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UNIVERSITY OF CALIFORNIA
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Vulnerability of *Erythranthe* Species in the California Floristic Province
Under Climate Change and Land-Use Change

A Thesis submitted in partial satisfaction
of the requirements for the degree of

Master of Science

in

Evolution, Ecology, and Organismal Biology

by

Su Yeon Kim

March 2024

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ABSTRACT OF THE THESIS

Vulnerability of Erythranthe Species in the California Floristic Province Under Climate Change and Land-Use Change

by

Su Yeon Kim

Master of Science, Graduate Program in Evolution, Ecology, and Organismal Biology
University of California, Riverside, March 2024
Dr. Helen M. Regan, Chairperson

Species extinction is increasing due to anthropogenic threats such as climate change and land-use change. Thus, there is increasing interest in predicting the future fate of species and implementing effective management strategies. In this study, we used spatially-explicit stochastic population models to simulate future projections of three Monkeyflower species, *Erythranthe cardinalis*, *Erythranthe lewisii*, and *Erythranthe guttata*, under climate and land-use change in their regional habitat range in the California Floristic Province. We compared future population projections of two of the three Monkeyflower species, sub-divided into lower and higher elevation ranges, to examine the role of elevational differences in life history parameters in the persistence of the species under projected habitat changes. Lastly, due to the appearance of oscillations and declines in population trajectories of one Monkeyflower species, we explored the role of small, colonized patches on population trajectories. The modeling framework linked species

distribution models (SDMs) with population models and dispersal modes parametrized with a combination of multi-year population census data, information from the literature, and publicly available environmental data, including temperature and precipitation projections under two climate scenarios and two climate models. Due to high population growth rates, all three species were constrained by changes in habitat due to climate and land-use change. However, subpopulations of *E. cardinalis* had a low population growth rate at lower elevational ranges leading to extirpation in that region. Conversely, *E. lewisii* had a high population growth rate but experienced substantial declines in suitable habitat. In the population trajectories of *E. lewisii*, damped oscillations were observed stemming from a combination of high growth rates and colonization of new small patches which paradoxically reduced the overall population size across the metapopulation. This study highlights the importance of examining small-scale local spatial and demographic characteristics and dynamics, as opposed to large-scale regional habitat and population projections, in understanding the drivers of declines and extinction.

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Introduction

Species extinction is occurring at rates much higher than background due to anthropogenic threats (Cowie et al. 2022, Ceballos et al. 2015). After industrialization in the mid-twentieth century, greenhouse gas emissions caused by anthropogenic stressors such as pollution, urbanization, deforestation, and agriculture led to a rise in ambient temperature, causing human-induced disturbances including sea-level rise, geographic shifts of vegetation, desertification, increases in evapotranspiration and primary production and altered disturbance regimes such as fires and flooding (Blondel & Aronson 1995, Marraccini et al. 2015; Rosenzweig et al. 2008). A metaanalysis of 131 studies showed that 7.9% of species are predicted to become extinct due to the impact of climate change, and the global extinction risk is projected to increase from 2.8% to 15.7% under the current, business-as-usual trajectory of a 4.3°C rise in global temperatures (Urban 2015). Globally, species richness in terrestrial ecosystems has decreased by 13.6% on average and is projected to decrease by another 3.4% by 2100 under current land-use scenarios with high rates of human population growth (Newbold et al. 2015). As urban and agricultural land-use continue to expand, a greater number of species are at risk of extinction due to habitat loss and fragmentation (Midgley et al. 2002; Underwood et al. 2009).

The Californian Floristic Province (CFP), a Mediterranean-type ecosystem (MTE) in North America and the focus of this study, is a highly threatened biodiversity hotspot with high biodiversity and endemism (Thomas et al. 2004; Harrison 2013). The 36 biodiversity hotspots (i.e. regions with more than 1,500 endemic species with less than

30% of natural habitat remaining) comprise 2.3% of the Earth's land surface but are home to more than half of known plant species (Mittermeier et al. 2011; Myers et al. 2000, Noss et al. 2015). Climate change, land-use change, and altered fire regime are three main threats to MTEs. These stressors not only alter the environmental conditions of MTEs, but they also influence the plant communities within them (Matesanz & Valladares 2014; Sala et al. 2000). Loarie et al. (2008) concluded that up to two thirds of endemic plants in the CFP will experience a decrease of more than 80% of their range sizes within a century, under an assumption of no dispersal. Agricultural land-use and urban expansion were and remain major threats to biodiversity hotspots with urban expansion having had larger effects in the developed regions of North America (Underwood et al. 2009; Jantz et al. 2015; Kong et al. 2021). Historically, an estimated 64% to 75% of plant cover in the CFP was lost from 1500 to 2005 by land-use change and up to 92% of natural plant cover that was present around the sixteenth century is predicted to be lost by the end of 21st century (Mittermeier et al. 2005; Jantz et al. 2015).

Species' geographic ranges are expected to shift due to climate change (Kelly & Goulden 2008, Lenoir et al. 2008, Lenoir et al. 2010, Wolf et al. 2016) with plant species in MTEs at considerable risk of range contraction due to their poor dispersal abilities (Franklin et al. 2014). Forest plant species have been estimated to have shifted upwards in elevation an average of 29 m per decade in the 20th century to track cooler temperatures at higher elevation (Lenoir et al. 2008). In California, 14.6% of native plant taxa and 12% of endemic plant taxa are estimated to have shifted upwards an average of 3.9 m and 9 m, respectively, during the past century (Wolf et al. 2016). Lenoir et al.

