



Life at the top: Long-term demography, microclimatic refugia, and responses to climate change for a high-elevation southern Appalachian endemic plant



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ABSTRACT

Plants existing in small and isolated populations often depend on microclimatic refugia that create local environments buffered from macroclimatic conditions. Currently much effort is devoted toward identifying features that create refugial conditions in the expectation that they will continue to serve as refugia into the future. However, the ability of a refuge to resist macroclimatic change is a biological question, not an abiotic one, since species can persist in these conditions while suffering slow decline. Here we test the ability of current refugial habitats of *Geum radiatum*, a narrowly endemic perennial herb specializing in cool, humid, high elevation sites, to continue to serve as refugia under present and future climatic conditions. We constructed integral projection models to characterize demography, and macro- and topoclimatic niche models to predict dynamics given climate change through 2070. This species' demography is characterized by high adult survival (about 97% annually), variable growth, frequent flowering, and rare seedling recruitment. Site relative humidity affected survival and reproduction, but predicted population growth rates under current conditions were similar for dry, wet, sheltered, and exposed sites ($\lambda = 0.994\text{--}0.998$). Augmentation by planting 20–70 seedlings annually would raise population growth rates to 1. Demographic modeling under future lower relative humidity predicted further reductions in population growth. Models of the species' macro- and microclimatic niche indicated that all populations had reduced climatic suitability by 2050 or 2080, with 58–83% falling below minimum suitability levels, depending on the climate scenario. *G. radiatum*'s stable demography and habitat protection mean that, barring catastrophes, most populations are not facing extinction under current conditions. However, this species is extremely vulnerable to projected climate change even within its current refugial habitats. This study demonstrates that climate refugia that currently buffer rare species from macroclimatic extremes may not be able to do so under anticipated climate change.

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1. Introduction

Climate change has the potential to affect nearly all organisms, and conservation planning is increasingly incorporating climate change effects (Staudinger et al., 2013; Jones et al., 2016). Small and isolated populations of wild plants face myriad threats, including habitat loss; competition from invasive species; genetic, environmental, and demographic stochasticity; degradation of mutualistic relationships; edge effects; and altered metapopulation dynamics (Schemske et al., 1994; Wilcove et al., 1998). Climate change is another threat to both common and rare species, but small populations and endemic species may be particularly sensitive to its effects (Schwartz et al., 2006). Many

examples of impacts on rare species exist. In the Colorado plateau for example, endemics tended to occur in habitats that are more likely to become climatically unsuitable and most lack strong dispersal abilities (Krause et al., 2015). Climate change is projected to cause drastic reductions in the ranges of 2/3 of California's large endemic flora (Loarie et al., 2008). High elevation endemic organisms are under disproportionate extinction risk due to climate change (Dirnbock et al., 2011).

In particular, identifying areas that protect species from macroclimatic trends has become a critical exercise (Keppel et al., 2012). In contrast to macroclimate refugia which are represented by large regions to which species retreated during past episodes of climate change, microclimatic refugia (hereafter just "refugia") are represented by small areas that harbor special features that buffer exposure to or otherwise alter local climates (Ashcroft, 2010). Refugia can be associated with mountain tops (Gollan et al. 2014), uncommon vegetation

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cover (Lenoir et al., 2013), poleward- and westward facing cliffs and slopes (Loarie et al., 2008), and even edaphic conditions that mimic climate conditions otherwise rare in the surrounding region (Damschen et al., 2012). To date much work has been devoted toward identifying landscape features that create buffered conditions on the basis of the assumption that they will serve as refugia in the future (e.g., Dobrowski, 2011; Ashcroft et al., 2012; Davis et al., 2013).

However, the ability of a refuge to resist macroclimatic change is really a biological question, not an abiotic one. Species in specialized, protected habitats are often assumed to be buffered from effects of climate change (Ashcroft et al., 2009; Serra-Diaz et al., 2015). Nonetheless, there are important exceptions to this generalization. For example, modeled vegetation in California in more mesic, wetter habitats actually were likely to be more sensitive to climate change than vegetation in less protected, drier sites (Ackerly et al., 2015). The effectiveness of a refuge should be measured by its ability to harbor populations that maintain themselves at least at replacement level over periods of environmental change. The mere presence of a species in a refuge and absence in the surrounding region alone is not enough to indicate effectiveness, as populations can persist for long periods in purported “refugia” while suffering slow decline. In light of the growing effort to identify landscape features conducive to maintenance of refugia, concurrent measurements of the actual biological effectiveness of refugia are necessary.

Of special concern is the ability of refugia to protect small and isolated populations of wild plants that occur at high elevations. These species already exist near their environmental limits and presumably will be greatly affected by changes in climate owing to the limited availability of habitat at higher elevations and difficulty in dispersing to newly favorable mountain tops (Dirnbock et al., 2011). In particular, the southern Appalachian Mountains of the southeastern United States are a biodiversity hotspot (Estill and Cruzen, 2001) due in part to biogeographic events that occurred during the Pleistocene (Russell et al., 2009). Many narrow endemics are restricted to these mountains, often in specialized habitats or high elevations. These species persist in what are presumably microclimatic refugia, although the ability of these sites to maintain these populations in light of oncoming anthropogenic climate change remains an open question.

Integral projection models are being increasingly used for demographic analyses, including assessments of population viability for rare plants (e.g. Raventos et al., 2015; Tye et al. in revision) and at least one study on the effects of climate on demography (e.g. Dalglish et al., 2011). Demographic modeling can provide insight into short-term possible trajectories and also, when used with environmental drivers, allow scenarios based on responses to climate change (Molano-Flores and Bell, 2012; Shryock et al., 2014). Demographic models are preferred to abundance-based models in understanding potential population responses to changing conditions (Bin et al., 2016) and among these models, integral projection models are more efficient with limited data than traditional matrix projection models (Ramula et al., 2009).

Ecological niche modeling (species distribution modeling) is commonly an important part of analyzing species future ranges and their ability to persist in current sites (Wiens et al., 2009). Despite their widespread application, niche models ignore demographic processes even though demography can have profound influences on range dynamics (Holt and Keitt, 2000; Merow et al., 2014; Swab et al., 2015). As a result, combining the predictions of niche models with predictions from integral projection models provides a more relevant measure of population persistence than either method alone.

This study considers *Geum radiatum*, a high elevation Southern Appalachian endemic plant specializing in cool, wet, high elevation microsites. We combined two approaches to measure the biological effectiveness of presumed refugia for *G. radiatum*. First, we use integral projection models to estimate population growth and relate this growth to a key climatic parameter, relative humidity. Second, we develop macroclimatic niche models that are sensitive to microtopographic

features associated with locally buffered climates favored by *G. radiatum*. Finally, we compare predictions from these models to develop a better understanding of the effectiveness of high-altitude refugia for protecting rare species in this biodiversity hotspot. This combination of approaches evaluates both the current ability of climate refugia to support viable populations of a rare species and whether these refugia are likely to buffer rare species from altered conditions given anticipated climate change.

2. Methods

2.1. Study species

This study considers a high elevation endemic to the Southern Appalachian Mountains, the major mountain chain in eastern North America. *Geum radiatum* (Rosaceae), a federally-endangered species, listed in 1990, is found mainly in cooler, wetter microsites and has only 15 extant populations, 11 on public land (USFWS, 2013). *G. radiatum* is a rhizomatous, perennial herb with mainly basal leaves, yellow flowers, and an aggregate fruit of beaked achenes (Massey et al., 1983). Based on limited germination trials, the species is not known to form a persistent seed bank. It grows mostly on northwest to north facing cliffs and talus slopes above 1300 m in elevation, within a matrix of spruce-fir, northern hardwood, or red oak forests (USFWS, 2013), as the treeline predicted by climate in the southern Appalachians is higher than the tallest summit (Cogbill et al., 1997). A few populations of *G. radiatum* occur in wet meadows or grassy balds. *G. radiatum* is one of a suite of southern Appalachian high-elevation outcrop plants, many narrowly endemic, with affinities to rock outcrop communities in the northeastern United States (Wiser, 1998). It is closely related to *Geum peckii*, endemic to the White Mountains of New Hampshire, but the two species are distinct based on RAPD markers (Paterson and Snyder, 1999). A limited study of five populations spanning the 250 km species range showed that *G. radiatum* had low genetic diversity (typical of endemic plant species) and low levels of gene flow (Godt et al., 1996).

G. radiatum appears to have specific microhabitat requirements for high elevations, wet, shady conditions, and rock surfaces with ledges and cracks. Populations are found at elevations from about 1300–2000 m (Table 1), usually on cliffs, sometimes on rocky outcrops in heath or grassy balds. Many sites are wet and steep. Soils are generally wet from fog, downslope drainage, or rain, and many locations do not receive direct sun due to their northerly exposure. Cliff sites may be unstable due to rock movements or erosion. Many plants grow in narrow ledges or in cracks on cliffs that require climbing equipment to access. Within habitat patches, *G. radiatum* occurrence and cover were positively associated with soil moisture and negatively correlated with light levels (Johnson, 1995). Occurrence at the 100 m² scale was positively associated with a fracturing index (rocks with cracks and ledges), negatively associated with solar radiation, and unimodally related to soil iron (Wiser et al., 1998). At a smaller scale, *G. radiatum* occurred more on exposed rock, less with high solar radiation and soil cations (Wiser et al., 1998).

G. radiatum is endemic to North Carolina and Tennessee (Fig. 1) and listed as federally endangered (USFWS, 2013). Most of the populations are protected on lands managed by federal or state agencies, or private conservation organizations (USFWS, 2013). Three populations are known to have been extirpated (USFWS, 2013). Listed threats include heavy recreation use (USFWS, 1993), trampling, ski slope development, and acid rain although the most recent analysis emphasizes habitat loss, habitat degradation from trampling, and inadequate regulation (USFWS, 2013). No objective criteria for self-sustaining populations have been identified (USFWS, 2013).

Efforts to restore sites supporting *Geum radiatum* have included soil reintroduction and stabilization, followed by transplantation, of 575 plants to at least three sites (Johnson, 1996). Moderate initial mortality occurred, some of which was due to erosion and displacement of fabric

Table 1
 Characteristics of *Geum radiatum* study populations. Population numbers are arbitrary; two study populations are not included in this paper because of limited data. “Wet” refers to whether site is wetter (Wet) or drier (Dry); see text for more details. “Exp” refers to whether site is sheltered (Sh) or exposed (Ex); see text for more details. “1st yr”: first year studied (data through 2013 for all populations with missing years for a few), N = number of plants in database, Surv = mean annual percent adult survival, Sdlg = total seedlings observed; % Flw = mean percent of plants flowering; Mn Len refers to mean length of plants (all years) in cm.

