differentiation was significant but small for gamma diversity, for which the error in ANOVA was 95% of the model, and individual variability did not have a significant effect (Table 2). For Shannon diversity, niche differentiation had a large,

Table 1

Mean (and standard deviation) for diversity metrics for cases with exclusion (N) or inclusion (Y) of volatility, niche differentiation, and individual-level variability.

Volatility/Niche/Individuality	Gamma diversity	Shannon diversity, H'
N/N/N	9(0)	2.20(0.000)
N/Y/N	9(0)	2.182(0.002)
N/N/Y	9(0)	2.172(0.011)
N/Y/Y	9(0)	2.043(0.035)
Y/N/N	7.98(1.286)	1.64(0.259)
Y/Y/N	8.98(0.141)	2.09(0.052)
Y/N/Y	8.94(0.240)	1.860(0.144)
Y/Y/Y	8.90(0.303)	2.011(0.064)
Proportional change caused by volatility		
Y/N/N	0.887	0.745
Y/Y/N	0.998	0.958
Y/N/Y	0.993	0.856
Y/Y/Y	0.989	0.984

significant effect, and accounted for slightly more than half of the ANOVA model.

4. Discussion

Individual-based simulations were run that combined climatic volatility with ecotypic niche differentiation and individual-level variability. In the absence of volatility neither niche differentiation or individual variability, or their combination, increased diversity, whereas niche differentiation mitigated losses of diversity with volatility. Maintenance of diversity without either niche differentiation, or individual-level variability and no volatility, would seem to contradict Gause's (1934) principle; but a minor competitive advantage for one ecotype would have to be maintained indefinitely – and this is unlikely to occur with stochastic demographics. This result illustrates the potential usefulness of simulations, showing iterations or time, versus analytical solutions.

The effect of niche differentiation but not of individual variability might resolve the contrast in earlier results wherein intraspecific variability increased (e.g., Clark, 2010; Clark et al., 2011) or decreased (e.g., Barabas and D'Andrea, 2016; Hart et al., 2016) diversity or co-existence. First, our simulation specifically increased the type of niche differentiation that Clark (Clark, 2010; Clark et al., 2011) had argued would be developed by individuals. On the other hand, our representation of individual-level variability in the mode and standard deviation of the fitness functions increased the blurring of niche differentiation, which was the process posited by Hart et al. (2016) to explain loss of diversity with greater individual variability.

Reduction of competitive exclusion would be expected to maintain greater diversity at intermediate levels of volatility. However, in our simulated level of volatility the primary effect was to increase density-independent extinction. Iterations where the environment moved outside of the niche dimensions of ecotypes or individuals reduced populations and eliminated some. The greater effect was to increase the unevenness of the populations. Among replications the smaller and larger populations vary among the nine ecotypes.

Simulations could inform expectations of consequences of increased climatic volatility with global climate change by recognizing niche differentiation in existing adaptations to disturbance or stress. Adaptations to temporal gradients as proposed by Clark (2010) and Scranton and Vasseur (2016), e.g., demographic strategies to increase fitness with temporal variation such as masting, could mitigate the impacts of increased climatic volatility. Predictions will need to incorporate such adaptations as opposed to including simple individual variability. A framework, beginning with that presented by Turcotte and Levine (2016), could be developed that explicitly incorporates both niche and individual variability in multiple dimensions of resources,

Table 2

ANOVA of gamma and Shannon diversity for cases with volatility, with niche differentiation and individual-level variability as factors.

Gamma diversity							
Source	DF	Seq SS	Contribution	Adj SS	Adj MS	F-Value	p-Value
Niche	1	11.52	9.29%	11.52	11.52	22.08	< 0.000
Variability	1	9.68	7.81%	9.68	9.68	18.55	< 0.000
Error	197	102.8	82.90%	102.8	0.5218		
Lack-of-Fit	1	13.52	10.90%	13.52	13.52	29.68	< 0.000
Pure Error	196	89.28	72.00%	89.28	0.4555		
Total	199	124	100.00%				

Shannon diversity							
Source	DF	Seq SS	Contribution	Adj SS	Adj MS	F-Value	p-Value
Niche	1	4.5022	42.93%	4.5022	4.50218	154.31	< 0.000
Variability	1	0.2381	2.27%	0.2381	0.23807	8.16	< 0.000
Error	197	5.7475	54.80%	5.7475	0.02918		
Lack-of-Fit	1	1.1101	10.58%	1.1101	1.11006	46.92	< 0.000
Pure Error	196	4.6375	44.22%	4.6375	0.02366		
Total	199	10.4878	100.00%				

time, and space. However, increases in volatility at levels observed over the past century, i.e., localized doubling of variability in tree-ring records (Millar et al., 2007; Malanson, 2017) could cause extinctions.

5. Conclusions

Both ecotypic niche differentiation and individual variability can be factors in a species' response to climate change. For modeling, including both requires procedures for parameterization and for implementation. We introduced a procedure to derive an indicator of variability for ecotypes from the CV of tree-ring widths across space. While we used a range of trees to derive a single number which we then used with theory to evenly distribute the modes of fitness functions on an environmental gradient, actual differences in modes for populations of observed ecotypes could add realism. Our use of the variability of the CV of tree-ring widths across space to represent individual-level variability could be done within those populations. Applying these representations of variability in individual-based models, by application to the mode and standard deviation of fitness functions, is useful for generalization and can lead to observations not attainable by current analytical approaches alone. Empirically based fitness functions could be changed similarly, and other types of models, such as species distribution models (already incorporating intraspecific variability, e.g., Valladares et al., 2014; Theodoridis et al., 2018), could also incorporate changes analogous to shifting modes and changing breadths.

Credit statement

GPM conceived the problem and wrote and executed the model.

JR and MB provide training data for tree ring analyses and guided the tree ring parameterization.

GPM, JR and MF analyzed the model outcomes and wrote the manuscript.

Acknowledgment

This paper was prepared in part by an employee of the US Forest Service as part of official duties and is therefore in the public domain.

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