(2010) also reviewed past studies and found that 65% of plant and animals species surveyed shifted their mid-range positions upwards while 25% shifted downwards. The long-term survey conducted in Kopp & Cleland (2014) showed that some alpine plant species increased in abundance in the upper limits of their distributions or decreased in abundance in the lower limits of their distributions suggesting more favorable environmental conditions at higher elevations. Many factors such as adaptation, traits, habitat quality and availability, and environmental conditions (Chen et al. 2011, Conlisk et al. 2017, Dickman et al. 2019, Eckhart et al. 2011, Lenoir et al. 2010, Midolo & Wellstein 2020, Urley et al. 2016, Wolf et al. 2016) affect the direction, speed and extent of these range shifts caused by climate change (Serra-Diaz et al. 2014). Species with larger population size, high growth rates, high reproduction, long-lived seeds, fast life-history, dispersal capabilities that match the speed of habitat shifts, wide altitudinal range, low habitat specificity, and/or drought-tolerant traits are predicted to have the best chances of persistence under climate change (Chichorro et al. 2022, Craine et al. 2013, Elizabeth 2007, Jeppsson & Forslund 2012, Mortiz & Agudo 2013, Pearson et al. 2014, Saar et al. 2012, Stöcklin & Fischer 1999). However, the specific combination of traits that are typically associated with resilience will interact with their spatial context in complex ways (Franklin et al. 2021).

There is evidence that different species have adaptations or phenotypic plasticity to different environmental conditions across their range and this may make subpopulations in some parts of the species' range more resilient to a changing environment than in other parts (Valladares et al. 2014). For instance, cutleaf

monkeyflower (*Mimulus laciniatus*) exhibits variation in demographic traits, such as plant size, growth rate, days to first flower and flowering period, in lower and higher elevations of its range after drought years (Dickman et al. 2019). Studies have observed different traits and substantial variance across subpopulations of *Erythranthe guttata* (Twyford et al. 2020); in dry conditions, such as drought or montane sites with dry soils in summer, plants are characterized by early flowering (Kooyers et al. 2015, Hall & Willis 2006), whereas in temperate coastal sites or permanently wet conditions, intermediate flowering dates, vegetative reproduction, and faster growth were apparent (Hall & Willis 2006, van Kleunen 2007). A question of conservation concern then is: are observed adaptations to different environmental conditions sufficient to confer resilience to species in the face of range shifts due to climate change? Studies that document differences in life history within species along elevational gradients are scarce. However, matrix population models in Angert (2006, 2009) constructed from the censuses of two monkeyflower species, *Erythranthe cardinalis* and *Erythranthe lewisii*, showed that there is a difference in population growth rates of subpopulations that are located in different elevational ranges. The wide range of demographic data from the study allows an examination of the subpopulations that are more likely to persist across the landscape in the face of climate change.

Climate change is not the only threat that is present in California and land-use change should not be overlooked when it may pose greater danger to biodiversity (Riordan & Rundel 2014). In California, it is expected that 28% more land will be used by humans by 2100 (Sleeter et al. 2017) and urban development is the fastest growing

cause of land-use change in recent years (Chen et al. 2010). Land-use change has degraded, destructed, or fragmented species' habitats leading to isolation of populations, transition of core habitat to edge and increased susceptibility to invasive species and is expected to continue (Fischer & Lindenmeyer 2007, With 2004). For instance, four percent of the forest in western United States was lost to residential and transportation land use, with the mean forest patch size drastically reduced and highly fragmented (Theobald et al. 2011). Coastal sage scrub in coastal southern California is also affected by residential development and the local species experience population declines and habitat reduction and fragmentation into smaller patches (Bolger 2002).

Under climate change projections, species distributions can be affected in a few different ways. Much of the scientific literature focuses on contractions and/or shifts upslope of suitable habitat which usually results in projections of population decline (Auld et al. 2022, Conlisk et al. 2017, Feeley & Silman 2010). However, changes in temperature and precipitation due to climate change can also lead to habitat fragmentation into small patches of occupied suitable habitat or the creation of small patches of newly suitable habitat that can be colonized if the species has sufficient dispersal capabilities; the ability of the latter of these to bolster populations is not yet fully understood and is likely to be context dependent. The field of conservation biology has long debated the value of small patches which is inevitably related to habitat fragmentation. Diamond (1975) asserted that a single large patch would be more beneficial than the several small patches in conserving biodiversity thus initiating the Single Large Or Several Small (SLOSS) debate. Simberloff & Abele (1976) suggested

that this is not always true theoretically and empirically; many studies have supported different sides of the debate since (Simberloff & Abele 1982, Quinn & Harrison 1988, Fahrig 2017, Wilson & Willis 1975, Wilcox & Murphy 1985, Järvinen 1982). Factors such as distance between patches, connectivity, spatial autocorrelation, degree of fragmentation, nestedness, heterogeneity, risks from disturbances, dominance of extinction or colonization, presence of environmental stress, and facilitation or hindrance of disease spread have been mentioned to support either side of the debate (Diamond 1976, Fahrig 2020, Fahrig et al. 2022, Lesica & Allendorf 1992, Riva & Fahrig 2022, Simberloff 1988). Additionally, in recent studies there has been an emphasis on the value of small habitats to conservation of biodiversity (Riva & Fahrig 2022, Lindenmayer 2019, Wintle et al. 2019). The crisis of climate change and its effects on biodiversity requires a re-examination of the conditions under which small patches can provide a mechanism for the persistence of species, if at all.