Population	Elevation	Aspect	Habitat	Wet	Exp	1st year	N	% Surv	Sdlg	% Flw	Mn Len
1-RHB	6260	NW	Cliff	Wet	Ex	2005	19	98.3	0	36.3	33.4
2-RHBC	6240	NW	Cliff & Base	Wet	Ex	2005	150	99.1	5	48.9	42.8
4-CE	5800	N	Cliff	Wet	Sh	2003	46	97.5	3	37.6	43.4
5-CP	5900	W	Cliff	Wet	Ex	2005	15	95.5	2	50.6	50.7
6-CW	5750	N	Cliff	Wet	Sh	2005	54	98.6	8	20.5	30.4
7-DCC	5680	W	Cliff & Base	Dry	Ex	2004	41	96.8	4	46.4	40.2
8-DCL	5400	W	Cliff Base	Dry	Sh	2004	28	90.1	14	37.4	30.0
9-GC	6000	NW	Cliff	Dry	Ex	2005	66	87.2	16	52.4	29.7
10-U	6150	N	Cliff	Wet	Sh	2006	19	96.0	0	16.8	35.3
12-Re	5900	NW	Cliff	Wet	Sh	2006	112	96.2	0	32.3	38.4
13-RGR	6120	S	Rock Outcrops*	Wet	Ex	2006	27	99.5	0	68.5	35.2
14-MC	6580	W	Cliff	Wet	Ex	2008	11	100	0	84.8	42.0
15-GFI	5800	NW	Cliff	Dry	Ex	2008	21	99.1	0	48.2	42.0
16-GFL	5250	NW	Cliff	Dry	Ex	2008	37	97.9	0	60.0	37.8
17-DCT	5680	W	Cliff	Dry	Ex	2007	20	94.5	0	57.7	40.6
18-RCM	6080	NW	Cliff	Wet	Sh	2008	85	96.9	0	20.7	30.9
19-RCW	6080	NW	Cliff	Wet	Ex	2008	7	100	0	45.2	41.6
20-BM	4650	NE	Cliff	Wet	Ex	2009	8	100	0	53.3	51.8
21-P	5100	NW	Cliff	Wet	Ex	2009	74	99.7	0	56.1	58.2
23-RHBW	6140	NW	Cliff Base	Wet	Ex	2009	22	100	0	46.0	63.5

* Rock outcrops surrounded by grassy bald.

holding patches of soil and plants. The ultimate success of this introduction is not known, as complete records are not currently available to the National Park Service or US Forest Service.

2.2. Study region

The southern Appalachians are a prominent geographic feature of the southeastern United States and are a biodiversity hotspot due in part to biogeographic events that occurred during the Pleistocene. Many narrow endemics are restricted to these mountains, often in specialized habitats or high elevations. The Blue Ridge province is particularly rich in endemic plants; many of which (*Abies fraseri* Lindl., *Calamagrostis cainii* Hitchc., *Carex misera* Phil., *Geum radiatum* Michx., *Hydatica petiolaris* (Raf.) Small, *Krigia montana* Nutt., *Solidago spithamea* M.A. Curtis ex. A. Gray.) are alpine relicts with their closest relatives in mountains further north. The Blue Ridge also supports endemic salamanders, fish, mussels, and crayfish.

High elevation plants (greater than 5000', 1524 m) in the southern Appalachians and the Blue Ridge province face several threats. High elevation endemics often exist in small populations due to limited habitat extent and microhabitat availability. While many high elevation areas are well-protected as conservation areas, high elevation areas that are accessible to humans may face additional threats. Because even the highest elevations are often accessible by trails or roads, human visitation can impact rare plant populations. Trampling by hikers, climbers, and other recreationists has had deleterious effects on many of these sensitive alpine relict plants (USFWS, 1993, 2013). Acid rain and climate change are also threats. Because many high-elevation plants are adapted high moisture conditions caused by frequent immersion by clouds (Berry and Smith, 2013); some endemics may not be able to adapt to climate change that alters these conditions (Culatta and Horton, 2014).

Climate in the southern Appalachians is projected to rapidly change over the coming few decades. In general, the southeastern United States is projected to have increasing temperature and growing season length (Ingram et al., 2013). Precipitation forecasts have more uncertainty, although overall precipitation is expected to increase across the northern tier of the southeastern US (Ingram et al., 2013). The frequency of extreme precipitation events is also expected to increase. Increases in

temperature are expected to endanger the high elevation spruce-fir forests (Ingram et al., 2013), which often surrounds the rocky cliffs that support *G. radiatum*.

2.3. Study populations

We studied *Geum radiatum* at all known study sites to which we could obtain consistent access (Table 1). These included sites spanning the known range of elevation, aspect, and vegetation for this species. Limited resources and access issues prevented us from including all known populations. We defined 20 study populations in total (Table 1); these are encompassed within 9 of the 15 more broadly-defined populations as defined by USFWS (2013). Populations are separated from the nearest population by 12 to 63 km.

2.4. Field methods

We visited study populations of *Geum radiatum* annually (2003–2013; not all populations in each year) in July (the month of peak growth and flowering) to assess plant survival, size, fecundity, and recruitment. Additional visits to some study populations in some years occurred in June (seedling recruitment) and September (seed collections). In most study populations, we attempted to follow all plants. This involved rappelling at most sites and the use of ladders or extensive scrambling at other sites. Individual plants were marked with aluminum tags, usually anchored into rocks by drilling a hole with a portable drill and inserting a metal expansion anchor that would accept a nail. Plant locations were described by measurements of X and Y coordinates in flatter terrain and by descriptions of locations on cliff faces and along rappel lines on cliffs.

We measured the length (longest axis, cm) and 1–5 widths (perpendicular to length, at approximately equal distances along the length) along the canopy of each study plant. We also counted the number of rosettes for each plant, using counts of subsets to estimate rosettes for very large plants. Additionally, we counted the number of flowering stems. We also observed herbivory on each plant. If plants were not found near a tag, we coded them as dead. Tags not found were coded separately as missing. We identified plants as adults, seedlings (new, tiny plants with cotyledons), or yearlings (tiny plants without

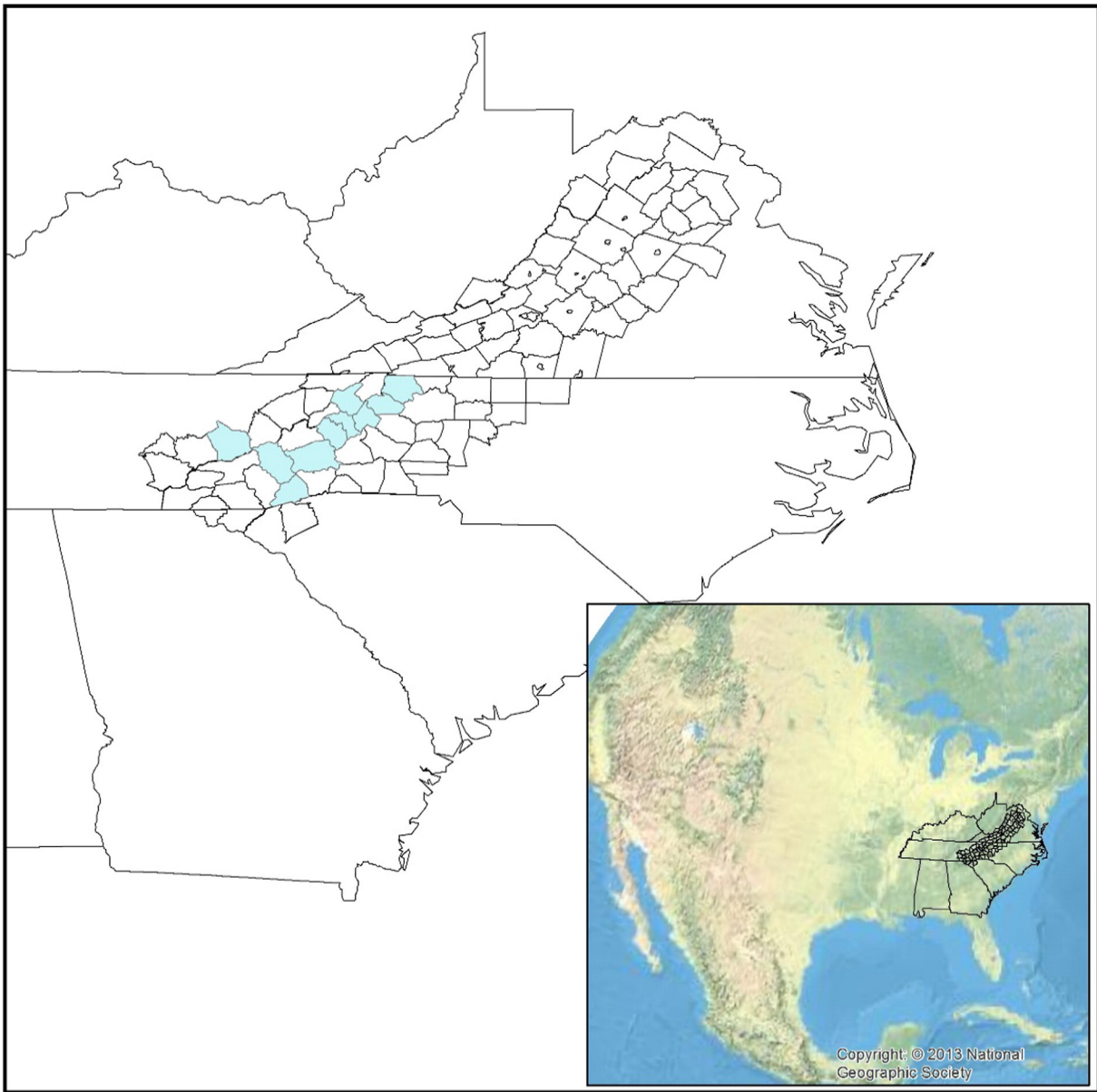


Fig. 1. Map showing range of *Geum radiatum* within the Blue Ridge geographic province of North Carolina, Tennessee, Virginia, West Virginia, and Georgia. Polygons show counties within province. Blue shading shows counties supporting one or more populations.

cotyledons, presumed as second year plants). Plants were defined as groups of rosettes separated from other plants by at least 25 cm or by bare rock.

We collected weather data at five sites from July 2010–July 2014. We placed portable weather stations at the field sites, attaching them to rock faces through the use of drilled holes. These devices provided temperature and relative humidity readings at 20 min intervals. We scaled weather data up to monthly, seasonal, and annual averages. These allowed us to classify sites with weather data as wet (higher humidity) or dry (lower humidity). Logistical constraints prevented us from installing weather stations at all sites. Therefore, we classified sites without weather data as wet or dry based on field observations (before any analyses). Wetter sites usually had groundwater seeping across the cliff faces although some were affected more by persistent ground-level fog and rain. We also categorized sites as exposed or sheltered based on field observations; exposed sites were windy and on convex landforms. Sheltered sites had less wind and were on concave landforms. Site exposure was not correlated with site wetness, so we used both variables in subsequent analyses and modeling.