In this study, we utilize a multi-year demographic data set for three *Erythranthe* (monkeyflower) species—*Erythranthe cardinalis*, *Erythranthe lewisii*, and *Erythranthe guttata*—in the CFP, to address three questions. First, is the persistence of these species under climate change and land-use change constrained by habitat availability or demography? Second, what role do elevational differences in the life history parameters of subpopulations of *E. cardinalis* and *E. lewisii* play in the persistence of these species under projected habitat changes? Third, do small patches of newly created and colonized suitable habitat benefit populations of *E. lewisii*?

To address these questions, we use an integrated modeling framework, that links species distribution models (SDMs) with population models constructed from empirical data for three *Erythranthe* species. The SDMs project how suitable habitat of the *Erythranthe* species is projected to change in 90 years as a result of climate change and land-use change (Elith & Leathwick 2009; Kearney & Porter 2009) while the population models take demographic parameters such as survival and reproduction of the species into account and simulate population dynamics in the suitable patches that are generated from the SDMs. Additionally, dispersal models were also added to incorporate colonization of new habitats into the models. This integrated modeling framework takes both intrinsic (e.g. species demography) and extrinsic factors (e.g. climate change) into account in estimating the extinction risks of the species (Fordham et al. 2012, Murray et al. 2014, Franklin et al. 2014, 2021).

Methods

Study System and Demographic Data

E. cardinalis and *E. lewisii* are rhizomatous perennial herbs (Nesom 2013). *E. cardinalis* is found across a broad geographical range, from sea level to 2,400 m, and from southern Oregon to northern Baja California and in coastal California. *E. lewisii* occurs mostly in higher elevations of 1,200 m to 3,100 m in the Sierra Nevada mountains of California. *E. guttata* (syn. *Mimulus guttatus*), found in areas with elevations up to around 2,438 m in California (Campbell 1950), has more variable ecotypes than *E. cardinalis* or *lewisii*, exhibiting two different life history types: a perennial life history

with clonal rosettes and an annual life history that does not reproduce clonally (DeMarche et al. 2016). *E. guttata* populations with a perennial life history are found in habitats that have accessibility to moisture throughout the year, usually in coastal areas, whereas populations with an annual life history are typically found in habitats with dry seasons, mostly in inland areas (Hall & Willis 2006). The two different ecotypes of *E. guttata* went through different genetic adaptations, reproductive isolation, and show differences in various physiological, phenological, life history and disturbance-related traits (DeMarche et al. 2015, Hall & Willis 2006, Holeski et al. 2013, Kleunen 2007, Twyford et al. 2020).

Life history parameters for each species were obtained from published empirical studies (Angert 2009; DeMarche et al. 2016) and/or directly as life history matrices constructed from census data (A. Angert pers. comm.). The detailed information about each matrix population model and where they were obtained are reported in Table 1. *E. cardinalis* was censused at two low elevation and two mid-elevation sites, whereas *E. lewisii* was censused at two mid-elevation and two high elevation sites (Angert 2009; pers. comm.). Censuses were conducted annually from 2000 to 2007 for each subpopulation listed in Table 1, producing a total of 56 stage matrices across both species. Life history parameters for *E. guttata* were calculated from census data collected from a common garden transplant experiment in central Sierra Nevada, California (DeMarche et al. 2016). Seeds were collected from 11 subpopulations in 2010 and transplanted in Eagle Meadows, Stanislaus National Forest (Table 1), along with a control. We used the 2012 and 2013 census data from the Eagle Meadow control

subpopulation (i.e. of plants that had germinated from seed collected at that site) to calculate the demographic parameters for the stage matrix.

Species Distribution Models

SDMs were generated for current climate conditions and under climate and land-use change projections using the *flexsdm* workflow package in R (Velazco et al. 2022). SDMs with 270 m x 270 m spatial resolution were used to estimate habitat suitability of each species and were produced using species occurrence and environmental data. For the two species *E. cardinalis* and *E. lewisii*, presence-only models were built from the Consortium of California Herbaria, the Global Biodiversity Information Facility (DOI: 10.15468/dl.nrdmke) data due to lack of data from vegetation surveys. For *E. guttata*, presence-absence models were built using data from vegetation surveys (Hannah et al., 2008) and Calflora.org collected between 1980-2010 (Table 2b). Environmental data included climate, hydrological, terrain and soil predictors that are closely associated with Mediterranean ecosystems (Stephenson 1998). Climate and hydrological predictors for the years 1981-2010 at 270 m x 270 m spatial resolution derived from the Basin Characterization Model (BCM) (Flint et al. 2013), 10 m resolution soil parameters from the gridded National Soil Survey Geographic Database (gNATSGO, Soil Survey Staff, 2020), and landform types based on hillslope position and dominant soil formation processes (Theobald et al. 2015) were used in our models (Table 2a). Integrated Climate Land Use scenarios (ICLUS) that predict increases in urban development and decreases in agricultural and forest lands were used to make land-use projections (Bierwagen et al. 2010, Theobald 2005).