2.5. Demographic modeling

Demographic data on *G. radiatum* were organized as seedlings, yearlings (small plants without cotyledons, presumably in their second year, about one year old), and adults. Data were extensively checked for errors and outliers. These data were used to build explanatory models for vital rates (individual survival, growth, fecundity) based on plant size (either elliptical area, length, number of rosettes, or their products), weather data, site wetness, and microhabitat. We implemented model selection using AICc criteria to choose the most plausible models among a range of alternative models. Because we had weather data for only a subset of our sites, we instead used wetness and exposure classifications to characterize each site (see below). For the sites with data, site level relative humidity was positively associated with survival, reproduction, and population growth rates (see results). The vital rate models provided the basis for construction of integral projection models.

We constructed multiple stage integral projection models (IPMs, Easterling et al., 2000; Ellner and Rees, 2006) to model the full life

cycle of *Geum radiatum* in R (3.0.1, R Development Core Team). We used an integrative measure ($\ln(\text{elliptical area} * \text{number of rosettes})$) as the size variable to construct models. This size measure proved superior (as judged by AICc) to any individual size variables in predicting vital rates. We considered separate IPM models for sites grouped by four combinations of site wetness (wetter or drier) and site exposure (exposed or sheltered). We evaluated models assessing the effect of the variables and their interactions on each vital rate using general linear mixed models (GLMMs) with random intercepts that varied by year. We did not include random variation by population because not every population was studied in every year. This is a compromise to minimize discarding data while balancing the design for statistical analysis.

Models were ranked using AICc. All models of similar AICc score (within 2; see Burnham and Anderson, 2002) were individually inspected.

The IPM integrates models for individual survival, changes in size, and fecundity. The models for individual survival used a logit link and binomial distribution. The model to assess changes in size used a Gaussian error distribution. We estimated size-dependent fecundity of reproductive individuals. Fecundity was the product of size-specific probability of successfully producing a reproductive stem (estimated with a logit link and binomial errors), the size specific number of flowering stems produced (with Poisson distribution) and the annual average count of seedlings per previous year's flowering stem (as the model assumes no persistent seed bank) and seedling survival. This gives an estimate of the number of seedlings produced by plants of different sizes. We integrated over 100 bins (+ one for yearlings). The dominant eigenvalue of the overall square matrix corresponds to population growth rate.

We modeled *Geum radiatum* population growth given current conditions, for populations classified by combinations of wetness and exposure. We also considered scenarios that represented potential augmentation of *G. radiatum* to extant small populations. Scenarios included augmentation of seedling recruitment by adding 0–80 seedlings to a population annually. We also modeled population growth based on current and future relative humidity values predicted by climate modeling (see below).

2.6. Modeling macro- and topoclimatic niche

We modeled the climatic niche of *G. radiatum* with three modeling algorithms (boosted regression trees—Elith et al., 2008; Maxent—Phillips et al., 2006; and 2-class support vector machines—Guo et al., 2005), plus the minimum, maximum, and median prediction across all three models. We used climatic variables for the period 1981–2010 from the ClimateNA data set (Hamann et al., 2013). From these data set, we calculated seven climate variables over based on the expectation they establish “envelope” conditions for site-level environments favorable to the species: mean diurnal temperature range, isothermality, temperature seasonality, temperature of the warmest month, mean annual precipitation, precipitation of the wettest month, precipitation of the driest month, and mean annual relative humidity. We used two sets of models, one with all climate variables and one with just the variables related to moisture (mean annual precipitation, precipitation of the wettest and driest months, and relative humidity). Several of these variables were highly correlated with one another, so we simplified them using principal components analysis (PCA). The first two (moisture variables only) or three (all variables) axes comprised >89% of the variance, so these were used as predictors in the models. Climate variables were available at 1×1 -km resolution. To account for microclimatic influences that cannot be reflected in coarse-resolution climatic data, in addition to the macroclimatic variables we included three “topographic-climate” variables (Gutiérrez Illán et al., 2010) representing slope and aspect calculated from a 90-m digital elevation model. Because aspect is measured on a circular scale it was transformed into two variables, “northness” using $\sin(x)$ and “eastness” using $\cos(x)$

(where x is aspect in radians). Topoclimatic variables were not simplified using PCA.

We used all known extant sites for niche modeling. Background points for model training were drawn from the southern portion of the US Environmental Protection Agency's Blue Ridge Level III ecoregion (Omernik, 1987). We tried modeling with and without correction for potential bias in sampling sites (cf. Stolar and Nielsen, 2015). For model testing all presences and background sites were divided into three mutually exclusive geographic subsections (roughly the northern, middle, and southern sections of the range, leaving 5–11 presences in each section). Each section was used once as test data for models trained using the other two sections (Radosavljevic and Anderson, 2014). We evaluated model performance with the Continuous Boyce Index (CBI; Boyce et al., 2002; Hirzel et al., 2006). CBI represents the models' ability to predict the probability of presence and ranges from -1 to 1 , with values >0 better than random. Finally, models using all presences were projected to two time periods centered on the 2050s (2041–2070) and 2080s (2071–2100) under the IPCC's RCP 4.5 (less warming) and 8.5 (most warming) greenhouse gas emissions pathways based on the average of 15 general circulation models from the ClimateNA data set (Hamann et al., 2013). Ecological niche models generally do not account for dispersal limitation, biotic interactions, or other factors known to affect range limits (Araújo and Luoto, 2007; Wiens et al., 2009). Hence, we interpret projections as an index of climate exposure rather than predictions about the range of the species (Summers et al., 2012). Monthly values of relative humidity for climate scenarios obtained from the ClimateNA data set were used to predict demographic trends. A new set of IPMs were built using these values of relative humidity for current and future conditions and the original size measures as predictors for the different vital rates.

3. Results

3.1. Current weather at *Geum radiatum* sites

The local weather at study sites from 2010–2014 was cool and humid. Temperatures averaged 6–9 °C (42–48 °F) among sites for the entire year and were very seldom above 24 °C (75 °F). Relative humidities averaged 78–90% among sites for the entire year, but were generally above 90% at most sites during the growing season. High relative humidities were likely due to a combination of frequent fog, ground water seepage, and limited direct sunlight on north facing cliffs. Sites varied somewhat in local weather, which reflected the elevation, aspect, and relative protection at each site. The overall local weather reflects high elevation, northerly aspect, and generally steep slopes.

3.2. Life history of *Geum radiatum*

Geum radiatum has consistently very high adult survival, averaging well over 90% annually by population (Table 1). Adult survival varied only modestly among study populations (Table 1) and years (from 93.5% to 100% for the eleven pairs of years of the study), with most ranging only from 97.2%–98.6%.

Individual plants could grow or shrink in area or number of rosettes from year to year. When all plants were considered, there was not a consistent increase in size from year to year. For plants with data from 2006–2013, the mean elliptical area decreased in 4 of 7 years. Smaller plants, however, did show consistent growth over time. Single rosette plants doubled in size about every 4 years.

Among study populations, 21–85% of plants flowered (Table 1). Flowering was commonly observed in larger plants. The minimum canopy area for flowering was 7.07 cm² with one rosette, but many plants did not consistently flower. Mean total area (canopy area * number of rosettes) was 9.4 cm² for non-flowering plants that subsequently died during the next year, 500.5 cm² for surviving non-flowering plants, and 14,842.6 cm² for flowering plants. In some years, no flowering

Table 2

Statistics on known seedlings and yearlings of *Geum radiatum*. Data are for all study populations combined. Some seedlings were first observed as second year plants (yearlings). NA = not applicable.

Year	No. recruited (no. with subsequent data)	Seedlings recruited as % of population	Number (%) surviving three years	Rosette area in cm ² (n)		
				As seedling	As 3 yr old	In 2013
2003	0	0	–	–	–	–
2004	10 (7)	12.6	0	–	–	–
2005	12 (12)	5.3	0	–	–	–
2006	9 (9)	2.6	2 (22%)	1.0 (2)	2.5 (2)	190 (1)
2007	12 (12)	2.9	2 (17%)	1.0 (2)	7.0 (2)	15 (1)
2008	17 (5)	3.2	5 (100%)	1.0 (5)	–	–
2009	4 (3)	0.6	3 (100%)	1.0 (3)	2.0 (1)	3.3 (3)
2010	3 (3)	0.5	1 (33%)	1.0 (3)	2.0 (1)	2.0 (1)
2011	0	0	NA	–	NA	–
2012	0	0	NA	–	NA	–
2013	1 (1)	0.2	NA	1.0 (1)	NA	1.0 (1)
Total	68 (52)	–	13	–	–	–
Mean	6.2 (4.7)	2.5	2.6 (25%)	1.0 (16)	3.8 (6)	30.2 (7)

plants died. Flowering status in successive years was inconsistent for small and medium sized plants but consistent for larger plants.

We rarely observed seedling recruitment, with fewer than five seedlings observed annually across all of our study populations (Table 2). Seedlings made up less than 6% of all *G. radiatum* plants in most years. Seedling survival was moderate, averaging 25% over the first three years of life. Growth was initially slow, but some seedlings had grown substantially after many years (Table 2).

3.3. Predictors of vital rates

Survival was predicted by our chosen size variable (canopy area × number of rosettes; Table 3). Each other size variable individually was less influential in predicting this vital rate. Smaller plants had lower survival than larger plants, which rarely died (Fig. 2). Site wetness and population status rarely affected survival (Table 3).

The probability of flowering was dependent on plant canopy area. Few plants with a canopy area below a minimum size (natural log = 4) ever flowered, and nearly all plants above a larger size (natural log = 8) flowered (Fig. 2). The transition from seldom to nearly always flowering was affected by the site's wetness, with drier sites requiring larger sizes for a given probability of flowering than wetter sites.

Fecundity also increased with plant canopy area. Population effects on fecundity were more pronounced than their effects on survival. Site wetness had positive effects on fecundity (Table 3). Equations predicting the vital rates were the basis for integral projection models (Table 4).

3.4. Integral projection models

The integral projection model emphasizes stability for the demography of *Geum radiatum*. Size was closely related among years and this variation was smaller for larger plants than for smaller plants (note

Table 3

Top five most plausible GLMM models after AICc (of eleven initial models) and null model, predicting survival, fecundity, probability of reproduction, and growth for *Geum radiatum*. S = ln (elliptical area × number of rosettes) Ro = number of rosettes, E = exposure, W = wetness, Ea = elliptical area, and R(Y) = random intercept for year effects.

Model	df	k	LogL	AICc	Delta	Weight	Evidence
Survival (logit link, binomial distribution)							
y ~ S + E + W + SE + SW + WE + SEW + R(Y)	3709	9	–313	644	0.0	0.9	1.0
y ~ S + R(Y)	3710	3	–322	649	5.4	0.1	14.1
y ~ S + E + W + SE + SW + R(Y)	3706	7	–318	650	6.4	0.0	25.1
y ~ S + E + W + R(Y)	3708	5	–321	652	8.2	0.0	61.1
y ~ Ea + R(Y)	3743	3	–330	666	22.0	0.0	5.9E + 04
y ~ 1 + R(Y)	3744	2	–504	1012	368.0	0.0	8.3E + 79
Fecundity (log link, poisson distribution)							
y ~ S + E + W + SE + SW + WE + SEW + R(Y)	955	9	–3265	6548	0.0	1.0	1.0
y ~ S + E + W + SE + SW + R(Y)	957	7	–3285	6585	36.5	0.0	8.54E + 09
y ~ S + E + W + R(Y)	959	5	–3315	6641	92.8	0.0	1.4E + 20
y ~ Ro + R(Y)	961	3	–3451	6908	360.4	0.0	4.8E + 78
y ~ Ea + R(Y)	961	3	–3530	7065	517.5	0.0	2.36E + 112
y ~ 1 + R(Y)	978	2	–5294	10,591	4043.5	0.0	Inf
P(reproduction), (logit link, binomial distribution)							
y ~ S + E + W + SE + SW + WE + SEW + R(Y)	3369	9	–1359	2736	0.0	1.0	1.0
y ~ S + E + W + R(Y)	3373	5	–1381	2771	35.3	0.0	4.61E + 07
y ~ S + E + W + SE + SW + R(Y)	3371	7	–1380	2774	37.6	0.0	1.44E + 08
y ~ S + R(Y)	3375	3	–1499	3003	266.9	0.0	9.35E + 57
y ~ Ea + R(Y)	3408	3	–1526	3058	321.9	0.0	7.79E + 68
y ~ 1 + R(Y)	3409	2	–2294	4591	1852.9	0.0	Inf
P(reproduction), (identity link, Gaussian distribution)							
y ~ S + R(Y)	3366	4	–4018	8043	0.0	1.0	1.0
y ~ S + E + W + + R(Y)	3364	6	–4019	8050	6.6	0.0	27.0
y ~ S + E + W + SE + SW + R(Y)	3362	8	–4026	8069	25.2	0.0	3.0E + 05
y ~ S + E + W + SE + SW + WE + SEW + R(Y)	3360	10	–4029	8079	35.5	0.0	5.1E + 07
y ~ Ea + R(Y)	3487	4	–4828	9664	1621	0.0	Inf
y ~ 1 + R(Y)	3488	3	–8392	16,790	8747	0.0	Inf

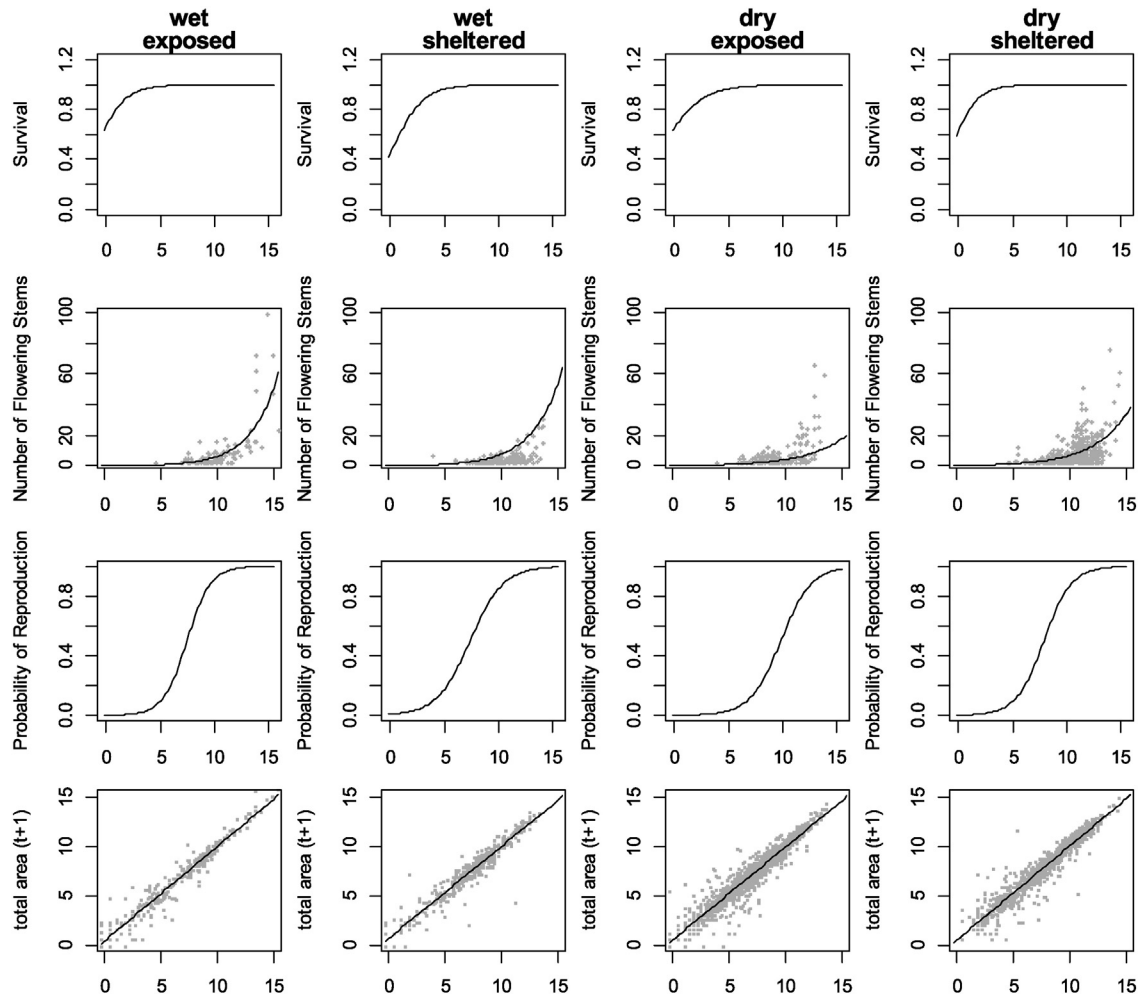


Fig. 2. GLMMs (with random year effects) of survival (top; with Logit link and binomial errors), fertility (production of flowering stems; with log link and Poisson errors), probability of reproduction (with Logit link and binomial errors) and plant growth (bottom; with identity link and Gaussian errors), for *Geum radiatum* in different environments, as a function of (canopy area * number of rosettes).

diagonal in Fig. 3). The size dependence of fecundity is also evident by the increases in this feature along the X axis (Fig. 3).

3.5. Population growth

Predicted equilibrium population growth rates (lambdas) were nearly one, with only minor differences among all sites varying in wetness and exposures (Fig. 4). In the two years (2007 and 2008) with the least rainfall recorded at Asheville, NC during the study, estimated population growth rates with random effects were particularly low (Fig. 4). When considering only the five sites with weather data, relative

humidity rankings were perfectly ordered with mean population growth rates, with population growth increasing with humidity (Spearman's rho = 0.872, $p = 0.054$, $n = 5$).

3.6. Results of modeling scenarios

Given the low levels of natural seedling recruitment and the potential for introducing seeds or seedlings, we simulated effects of different levels of seedling recruitment on population growth rate. Depending on habitat, between 20–70 seedlings would need to be added each year to bring population growth rates (λ) up to one (Fig. 5).

Table 4

Coefficients for functions predicting vital rates for *Geum radiatum*. Italic + bold entries are significant at $p < 0.05$; bold entries are significant at $p < 0.1$. Numbers in parentheses are standard errors.

	Survival	Flowering stems	Probability of reproduction	Growth
Intercept	0.75 (0.38)	-2.39 (0.18)	-6.89 (0.82)	0.38 (0.11)
Size(S)	0.75 (0.17)	0.42 (0.01)	0.93 (0.11)	0.96 (0.01)
Exposure (E)	-0.91 (0.49)	0.53 (0.25)	2.05 (1.00)	0.27 (0.15)
Wetness (W)	-0.08 (0.46)	0.92 (0.29)	-0.13 (0.92)	0.11 (0.11)
S E	-0.04 (0.20)	-0.03 (0.02)	-0.27 (0.13)	-0.03 (0.02)
S W	0.19 (0.18)	-0.13 (0.03)	-0.21 (0.11)	-0.02 (0.01)
E W	0.82 (0.80)	-0.32 (0.36)	-1.28 (1.14)	-0.28 (0.17)
S W E	0.32 (0.27)	0.06 (0.03)	0.35 (0.14)	0.04 (0.02)
Random effects: time intercept sd	0.152	0.156	0.185	0.152

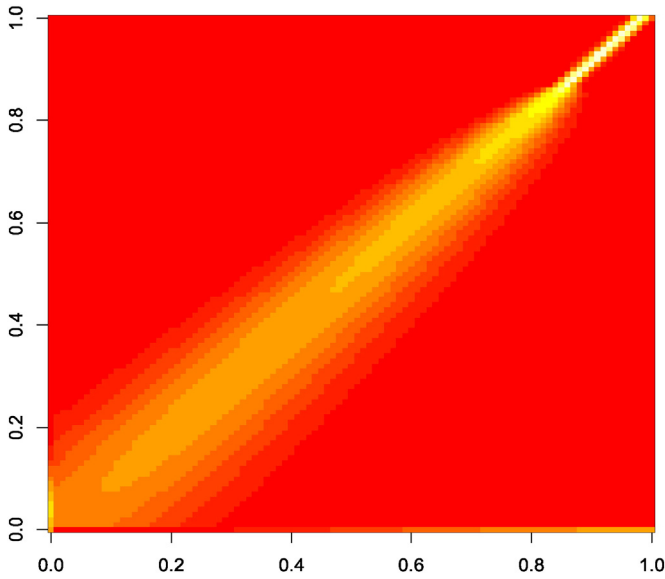


Fig. 3. Heat color image of an example IPM of a *Geum radiatum* in Dry Sheltered environment. The X axis represents size (log(plant area × number of rosettes, in 100 bins) for the first of a pair of years; the Y axis represents the size for the second year of the pair. The lighter colors indicate higher values and emphasize that most plants remain a similar size from year to year, especially the larger plants. Fecundity (seedlings produced by plants of different sizes) shows as the row at the bottom.