Eight SDM algorithms were used to project suitable habitat following the procedures described in Velazco et al. (2022) and Rose et al. (2023). Generalized linear models (glm), generalized additive models (gam), boosted regression trees (gbm), random forests (raf), artificial neural networks (net), support vector machines (svm), maximum entropy (max), and gaussian process (gau) (Franklin, 2010), were used for *E. cardinalis* and *E. lewisii*. Maximum entropy and Gaussian processes were excluded for *E. guttata* to utilize the presence-absence data available for this species. Continuous suitability values were retained for the habitat suitability values above the threshold level to remove areas with low habitat suitability while retaining variation in suitability within remaining species' habitat (Muscatello & Kujala 2021). Thresholds for SDMs were chosen that maximized the sum of sensitivity and specificity; habitat suitability values of 0 were assigned to the cells below the threshold. Threshold values of 0.203, 0.219 and 0.087 were used for *E. cardinalis*, *E. lewisii*, and *E. guttata*, respectively. The suitability values from each SDM were averaged across all models to produce a “mean above threshold” ensemble. In the ensembles, any models that had a Boyce index < 0.5 , F-measure on presence-background (Fpb) < 1.0 , or a Sorenson value < 0.7 were excluded for *E. lewisii* and *E. cardinalis* and ensemble individual model predictions with an AUC < 0.7 were excluded for the *E. guttata*. The individual SDM models that were included in the final ensemble models for each species are listed in Table 2b (Rose et al. 2023; pers. comm.).

Species distributions for the year 1995 were used as an initial habitat suitability map (Figure S1). For distributions projected into the future, 4 different climate scenarios

were used to examine the effect of climate change on each of the species: CNRM-CM5 RCP 4.5, CNRM-CM5 RCP 8.5, HadGEM2-ES RCP 4.5 and HadGEM2-ES RCP 8.5 (IPCC 2013). Representative Concentration Pathways (RCP) 4.5 scenarios are low emission scenarios that stabilize radiative forcing at 4.5 W/m^2 by the year 2100 (Thomson et al. 2011), and RCP 8.5 scenarios are high emission scenarios that are baseline scenarios without any climate mitigation targets raising radiative forcing up to 8.5 W/m^2 by the year 2100 (Riahi et al. 2011). Climate models CNRM-CM5 and HadGEM2-ES represent warm and wet, and hot and dry scenarios, respectively. Annual maps with habitat change due to climate change were generated for a duration of 90 years from 1995 to 2085 (Figure S4). The land-use projections were overlaid on to the SDMs and modified the final habitat suitability values. Cells in developed regions that were unsuitable for plants were assigned a habitat suitability value of 0, the habitat suitability in cells of exurban categories were halved and habitat suitability in natural lands were unmanipulated (Rose et al. 2023). The RAMAS GIS software (Akçakaya and Root, 2005) was used to convert SDM maps into patches that served as subpopulations for each species under each climate change scenario. These patches of suitable habitats were converted to total carrying capacity of cells making up each patch and changes in suitable habitats were assessed as changes in carrying capacity. These time series of annual habitat patch maps form the spatial context of the metapopulations to which a stochastic stage-based population model is linked.

Population Models

Population models for the three species were constructed as stochastic stage-based matrix models (Figure 1, Table 3). The life histories of *E. cardinalis* and *E. lewisii* are structured into four life stages: seeds, small non-reproductive plants, large non-reproductive plants, and reproductive plants. The small non-reproductive stage was defined as non-reproductive plants with stems <3cm and <5cm for *E. cardinalis* and *E. lewisii*, respectively (Angert 2009). Seven annual stage-structured matrices from 2000 to 2007 for 4 subpopulations gave rise to 28 matrices for each species (Figure S2; A. Angert pers. comm.) from which a grand mean matrix was calculated per species. In cases where a valid life history transition was measured as zero, these values were excluded from the mean calculation as ecologically implausible (however, see supplementary material for a sensitivity analysis of this choice; Figure S2). For *E. guttata*, the 2012-2013 stage-structured matrix for the Eagle Meadows subpopulation was used as that was the only subpopulation grown (from seed to adult plants) in its home site and it was unaffected by the severe drought event in 2013 (DeMarche et al. 2016). The life history for the perennial ecotype of this species was structured as three life stages: seeds, seedlings, and ramets (Figure 1, Table 3).

The resulting standard deviations calculated across individual annual and subpopulation matrices gave unrealistic ranges of variability that persistently resulted in extinction in simulations of population projections. Therefore, a coefficient of variation of 0.02 in a Lognormal distribution was used for all vital rates to characterize annual

variability in population sizes – this choice allowed for maximal variation in population sizes while avoiding extinctions solely due to extreme variability. Environmental stochasticity in survival and transition rates was captured by randomly selecting values from a Lognormal distribution with standard deviations calculated from the coefficient of variation in each time step of the projections and across all replications (Akçakaya and Root, 2015). To simulate demographic stochasticity, the number of survivors in each stage (in each year) was drawn from a binomial distribution with the randomly selected survival/transition rate as the distribution probability and the stage-specific number of individuals as the number of trials. The number of seeds produced in each stage was similarly drawn from the Poisson distribution.

For all three species, density dependence was implemented as a ceiling carrying capacity to reflect limited resources in a given area. Since all three species are similar in size, we standardized the carrying capacity (K) of each 270 m x 270 m grid cell of maximally suitable habitat to be 50 individuals across all stages of standing plants (not including seeds). Since the definition of each life stage in the original census method differed by only a few centimeters of total stem size (Angert 2006, Angert 2009), all plants across all stages were assumed to contribute to the carrying capacity equally. Carrying capacities for patches were calculated as the total patch habitat suitability (i.e. the habitat suitability summed over all grid cells in a habitat patch) multiplied by 50. Due to models producing large numbers of extremely small, low-quality habitat, patches with less than 250 individuals ($5 \times K$) were excluded from the simulations. The initial population size was arbitrarily set to be at 90% of the carrying capacity of each patch. For

E. guttata, the initial population size was distributed across the stages according to the stable stage distribution, in the proportions of 0.1, 0.3, 0.6 from the earliest to the latest life stages. For *E. cardinalis* and *E. lewisii*, the initial population size was distributed in the arbitrarily selected proportions of 0.40, 0.25, 0.15, 0.10 (in order of seeds to largest reproductive stage) across stages because the stable stage distribution resulted in an initial population dominated by seeds and insignificant numbers of standing plants. This arbitrary ratio was selected to reflect the general trend of smaller life stages constituting greater proportions in a population. The total population size in each time step was calculated as the sum of abundances across all stages except the seed stage.

Erythranthe species disperse by wind, water, hummingbirds, bees, or deer depending on the species (Nelson et al. 2021, Twyford et al. 2020, Vickery Jr et al. 1986). The dispersal distances due to wind and water are negligible relative to the size of a patch in the spatial model. Therefore, we used home range size of the deer, *Odocoileus hemionus*, to estimate dispersal distances. We used Eqn 1 below (Akçakaya and Root 2005), to estimate the dispersal rates between two patches, where m_{ij} is the dispersal rate between the i^{th} and j^{th} patches, D_{ij} is the distance between the i^{th} and j^{th} patches, and b is the average dispersal distance. We referenced Fire Effects Information System (FEIS) page of *Odocoileus hemionus* species to estimate the parameters of the dispersal function (Innes 2013). The maximum dispersal distance, D_{max} , was estimated as the radius of deer home range in forested prairie break in Montana, assuming the home range is a perfect circle (3340 ha, $r = 3.26$ km) (Hamlin et al. 1989). Forested-area home range was used because the *Erythranthe* species of this study are mostly found in the forested mountain

range of Sierra Nevada. For the mean dispersal distance, b , the average summer home range of male deer in the Bridger Mountains of Montana was used in the absence home range information specific to California (240 ha, $r = 0.874$ km) (Pac et al. 1991). A dispersal-distance function was used to model a dispersal function where the dispersal rate declines as the distance between patches increases.

$$m_{ij} = \exp\left(\frac{-D_{ij}}{b}\right), \text{ when } D_{ij} \leq D_{max} \quad (\text{Eqn 1})$$

$$0, \text{ if } D_{ij} > D_{max}$$

All simulations were run for 90-time steps (years) and the average population for each time step was recorded across 1,000 replications. And for each replication, we used 90 years of burn-in period to get the initial population (Backus et al. 2023). To examine whether the projected population trajectories of the three *Erythranthe* species under climate and land-use change are constrained by habitat or their demographic traits, population projections for the four climate change scenarios, including land-use change, were run for each of the species for the 90 years of their SDM projections. To test the role of elevational adaptations, as observed in the empirical data, on population persistence of *E. cardinalis* and *E. lewisii*, we divided the species ranges into lower and higher elevation regions using an elevational threshold based on the midpoint of the highest and lowest elevations of the subpopulations for each species in the empirical study (Figure S3; Angert 2009). This midpoint was 1020.5 m for *E. cardinalis* and 2005 m for *E. lewisii*. For each species and elevational region, the average stage matrix for the region (lower or higher) was recalculated using demographic data specific to that region

(Table 4) and then applied to all subpopulations in the region as determined by the SDMs under each climate change scenario. Finally, to examine how the colonization of small habitat patches for *E. lewisii* created by climate change affected population dynamics, we compared and contrasted results across 4 different patch omission scenarios: omission of patches with carrying capacities up to 150, 250, 500, or 750 individuals.

Results

Q1. Vulnerability of *Erythranthe* species under climate and land-use change

For *E. cardinalis* (Figure 2a), suitable habitat was projected to increase under all climate models and emissions scenarios, with the exception of HadGEM2-ES RCP 4.5 in which habitat had declined only slightly by the end of the time horizon (-0.51%, i.e. 0.51% decrease of the initial carrying capacity; Table 5). Suitable habitat under the RCP 8.5 scenario initially declined to a greater extent than for the RCP 4.5 emissions scenario (CNRM-CM5: +16.91%; 16.91% increase of initial carrying capacity, HadGEM2-ES: -0.51%), under both climate models, however after around the year 2055 suitable habitat increased sharply for the RCP 8.5 scenarios (CNRM-CM5: +37.64%, HadGEM2-ES: +22.95%), resulting in more habitat at the end of the simulation than for the RCP 4.5 emissions scenario with both climate models. CNRM-CM5 (warm and wet) scenarios resulted in more habitat than the HadGEM2-ES (hot and dry) scenarios for the same RCP values. The population growth rates of the mean matrices for *E. cardinalis* was greater than one, indicating increasing populations on average. Population trajectories of *E.*

cardinalis (Figure 2b) tracked habitat changes, indicating that population abundance is not constrained by habitat availability and is primarily driven by demographic rates.