3.7. Potential effects of climate change on *Geum radiatum*

Of the niche models, Maxent with bias correction generally had the highest overall performance regardless of whether all climate variables or just moisture-related variables were used, so we report the results from the bias-corrected model with all climate variables. The average (± se) Continuous Boyce Index (CBI) of this model was 0.71 ± 0.02 , (across all models: 0.45 ± 0.04). Areas of high current suitability are restricted to high-elevation areas throughout the species' range (Fig. 6). The total area of suitable habitat declines sharply by the 2050s and

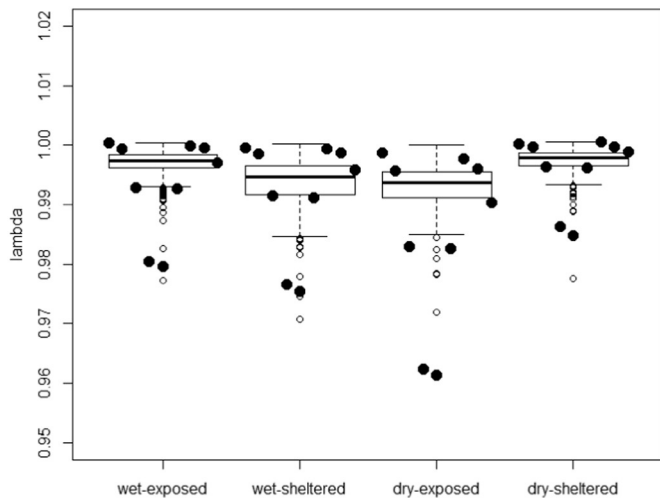


Fig. 4. Box plots showing *Geum radiatum* population growth rates (lambdas) and their variation as a function of site wetness and exposure. Variation was assessed by bootstrapping the data to calculate fixed effect coefficients of GLMMs (with random year variation) for the different vital rates that were integrated in IPMs. The dark line indicates the median, the limits of the box include the first (25%) and the third (75%) quartiles, the whiskers are the 9th and 91st percentiles, and the small open circles are outliers. Large black circles represent random year effects of original data (2004–2013, in annual sequence for each combination of site wetness and exposure).

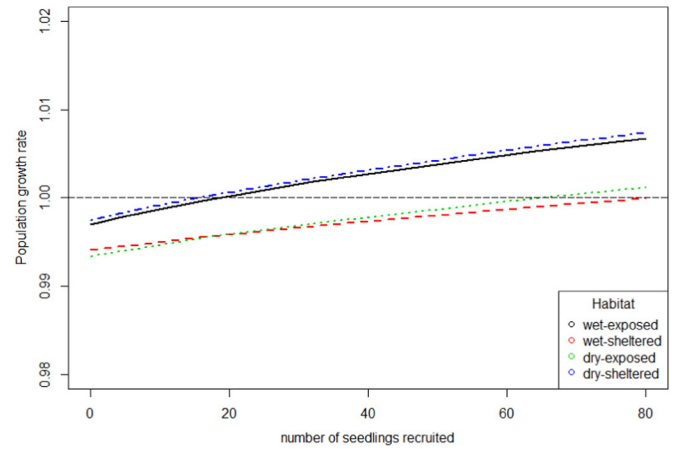


Fig. 5. Simulated effects of recruiting 0–80 seedlings per year to populations of *Geum radiatum* on population growth rate, for four habitat states. Natural recruitment averages 0–2 seedlings per year. We show a reference line for $\lambda = 1$.

2080s (Fig. 6) even under a scenario in which emissions are moderately abated (RCP 4.5). All sites declined in climatic suitability between the present and the 2050s and 2080s, regardless of emissions pathway (Fig. 7). Depending on the time period and scenario, from 17 (58%) to 24 (83%) of the 29 modeled locations have suitabilities that fell below the current minimum suitability across all sites (Fig. 7).

Because current population growth was affected by relative humidity, we can project population growth under future climate scenarios that also predict relative humidity. These analyses consistently predicted that population growth in the 2050s and 2080s will be slightly more negative than currently (Fig. 8). There were little effects of climate scenario on this prediction and the predictions were similar for the two future periods.

4. Discussion

Our research evaluates whether climate refugia are likely to support populations of a locally endemic, endangered species, *Geum radiatum*. While the current refugia support nearly stable populations with high annual adult survival (ca. 97%), our analysis using ecological niche models and climate projections predict climatic conditions will become less suitable in the coming decades. This result is relevant to many other rare species in the Southern Appalachian biodiversity hotspot, including *Liatris helleri* Porter, *Calamagrostis cainii*, *Houstonia purpurea* L. var. *montana* Chick., *Solidago spithamea*, *Carex misera*, and *Trichophorum cespitosum* (L. Hartm.) (Godt et al., 1996; Wisner, 1994; Wisner et al., 1998). It is also relevant to rare species in other areas that depend on climatic refugia. Our results call into question whether conservation strategies that rely on protecting currently suitable habitats will be sufficient. Will protected sites can provide long-term refugia buffered from climate change or will species specializing in these sites be particularly sensitive to climate change?

4.1. Demography, disturbance, and current refugia

This stable demography of *G. radiatum* might seem surprising given the potential for catastrophic disturbance in *G. radiatum* sites. Many sites occur on steep, wet cliffs with considerable groundwater seepage. Some plant locations are in cracks among rocks that are clearly unstable (and difficult to work on). These rocky areas are also subject to freezing winter temperatures that might be expected to de-stabilize the rocky substrates. Indeed, we have recovered tags and even dead plants at the base of cliffs after erosion events. Nonetheless, this potential for catastrophic population decline has not been realized at our 20 study sites during the ten years of our study.

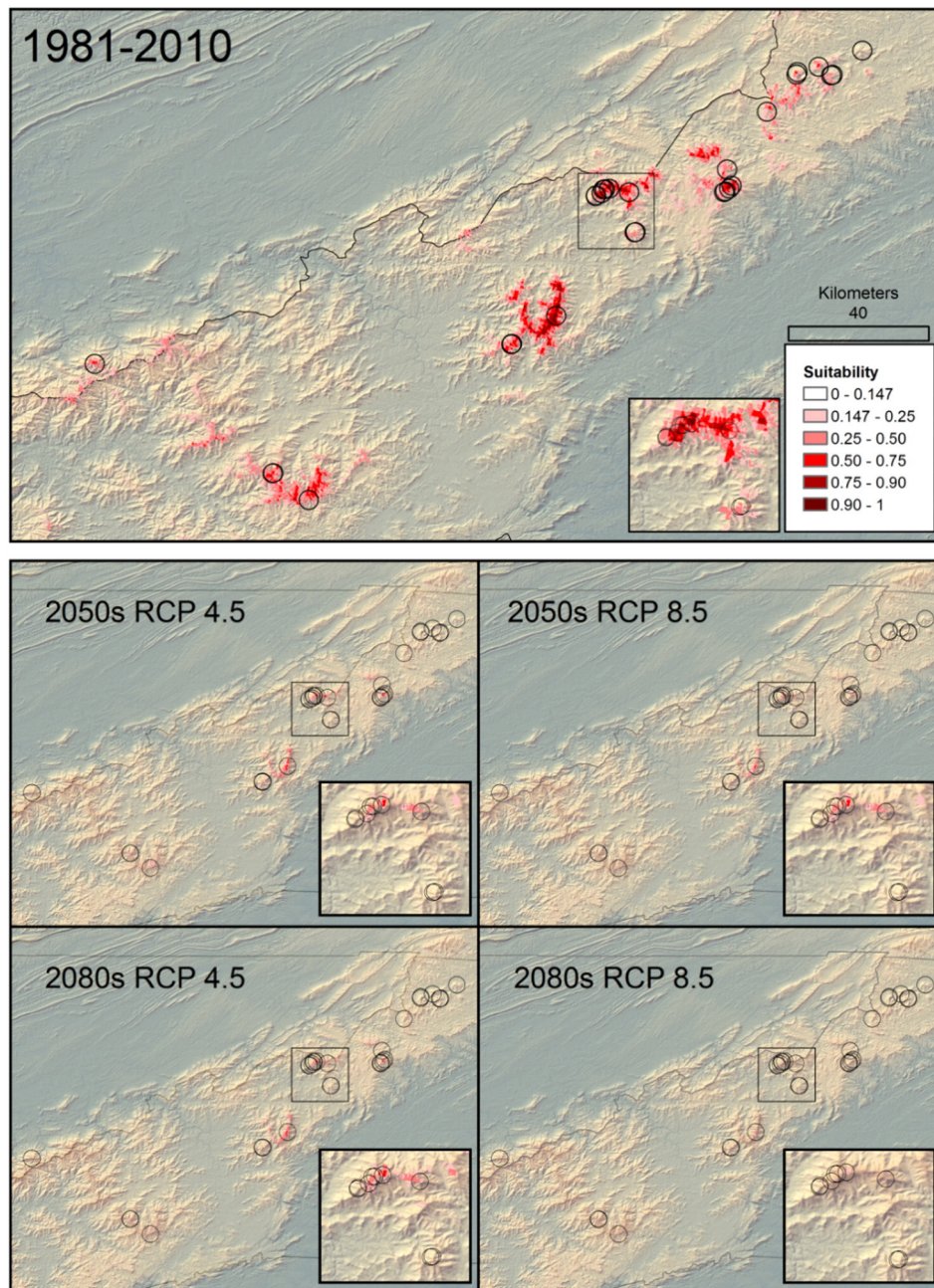


Fig. 6. Current (top) and future (bottom) macro- and topoclimatic suitability for *Geum radiatum*, modeled with Maxent. Each circle is a location of an extant population. Darker shades indicate greater suitability. Shading is clipped at the minimum value at which any site currently occurs. Overall climatic suitability declines severely under scenarios of future climate change regardless of the emissions scenario. Insets show that even fine-scale suitability declines with change in climate.

The low rate of seedling recruitment for *G. radiatum* does not have a clear cause. Flower production is usually consistent in large plants. Seed production appears abundant (Ulrey, personal observations), although there are few data on fecundity. Lack of available microhabitats may limit recruitment at many sites. Seed dispersal may be an issue, as it is likely that most seed will be dispersed away from suitable habitats. Strong winds are likely to remove many seeds from suitable microsites.

G. radiatum clones may extend many meters and may buffer genets from more local disturbances. This clonal structure allows it to spread vegetatively along cracks and crevices in cliff faces, in both vertical and horizontal directions. This is similar to *Oxyria sinensis* in China, which forms clones as large as 2.7 and 6.9 m in vertical and horizontal extent, respectively, along cliff faces (Liu et al., 2007).