For *E. lewisii* (Figure 2c), suitable habitats were projected to decrease under all climate model scenarios except for the low emission scenario coupled with the CNRM-CM5 climate model (+6.35%; Table 5). Suitable habitat for CNRM-CM5 (warm and wet) under the two emissions scenarios (RCP 4.5: +6.35%, RCP 8.5: -11.31%) and the low emission scenario coupled with the HadGEM2-ES climate model (hot and dry; -22.14%) was stable or increasing during the first two-thirds of the simulation until around year 2055 and decreased in the remaining third of the time horizon. Suitable habitat in the high emission scenario coupled with the HadGEM2-ES (hot and dry) climate model gradually declined from the beginning of the simulation and resulted in 54.90% of the initial habitat by the end of the time horizon. Population trajectories of *E. lewisii* (Figure 2d) tracked habitat change for the CNRM-CM5 RCP 4.5 scenario. Population trajectories for the other three scenarios experienced some declines, in alignment with habitat changes, but also exhibited significant population oscillations for different intervals in the time horizon. By the end of the time horizon, the population decline under the HadGEM2-ES RCP 4.5 scenario was the greatest (-63.13%; 63.13% decrease of initial population size; Table 5), a greater decline than for the more extreme HadGEM2-ES RCP 8.5 emissions scenario (-44.93%).

E. guttata (Figure 2e), exhibited a small decline in habitat by the end of the time horizon. Suitable habitat under the low emission (RCP 4.5) scenario showed slight

declines until around year 2055 of the simulation, followed by a gradual increase until the end of the simulation (CNRM-CM5: -9.48%, HadGEM2-ES: -6.28%; Table 5). Suitable habitat under the high emission scenario coupled with the CNRM-CM5 climate model experienced a gradual decrease throughout the simulation (-20.47%) while suitable habitat under the high emission scenario coupled with the HadGEM2-ES climate model declined after year 2055 (-11.81%). The population growth rate for was 1.7138, indicating a fast-increasing population. Population trajectories of *E. guttata* (Figure 2f) largely tracked the changes in habitat availability except for a small population decline around the year 2030 in the HadGEM2-ES RCP 8.5 scenario. This is possibly due to increasing habitat in the SDM that is not being colonized by *E. guttata* individuals. The ranking of the final percentage declines in population sizes match the ranking of the final percentage declines in suitable habitat for the four climate change scenarios of *E. guttata*. The population trajectories of RCP 8.5 scenarios (CNRM-CM5: -32.31%, HadGEM2-ES: -22.86%) exhibited a greater decline compared to those under the RCP 4.5 scenarios (CNRM-CM5: -9.52%, HadGEM2-ES: -7.77%) that showed a slight increase towards the end of the simulation.

Q2. Elevational differences in subpopulations

Projected habitat for the higher-elevation (> 1,020.5 m) region of *E. cardinalis* (Figure 3a) increased under all climate and emissions scenarios with the exception of the HadGEM2-ES RCP 4.5 scenario which experienced a slight decrease (2.38% decrease; Table 6). Changes in habitat suitability exhibited the same general pattern for the entire

range of the species (Figure 3a; Figure 2a). Population abundances across the 90-year time horizon also tracked changes in projected habitat suitability (Figure 3a,b). However, unlike the habitat trajectory, the population under of HadGEM2-ES RCP 8.5 (an increase of 3.28%) was lower than for the CNRM-CM5 RCP 4.5 scenario (an increase of 7.72%). The results for lower-elevation subpopulations of *E. cardinalis* are not included in the study because the population growth rate was 0.7846 (Table 3) which is insufficient for subpopulations to persist even with an increase in suitable habitat. The pattern of habitat change for the higher-elevation (> 2,005 m) region (Figure 3c) of *E. lewisii* also resembles that of the entire range of the species. The population trajectories of higher-elevation subpopulations (Figure 3d) tracked the pattern of habitat suitability while showing a dip in population with brief oscillations around year 2010 for the HadGEM2-ES (hot and dry) climate model. Habitat suitability and abundances for lower-elevation subpopulations (Figure 3e) decreased dramatically relative to the higher-elevation subpopulations (Figure 3f). Even though habitat suitability under the CNRM-CM5 RCP 8.5 scenario initially increased, it was followed by a steep decline in mid-2050 resulting in a different ranking of climate change induced habitat suitability, from lowest to greatest carrying capacity, than for the entire range of the *E. lewisii*.

Q3. Effect of small habitats on population abundances of *E. lewisii*.

For *E. Lewisii*, final population abundances were higher when the prevalence, duration, and amplitude of population oscillations were reduced (Table 7; Figure 4). Population oscillations disappeared as small habitat patches were removed from the

initial maps (Figures 2c, d; Figure 4) however, the size of small patch removal necessary to remove oscillations depended on the climate model and emissions scenario. All four climate model/emissions scenario resulted in oscillations in population abundances when only small patches with carrying capacities ≤ 150 individuals were omitted from the available suitable habitat (Figure 4a). When patches with carrying capacities ≤ 250 individuals were omitted, population oscillations disappeared under only one of the climate model/emissions scenarios: CNRM-CM5 RCP 4.5 (Figure 4b). When patches with carrying capacities ≤ 500 individuals were omitted, oscillations were absent under an additional climate model/emissions scenario—CNRM-CM5 RCP 8.5—resulting in a higher final population size under this scenario but a lowered final population size for CNRM-CM5 RCP 4.5 (Figure 4c). Finally, when patches with carrying capacities ≤ 750 were omitted, oscillations disappeared from populations under both HadGEM2-ES RCP 4.5 and 8.5 resulting in higher final population abundances under these two scenarios.