Currently, the microclimates where *G. radiatum* grows are buffered and constant. Temperatures are cool and rarely exceed 24 °C (75 °F),

even as regional temperatures in the summer are far higher. Even more notable are consistent and high relative humidity (generally above 85% with median RH values of 100% for many study populations in many months). Because of these conditions, it is likely that *G. radiatum* plants experience only occasional drought stress during their long lifetimes (e.g. droughts occurred in the region from 1999–2002 and 2007–2009; during the latter years we did not see any observable effects on *G. radiatum* plants). This may make these populations particularly vulnerable to any climate change that increases the frequency of droughts or results in consistently drier local conditions. Climate change, especially as it affects episodic climate events (Jackson et al., 2009), may have particularly strong effects on species with specialized microhabitat requirements (Beaumont and Hughes, 2002).

The lack of strong effects of local habitat factors on the current demography of *Geum radiatum* has several potential causes. First, the

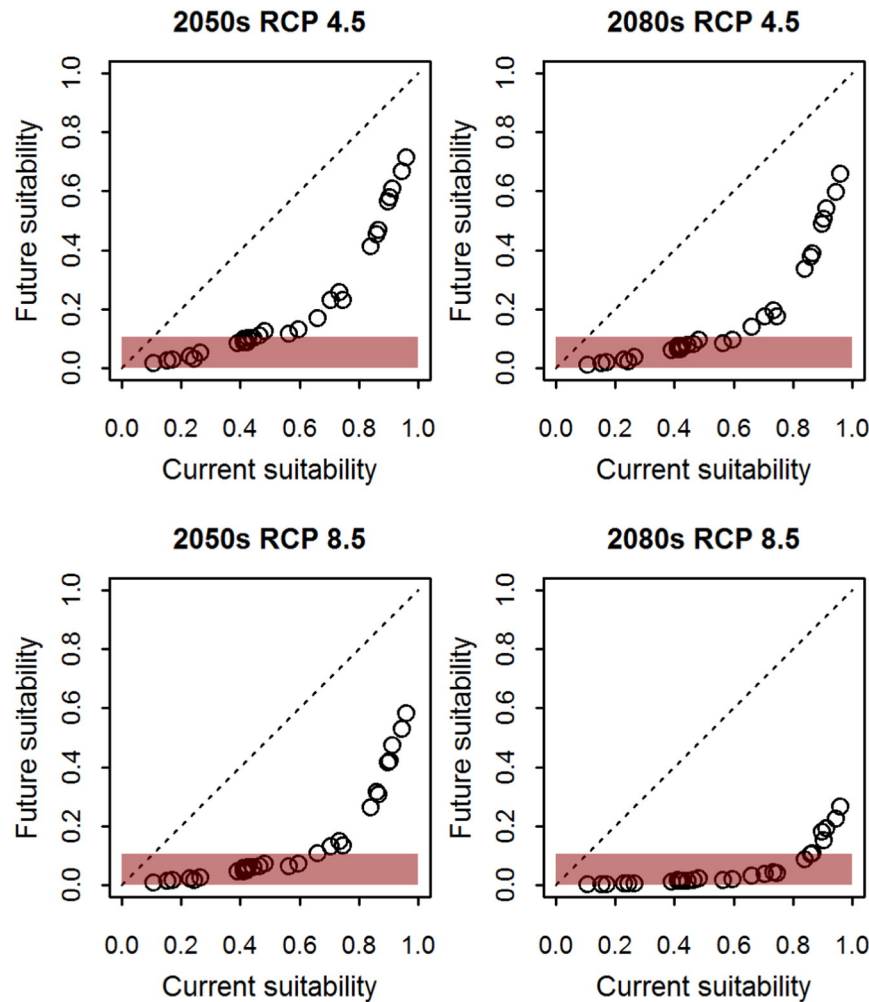


Fig. 7. Change in macro- and topo-climatic suitability among *Geum radiatum* populations across time periods and emissions scenarios. Each dot represents the current and future suitability of a site with a population (some populations are represented by more than one georeferenced site). No change in suitability would be represented by all points falling on the diagonal line. The bar demarcates values of suitability < the current minimum suitability across all sites. Depending on the time period and emissions scenario, between 13 and 22 of 29 sites fall into this zone. These sites tend to be in the northern portion of the species' range (not shown). In general there is little qualitative difference between the two time periods or emission scenarios, except that declines become especially severe under RCP 8.5 in the 2080s. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

range of habitat variation is relatively narrow. Second, plants may show plasticity in relation to changes in habitat factors. For example, other high elevation southern Appalachian species are able to plastically adjust physiological performance to reduced cloud immersion (Culatta and Horton, 2014). Finally, *G. radiatum* populations are dominated by slow-growing, high-surviving plants that may provide a great deal of demographic inertia, making responses to environmental gradients hard to detect.

Although we have been able to collect weather data for only a few years and from a subset of sites supporting *Geum radiatum*, these data suggest that population growth is sensitive to relative humidity. Changes in relative humidity forecasted by climate change models are predicted to reduce population growth in demographic models. Currently, this species is restricted to a very specific microenvironment with little variation in temperature and relative humidity. In general, global climate change is likely to create conditions far outside current climate envelopes and alter the relationships of demography to species' niches (Jackson et al., 2009). Thus, additional climate changes, such as extreme events, could have negative effects on *G. radiatum* and similar species in the future. In particular, extreme weather events could exacerbate erosion, the cause of some *G. radiatum* mortality, and affect groundwater seepage on which these habitats depend.

4.2. The effectiveness of climate refugia

Climate change is likely to be particularly threatening to rare plants because of their narrow distributions, small population sizes, and specific habitat requirements. All three of these components of rarity (Rabinowitz, 1981) apply to *Geum radiatum*. Macro- and topo-climatic ecological niche models predict that regardless of emission scenario, the species will experience a radical loss of habitat suitability at sites where it currently occurs and a widespread loss of climatically suitable habitat in the region by at least the 2050s. Fine-scale topographic heterogeneity (e.g., north- or west-facing cliff sides) could forestall some of this decline by leaving small areas still habitable.

A key question that remains unanswered is whether the specialized microhabitats currently favored by *G. radiatum*, by other rare plants in the Appalachians, and by plants in general, will be buffered from climate change that occur regionally (Williams et al., 2008; Maclean et al., 2015). Because *G. radiatum* is growing in the coldest and wettest sites in the southern Appalachians, it is likely to face problems with climate change unless its microhabitats remain particularly buffered (Williams et al., 2008). The spatial limitations of available data (90 m) relative to the small size of the occupied microhabitats, makes this question difficult to address. Our ecological niche models predicted loss of

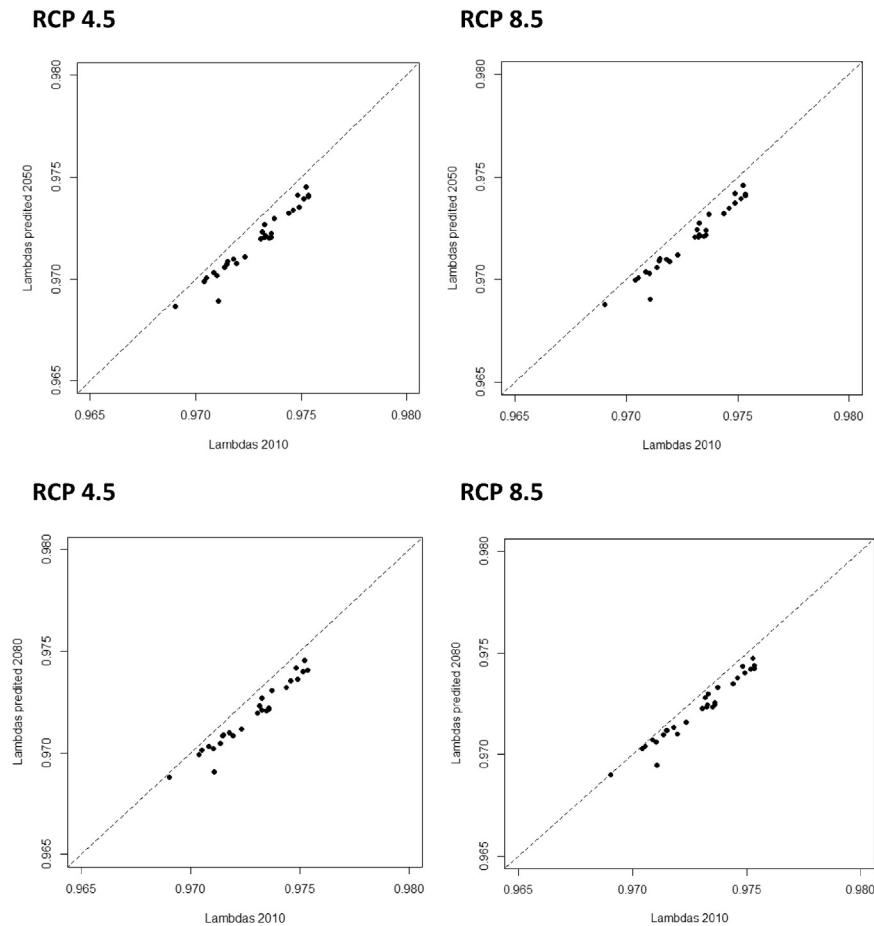


Fig. 8. Predicted population growth rate (lambda) under current conditions and in 2080, given four climate scenarios. Each point represents lambda of population. Each graph shows a 1:1 line; all populations are below this line indicating reductions in predicted population growth given climate change.

climatically suitable habitat across the species' range even though the models included 90-m resolution topo-climatic variables as predictors. Hence, fine-scale topographic features are unlikely to offer sufficient buffering against macroclimatic change.

Changes in climate are likely to affect vital rates and population viability of existing *G. radiatum* populations. The issues include increased mortality due to warmer and drier summers and increased disturbance by more frequent freeze-thaw cycles during warmer winters. In addition, predicted increases in the elevation of cloud cover will likely have negative effects on photosynthesis of plants adapted to foggy conditions (Richardson et al., 2003; Johnson and Smith, 2006). Unlike species that may have genetically based adaptations from lower elevation sites that would allow evolution in response to climate change (e.g. Lara-Romero et al., 2014), the limited elevational range and high population isolation in *G. radiatum* makes such adaptation unlikely.

The situation faced by *G. radiatum* is also a concern for rare flora in many parts of the world. In the Southern Appalachians future climate is expected to be warmer and, on average wetter, though whether precipitation increases or decreases overall remains an open question (Mitchell et al., 2014). Regardless, many species will experience drastically different climatic conditions. It is possible that microtopographic features like cliffs and sheltered ravines could provide refuge from regional climatic changes, but our results suggest that their ability to do so is limited (Fig. 6), especially for species living near the upper limit of elevational range. Surprisingly, wetter regional conditions do not necessarily translate into favorable levels of relative humidity, which had a direct bearing on population growth rates of *G. radiatum*. It is possible that elevated temperatures outweigh the effect of increased moisture to drive overall humidity lower at higher elevations (Berry et al.,

2014). Another important issue is changes in cloud/fog cover. Cloud immersion is common at sites currently supporting *G. radiatum*, but the height of the cloud cover is likely to increase with climate change (Richardson et al., 2003). Such immersion has strong physiological effects and reductions in cloud immersion could shift vegetation in the southern Appalachians (Johnson and Smith, 2008) as well as other cloud immersion ecosystems such as tropical montane cloud forests (Foster, 2001; Hu and Riveros-Iregui, 2016) and desert woodlands (Hildebrandt and Eltahir, 2006).

A key question for species facing changing climates is whether they can disperse to more suitable conditions and thus shift their ranges (Thuiller, 2004). *G. radiatum* is unlikely to be able to disperse to suitable sites during or after significant climate change. Its current sites are located at some of the highest elevations in North Carolina and Tennessee and, generally, on the coolest, moistest microsites. Because *G. radiatum* is usually on the most extreme microsites on any given mountain, short migrations to different microsites on the same mountains are not possible. Longer distance migrations to mountains in Virginia and West Virginia are also unlikely as these mountains are lower in elevation than current *G. radiatum* sites. Moving northward, mountains with comparable elevations are not found until upstate New York and New Hampshire, locations far in excess of unaided dispersal. The nearest relative to *G. radiatum* is *G. peckii*, a summer-flowering herb found in the alpine tundra, wet meadows, and stream-sides in the White Mountains of New Hampshire (Bliss, 1962; Fonda and Bliss, 1966; Paterson and Snyder, 1999). Although it seems unlikely that assisted migration of *G. radiatum* would occur over such a large latitudinal range, any plans to do so would have to consider the possible impacts of hybridization with the resident *G. peckii*.

4.3. Conservation alternatives

Geum radiatum, like many rare species and many habitat specialists, faces a range of challenges. These include site and demographic factors such as trampling, poor recruitment of seedlings, and limited safe sites. Limited genetic variation is another potential issue for this species. Augmentation is a potential tool for stabilizing extant populations and introductions could be used to respond to the threat of climate change.

Trampling has been cited as a major threat to populations of *Geum radiatum*. This has resulted in strong actions by multiple management agencies, particularly construction of overlooks that attempt to restrict visitor movement. These actions have been successful at several sites.

Currently, there is not strong evidence to suggest that narrow genetic variation is contributing to potentially low fecundity and subsequent seedling recruitment. Isozyme data from five *G. radiatum* populations showed that, compared to endemic plants in general, it had lower genetic diversity at the species level, typically low genetic diversity at the population level, and low levels of gene flow (Godt et al., 1996). Larger populations had higher genetic variation than medium-sized populations (Godt et al., 1996). Augmentations made during the 1990s may have provided immigrants from other populations and changed the landscape genetic structure of this species. In 2014, leaf collections were made from all of our study populations; ongoing microsatellite analysis of genetic structure is likely to provide new insights with potential management applications.

Because currently occupied microhabitats will probably become less suitable, and because natural migration is unlikely due to the fragmented nature of current habitats, augmentation of existing populations or introductions to new sites are tempting conservation actions that could forestall local extinctions in *G. radiatum*. Augmentation can be effective at increasing population viability (Halsey et al., 2015). Our modeling suggests that 20–70 seedlings would need to be added each year to balance population growth. Augmentation of larger individuals, if they could be successfully grown, would reduce these numbers. Previous augmentations and introductions to several areas have sometimes been successful to date, although some of the transplant locations were not into typical habitats and may not be viable in the long run due to shrub encroachment. In general, past augmentations have not been well documented.

One issue with augmentations is the availability of safe sites. Bare soil patches are usually quickly colonized by other species, although rockfalls and slides in the wet, steep habitats favored by *G. radiatum* are being continually created. Past augmentations by one of the authors have used coconut fiber mats anchored to cliffs to create fairly stable microsites, although these particular augmentations were unsuccessful due to dry weather and very limited post-transplant watering.

The niche modeling accomplished in this study can provide a model for potentially suitable, but unoccupied, sites that could be candidates for the creation of new populations. Populations within the current range of *Geum radiatum* would have the same climate change threats as extant populations. Whether there are suitable sites further north is an open question, although our modeling suggests that these sites will also become unsuitable in the next few decades. Nonetheless, having more populations (wild or introduced) will certainly decrease the likelihood of species extinction.

Most augmentations to date have used plants grown in high-elevation gardens. Although this method has produced plants, it takes several years of growth to produce plants large enough to have a good chance of survival. Another possibility is to sow seeds directly into microsites on-site. Ex situ collections of plants or seeds would be a good reservoir to use in future introductions and augmentations, and to serve as a backup source of material for responding to major disturbances. Current genetic studies will help elucidate whether genetically unique or unusual populations need to be augmented only from material derived from individual populations.

5. Conclusions

Our results provide an important, biologically meaningful test of the ability of climate refugia to support populations of rare endemic species both now and in the future. We found that those high-altitude microclimatic refugia in the southern Appalachian Mountains are currently able to support populations of *G. radiatum* at slightly less than replacement level. Moreover, conditions at these sites are expected to degrade as anthropogenic climate change progresses. This is a worrisome trend and raises the question as to whether relying on climate refugia identified using current locations of rare species is sufficient for guiding conservation in light of climate change. While these sites might provide short-term buffering from climatic extremes, it is unclear if they will serve this function in the longer term.

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References

- Ackerly, D.D., Cornwell, W.K., Weiss, S.B., Flint, L.E., Flint, A.L., 2015. A geographic mosaic of climate change impacts on terrestrial vegetation: which areas are more at risk? *PLoS One* (<http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0130629>).
- Aratijo, M.B., Luoto, M., 2007. The importance of biotic interactions for modelling species distributions under climate change. *Glob. Ecol. Biogeogr.* 16, 743–753.
- Ashcroft, M.B., 2010. Identifying refugia from climate change. *J. Biogeogr.* 37, 1407–1413.
- Ashcroft, M.B., Chisholm, L.A., French, K.O., 2009. Climate change at the landscape scale: predicting fine-grained spatial heterogeneity in warming and potential refugia for vegetation. *Glob. Chang. Biol.* 15, 656–667.
- Ashcroft, M.B., Grollan, J.R., Warton, D.L., Ramp, D., 2012. A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. *Glob. Chang. Biol.* 18, 1866–1879.
- Beaumont, L.J., Hughes, L., 2002. Potential changes in the distribution of latitudinally restricted Australian butterfly species in response to climate change. *Glob. Chang. Biol.* 8, 954–971.
- Berry, Z.C., Smith, W.K., 2013. Ecophysiological importance of cloud immersion in a relic spruce-fire forest at elevational limits, southern Appalachian Mountains, USA. *Oecologia* 173, 637–648.
- Berry, Z.C., Hughes, N.M., Smith, W.K., 2014. Cloud immersion: an important water source of spruce and fir saplings in the southern Appalachian Mountains. *Oecologia* 174, 319–326.
- Bin, Y., Spence, J., Wu, L., Li, B., Hao, Z., Ye, W., He, F., 2016. Species-habitat associations and demographic rates of forest trees. *Ecography* 39, 9–16.
- Bliss, L.C., 1962. Caloric and lipid content in alpine tundra plants. *Ecology* 43, 753–757.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. *Ecol. Model.* 157, 281–300.
- Burnham, K.P., Anderson, D., 2002. *Model Selection and Multimodal Inference*. Springer.
- Cogbill, C.V., White, P.S., Wiser, S.K., 1997. Predicting treeline elevation in the southern Appalachians. *Castanea* 62, 137–146.
- Culatta, K.E., Horton, J.L., 2014. Physiological response of southern Appalachian high-elevation rock outcrop herbs to reduced cloud immersion. *Castanea* 79, 182–194.
- Dalgleish, H.J., Koons, D.N., Hooten, M.B., Moffet, C.A., Adler, P.B., 2011. Climate influences the demography of three dominant sagebrush steppe plants. *Ecology* 92, 75–85.
- Damschen, E.I., Harrison, S., Ackerly, D.D., Fernandez-Goñi, B.M., Anacker, B.L., 2012. Endemic plant communities on special soils: early victims or hardy survivors of climate change? *J. Ecol.* 100, 1122–1130.
- Davis, J., Pavlova, A., Thompson, R., Sunnucks, P., 2013. Evolutionary refugia and ecological refuges: key concepts for conserving Australian arid zone freshwater biodiversity under climate change. *Glob. Ecol. Biogeogr.* 19, 1970–1984.
- Dirnbock, T., Essl, F., Rabitsch, W., 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Glob. Chang. Biol.* 17, 990–996.
- Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Glob. Chang. Biol.* 17, 1022–1035.