Discussion

These results show that, for the most part, population trends are constrained by habitat availability, however there are some exceptions depending on the species, elevation, and climate scenario. Habitat changes for *E. cardinalis* showed similar trends under climate change for each emissions scenario (Figure 2a). This species lost more habitat in the first half of the time horizon under the higher emissions scenario (RCP 8.5) but recovered with a greater habitat area than for the lower emissions scenario (RCP 4.5) by the end of the simulation, irrespective of the climate prediction model used. When

comparing climate models under the same emissions levels, the hot and dry (HadGEM-ES) climate model resulted in greater habitat loss than for the warm and wet model (CNRM-CM5). For *E. lewisii* (Figure 2c), more habitat was conserved in warm and wet scenarios than in hot and dry scenarios, while *E. guttata* lost more suitable habitat under high emissions scenarios than under low emissions, irrespective of the climate models (Figure 2e).

The extent to which populations respond to shifts or changes in suitable habitat depends on their ability to disperse into newly created suitable habitat and the population dynamics in the colonized patches. For two species, *E. cardinalis* and *E. guttata*, population trajectories largely track the changes in projected habitat suitability, and *E. cardinalis*, in particular, was able to colonize new habitat and sustain populations at higher abundances. However, *E. lewisii* exhibited damped population oscillations which are well established in population ecology theory (Hassell 1975); they occur with very high growth rates (here, with a mean λ of 1.4441; Table 3) in populations with a carrying capacity. Patch extirpation can occur when the amplitude of oscillations is sufficiently high, and carrying capacity sufficiently low, to plunge the population abundance to zero. Because seeds disperse into small occupied patches that are created through climate-induced habitat shifts or fragmentation, local extinction/colonization dynamics are generated which have the effect of lowering the overall population size (Oborny et al. 2005); in a series of time steps seeds disperse to empty small patches, the population increases rapidly due to a high growth rate, oscillations ensue, and the subpopulation hits zero on its downswing resulting in an empty small patch (possibly temporarily) (Figure

2d). In this study the size of patches is measured by carrying capacity which is a combination of habitat suitability and area. Hence, “small” patches include patches with small area, low habitat quality, or a combination of both. We therefore speculated that the observed population oscillations in *E. lewisii* were due to a type of source-sink dynamics of small patches. To test this, we reran the *E. lewisii* simulations with different sized small patches omitted from the original model (Table 5) to observe how different numbers of small or low-quality habitats affect overall population viability of *E. lewisii*. To confirm that the oscillations and lower total population sizes were the result of dispersal to “small” patches with high growth rates, we compared the number of patches of different carrying capacities at the initial time step for the HadGEM2-ES RCP 4.5 scenario (Table S1). This scenario was chosen for investigation because it had the most apparent oscillation patterns among the four climate change/emissions scenario combinations. Table S1 shows that there are no differences in the number of larger patches across the different scenarios and there were only differences in the number of patches with total carrying capacities of up to 250 individuals. Once these small patches were omitted, population dynamics stabilized allowing the total population to track the changes in habitat suitability/carrying capacity (Figure 4), albeit the number and size of patches it was necessary to omit to achieve this depended on the combination of climate model and emissions scenario.

The results in this study also show that population outcomes can depend on elevational regions. Restricting the spatial scope of the simulations from the entire species range to two different elevational regions (lower and higher) showed different

regional population trends for the two species considered. Trends of suitable habitat in the lower and higher elevations (Figure 3c, 3e) for *E. lewisii* were similar to those of the entire range, albeit with the lower elevational habitat decreasing by much greater proportions. Population trajectories at higher elevations (Figure 3d) also showed similar trajectories but the oscillations caused by the combination of small patches and high growth rate were observed much less in the higher elevation patches than for the total habitat range. This is due to a lower population growth rate in the higher elevation region where most small patches occur; population growth rates were 1.0567 (Table 4) and 1.4441 (Table 3) for the populations in the higher and entire regions, respectively (Figure 2d). These results reveal rapid reductions in *E. lewisii* population projections in the lower habitat range especially after the year 2055 under all the climate model/emissions scenarios. The population in the higher region was projected to increase until the year 2055, and then declined afterwards. This species tended to fare better under a wet and warm future climate than the hot and dry climate. As mentioned in the introduction, upward shift in habitat is a common trend predicted after the 20th century. However, this can be of no benefit to populations because plants are often not able to track environmental shifts due to limited dispersal, thus creating an extinction debt (Corlett & Westcott 2013, Dullinger et al. 2012, Feeley & Silman 2010, Geppert et al. 2023) or they are displaced by nonnative species that are able to disperse upwards more quickly (Dainese et al. 2017, Geppert et al. 2023).

Simulations for *E. cardinalis* species under different elevational ranges indicated that regional population projections may tell us more about the fate of the species, and

offer targeted conservation options, in different geographic or environmental conditions than focusing on the entire range of the species. Future populations in the lower elevational range of *E. cardinalis* were not sustainable due to the extremely low average population growth rate observed in Angert (2009). In that study, *E. cardinalis* exhibited greater population growth and reproduction at higher elevations. The present study has coupled these observed rates with habitat shifts due to climate change and land-use change to project possible spatial and demographic outcomes for these populations. The differences in growth rates across the lower and higher geographic regions in the present study highlight the importance of focusing on spatially explicit population dynamics in addition to species distributions which on their own can mask how plants will respond to global change. Indeed, previous studies have shown that even though habitat suitability degraded, populations can persist due to the demographic compensation for these environmental changes (Doak & Morris 2010, Oldfather & Ackerly 2019).