- Easterling, M.R., Ellner, S.P., Dixon, P.M., 2000. Size-specific sensitivity: applying a new structured population model. *Ecology* 81, 694–708.
- Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. *J. Anim. Ecol.* 77, 802–813.
- Ellner, S.P., Rees, M., 2006. Integral projection models for species with complex demography. *Am. Nat.* 167, 410–428.
- Estill, J.C., Cruzen, M.B., 2001. Phylogeography of rare plant species endemic to the Southeastern United States. *Castanea* 66, 3–23.
- Fonda, R.W., Bliss, L.C., 1966. Annual carbohydrate cycle of alpine plants on Mt. Washington, New Hampshire. *Bull. Torrey Bot. Club* 93, 268–277.
- Foster, P., 2001. The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Sci. Rev.* 55, 73–106.
- Godt, M.J.W., Johnson, B.R., Hamrick, J.L., 1996. Genetic diversity and population size in four rare southern Appalachian plant species. *Conserv. Biol.* 10, 796–805.
- Gollan, J.R., Ramp, D., Achcroft, M.B., 2014. Assessing the distribution and protection status of two types of cool environment to facilitate their conservation under climate change. *Conserv. Biol.* 28, 456–466.
- Gutiérrez Illán, J., Gutiérrez, D., Wilson, R.J., 2010. The contributions of topoclimate and land cover to species distributions and abundance: fine-resolution tests for a mountain butterfly fauna. *Glob. Ecol. Biogeogr.* 19, 159–173.
- Guo, Q., Kelly, M., Graham, C.H., 2005. Support vector machines for predicting distribution of Sudden Oak Death in California. *Ecol. Model.* 182, 75–90.
- Halsey, S.J., Bell, T.J., McEachern, K., Pavlovic, N.B., 2015. Comparison of reintroduction and enhancement effects on metapopulation viability. *Restor. Ecol.* 23, 375–384.
- Hamann, A., Wang, T., Spittlehouse, D.L., Murdock, T.Q., 2013. A comprehensive, high-resolution database of historical and projected climate surfaces for western North America. *Bull. Am. Meteorol. Soc.* 94, 1307–1309.
- Hildebrandt, A., Eltahir, E.A.B., 2006. Forest on the edge: seasonal cloud forest in Oman creates its own ecological niche. *Geophys. Res. Lett.* 33, L11401. <http://dx.doi.org/10.1029/2006GL026022>.
- Hirtzel, A.H., De Lay, G., Halfer, V., Randin, C., Guisan, A., 2006. Evaluating the ability of habitat suitability models to predict species presences. *Ecol. Model.* 199, 142–152.
- Holt, R.D., Keitt, T.H., 2000. Alternative causes for range limits: a metapopulation perspective. *Ecol. Lett.* 3, 41–47.
- Hu, J., Riveros-Iregui, D.A., 2016. Life in the clouds: are tropical montane cloud forests responding to changes in climate? *Oecologia* 180, 1061–1073.
- Ingram, K., Dow, K., Carter, L., Anderson, J. (Eds.), 2013. *Climate Change of the Southeast United States: Variability, Change, Impacts, and Vulnerability*. Island Press, Washington DC, USA.
- Jackson, S.T., Betancourt, J.L., Booth, R.K., Gray, S.T., 2009. Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *PNAS* 106 (supplement 2), 19685–19692.
- Johnson, B.R., 1995. *The Ecology and Restoration of a High Montane Rare Plant Community*. University of Georgia, Athens, Georgia, USA (PhD dissertation).
- Johnson, B.R., 1996. Southern Appalachian rare plant reintroductions on granite outcrops. In: Falk, D.A., Millar, C.I., Olwell, M. (Eds.), *Restoring Diversity. Strategies for Reintroduction of Endangered Plants*. Island Press, Washington, DC, USA, p. 443.
- Johnson, D.M., Smith, W.K., 2006. Low clouds and cloud immersion enhance photosynthesis in understory species of a southern Appalachian spruce–fir forest. *Am. J. Bot.* 93, 1625–1632.
- Johnson, D.M., Smith, W.K., 2008. Cloud immersion alters microclimate photosynthesis and water relations in *Rhododendron catawbiense* and *Abies fraseri* seedlings in the southern Appalachians Mountains, USA. *Tree Physiol.* 28, 385–392.
- Jones, K.R., Watson, J.E.M., Possingham, H.P., Klein, C.J., 2016. Incorporating climate change into spatial conservation prioritization: a review. *Biol. Conserv.* 194, 121–130.
- Keppel, G., Van Neil, K.P., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., Schut, A.G.T., Hopper, S.D., Franklin, S.E., 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. *Glob. Ecol. Biogeogr.* 21, 393–404.
- Krause, C.M., Cobb, N.S., Pennington, D.D., 2015. Range shifts under future scenarios of climate change: dispersal ability matters for Colorado Plateau endemic plants. *Natural Areas Journal* 35, 428–438.
- Lara-Romero, C., Robledo-Arnuncio, J.J., García-Fernández, A., Iriondo, J.M., 2014. Assessing Intraspecific Variation in Effective Dispersal Along an Altitudinal Gradient: A Test in Two Mediterranean High-Mountain Plants. *PLoS ONE* 9 (1), e87189. <http://dx.doi.org/10.1371/journal.pone.0087189>.
- Lenoir, J., Graae, B.J., Arrestand, P.A., Alsos, I.G., Armbruster, S., et al., 2013. Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Glob. Chang. Biol.* 19, 1470–1481.
- Liu, F.-H., Yu, F.-H., Liu, W.-S., Krusi, B.O., Cai, X.-H., Schneller, J.J., Dong, M., 2007. Large clones on cliff faces: expanding by rhizomes through cracks. *Ann. Bot.* 100, 51–54.
- Loarie, S.R., Carter, B.E., Hayhoe, K., McMahon, S., Moe, R., Knight, C.A., Ackerly, D.D., 2008. Climate change and the future of California's endemic flora. *PLoS One* <http://dx.doi.org/10.1371/journal.pone.1112502>.
- Maclean, I.M.D., Hopkins, J.J., Bennie, J., Lawson, C.R., Wilson, R.J., 2015. Microclimates buffer the responses of plant communities to climate change. *Glob. Ecol. Biogeogr.* 24, 1340–1350.
- Massey, J.R., Otte, D.K.S., Atkinson, T.A., Whetstone, D.R., 1983. *An Atlas and Illustrated Guide to the Threatened and Endangered Vascular Plants of the Mountains of North Carolina and Virginia*. Southeast Forest Experiment Station, Asheville, North Carolina, USA.
- Merow, C., Latimer, A.M., Wilson, A.M., McMahon, S.M., Rebelo, A.G., Silander Jr., J.A., 2014. On using integral projection models to generate demographically driven predictions of species' distributions: development and validation using sparse data. *Ecography* 37, 001–017.
- Mitchell, R.J., Liu, Y., O'Brien, J.J., Elliott, K.J., Starr, G., Miniati, C.F., Hiers, J.K., 2014. Future climate and fire interactions in the southeastern region of the United States. *For. Ecol. Manag.* 327, 316–326.
- Molano-Flores, B., Bell, T.J., 2012. Projected population dynamics for a federally endangered plant under different climate change emission scenarios. *Biol. Conserv.* 145, 130–138.
- Omerik, J.M., 1987. Ecoregions of the conterminous United States. Map (scale 1: 7,500,000). *Ann. Assoc. Am. Geogr.* 77, 118–125.
- Paterson, I.G., Snyder, M., 1999. Genetic evidence supporting the taxonomy of *Geum peckii* (Rosaceae) and *G. radiatum* as separate species. *Rhodora* 101, 325–340.
- Phillips, S.J., Anderson, R.P., Schapire, R.W., 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190, 231–259.
- Rabinowitz, D., 1981. Seven forms of rarity. In: Syngue, H. (Ed.), *The Biological Aspects of Rare Plant Conservation*. J. Wiley, Chichester, United Kingdom, pp. 205–217.
- Radosavljevic, A., Anderson, R.P., 2014. Making better Maxent models of species distributions: complexity, overfitting and evaluation. *J. Biogeogr.* 41, 629–643.
- Ramula, S., Rees, M., Buckley, Y.M., 2009. Integral projection models perform better for small demographic data sets than matrix population models: a case study of two perennial herbs. *J. Appl. Ecol.* 46, 1048–1053.
- Raventos, J., Gonzalez, E., Mujica, E., Doak, D.F., 2015. Population viability analysis of the epiphytic ghost orchid (*Dendrophylax lindenii*) in Cuba. *Biotropica* 47, 179–189.
- Richardson, A.D., Denny, E.G., Siccama, T.G., Lee, X., 2003. Evidence for a rising cloud ceiling in Eastern North America. *Am. Meteorol. Soc.* 16, 2093–2098.
- Russell, D.A., Rich, F.J., Schneider, V., Lynch-Stieglitz, J., 2009. A warm thermal enclave in the Late Pleistocene of the South-eastern United States. *Biol. Rev.* 84, 173–202.
- Schemske, D.W., Husband, B.C., Ruckelshaus, M.H., Goodwillie, C., Parker, I.M., Bishop, J.G., 1994. Evaluating approaches to the conservation of rare and endangered plants. *Ecology* 75, 584–606.
- Schwartz, M.W., Iverson, J.R., Prasad, A.M., Matthews, S.N., O'Connor, R.J., 2006. Predicting extinctions as a result of climate change. *Ecology* 87, 1611–1615.
- Serra-Diaz, J.M., Scheller, R.M., Syphard, A.D., 2015. Disturbance and climate microrefugia mediate tree range shifts during climate change. *Landsc. Ecol.* 30, 1039–1053.
- Shryock, D.F., Esque, T.C., Hughes, L., 2014. Population viability of *Pediocactus bradyi* (Cactaceae) in a changing climate. *Am. J. Bot.* 101, 1944–1953.
- Staudinger, M.D., Carter, S.L., Cross, M.S., Dubois, N.S., Duffy, J.E., Enquist, C., Griffis, R., Hellmann, J.J., Lawler, J.J., O'Leary, J., Morrison, S.A., Sneddon, L., Stein, B.A., Thompson, L.M., Turner, W., 2013. Biodiversity in a changing climate: a synthesis of current and projected trends. *Front. Ecol. Environ.* 11, 465–473.
- Stolar, J., Nielsen, S.E., 2015. Accounting for spatially biased sampling effort in presence-only species distribution modelling. *Divers. Distrib.* 21, 595–608.
- Summers, D.M., Bryan, B.A., Crossman, N.D., Meyer, W.S., 2012. Species vulnerability to climate change: impacts on spatial conservation priorities and species representation. *Glob. Chang. Biol.* 18, 2335–2348.
- Swab, R.M., Regan, H.M., Matthies, D., Becker, U., Brunn, H.H., 2015. The role of demography, intra-specific variation, and species distribution models in species' projections under climate change. *Ecography* 38, 221–230.
- Thuiller, W., 2004. Patterns and uncertainties of species' range shifts under climate change. *Glob. Chang. Biol.* 10, 2020–2027.
- Tye, M.R., Menges, E.S., Weekley, C., Quintana-Ascencio, P.F., Salguero-Gomez, R., 2016. A demographic ménage à trois: interactions between disturbances both amplify and dampen population dynamics of an endemic plant species. *J. Ecol.* (in revision).
- U.S. Fish and Wildlife Service, 1993. *Recovery Plan for Spreading Avens (*Geum radiatum*) Rafinesque*. Atlanta, Georgia, USA.
- U.S. Fish and Wildlife Service, 2013. *Spreading Avens (*Geum radiatum*) 5-year Review*. U.S. Fish and Wildlife Service, Atlanta, Georgia, USA.
- Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A., Snyder, M.A., 2009. Niches, models, and climate change: assessing the assumptions and uncertainties. *Proc. Natl. Acad. Sci. U. S. A.* 106, 19729–19736.
- Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. *Bioscience* 48, 607–615.
- Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A., Landham, G., 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol.* 6, e325.
- Wiser, S.K., 1994. High-elevation cliffs and outcrops of the southern Appalachians: vascular plants and biogeography. *Castanea* 59, 85–116.
- Wiser, S.K., 1998. Comparison of southern Appalachian high-elevation outcrop plant communities with their northern Appalachian counterparts. *J. Biogeogr.* 25, 501–513.
- Wiser, S.K., Peet, R.K., White, P.S., 1998. Prediction of rare-plant occurrence: a southern Appalachian example. *Ecol. Appl.* 8, 909–920.