This study also demonstrates the effect of high population growth rates on colonization and extinction dynamics in small patches; for *E. lewisii* these dynamics tended to resemble classic source-sink dynamics. Source populations are defined as good quality habitats where birth rates exceed mortality for a given species, whereas sink populations are characterized as poor-quality habitats where mortality exceeds birth rates thus relying on immigration for persistence Dias (1996). This definition of a sink population does not match the small populations apparent in this study because the oscillations are caused by a combination of high population growth rates and patches with low carrying capacity rather than extirpation due to high mortality rates typical of

sink populations. There has long been debate over the value of small patches in conservation. Historically, it was postulated that conserving one large habitat is more beneficial to species and biodiversity than several small patches and that extinction risk is much higher in small patches especially under isolation (Diamond 1975, Hanski 2015, McAuthur & Wilson 1967, Simberloff & Abele 1976). Increased dispersal between populations, causing greater loss of population from the source, has been observed to decrease regional populations and increase the risk of extinction (Heinrichs et al. 2019). However, recent studies have shown that while large habitat areas are important, small patches of habitat also contribute to biodiversity and can have high conservation value by serving as refuges for rare species or by promoting connectivity (Godefroid & Koedam 2003, Lindenmayer 2019, Riva & Fahrig 2022, Wintle et al. 2019). The results for *E. lewisii* show that the creation of newly suitable habitat through climate change that can be colonized through dispersal does not always lead to increases in total population size even when growth rates should indicate increasing subpopulation sizes. A combination of growth rates that are too high and patches that are too small can lead to a cycle of colonization, local extinction, and recolonization, ultimately dragging down the total population size. Therefore, close attention needs to be paid to the spatial and demographic context of new habitat creation under climate change and consideration given to strategies such as conservation thinning or removal and replanting of individuals from highly populated areas (Nicol & Possingham 2010; Gorrod et al. 2017; de Araujo et al. 2021).

The population growth rates we estimated for *E. cardinalis* and *E. lewisii* were substantially higher than growth rates reported in Angert (2009), rates which precluded the types of population oscillations we observed. The reasons for this are twofold. First, the purpose of the present study was to project stochastic population dynamics into the long-term future, rather than report growth rates for the time period of the data collection, as was the focus of Angert (2009). Hence, we omitted the zero entries in the annual stage-based matrices when calculating the average stage-based matrix across multiple years for each species. Zero entries, while present in the data, resulted in some growth rates < 1.0 in Angert (2009), reflecting declining populations that will surely reach extinct in a short period of time which is unrealistic for these species. Therefore, these low growth rates are unlikely to represent long-term population dynamics and could be a reflection of uncertainty in the data in some cases. Second, we averaged each rate in the stage-based matrices across years using an arithmetic mean and then calculated the overall growth rate as the positive eigenvalue of the resulting averaged matrix, whereas in Angert (2009) growth rates were calculated for each annual matrix and then a geometric mean was taken across these annual rates; it is well known that geometric means give lower estimates than arithmetic means. We believe that the low population growth rates presented in Angert (2009) do not align with the observed persistence of these species in the wild. However, it is also likely that the growth rates calculated in this present study overestimate growth rates in the wild. Nevertheless, if we included all the zero vital rates in our calculation of growth rates (see Figure S2) oscillations in small patches caused by

high growth rates would still be expected to occur and overall population trends driven by habitat change should be maintained.

The common challenge studies on extinction risk face are a lack of data for the species of interest. Fortuitously, thanks to Angert (2009), censuses for two of the three monkeyflower species in this study, *E. cardinalis* and *E. lewisii*, were conducted to build seven annual matrix population models for four subpopulations for each species. This provided an opportunity to explore the future possible fate of these species under anthropogenic threats and how subpopulations distinguished by different elevation range respond differently. However, the average growth rate of all populations used in these simulations were extremely high (*E. cardinalis* = 1.2585, *E. lewisii* = 1.4441; Table 3) and there seemed to be very high variability in vital rates across time and space (Angert 2009). Some individual matrices contained cells with no transitioning individuals – while these were excluded from calculations of the mean vital rates, sensitivity analyses were conducted to show that this omission did not have a big effect on the population trends (Figure S1). Extremely high temporal standard deviations caused by the frequency of cells with absent stage transition rates were replaced with a coefficient of variation selected to be large enough to simulate variability without routinely and unrealistically plummeting populations to extirpation in randomly selected “bad” years. This uncertainty could be resolved with more years of data collection. Studies have shown that at least 15 years of demographic time series data allows for reliable population trajectories over relatively short projections (McCarthy et al. 2003; Hovestadt and Nowicki 2008; Rueda-Cediel et al. 2015). Additionally, more data is needed for long-lived species and

projections of longer duration, such as the projections in this present study (Rueda-Cediel 2015). Considering this, 7 years of census data may not be sufficient to characterize the temporal variation in vital rates and to make projections about *Erythranthe* species under long-term climate change. Moreover, the results of simulations for separate elevational ranges (Figure 3) demonstrated that the oscillations observed in the simulations for *E. lewisii* can be reduced or removed altogether by taking the spatial variation into account and assigning spatially-explicit vital rates for subpopulations in different regions.

Finally, this study sheds light on the value of demographic traits as proxies for extinction risk across species for which such large temporal and spatial demographic datasets do not exist. Extensive analyses have found that species traits, including spatial traits, life history traits, and functional traits, have specific relationships to predicted extinction risk under anthropogenic threats such as climate change and land-use change (Andrew et al. 2022, Cardillo & Meijaard 2012, Hernández-Yáñez et al. 2022, Murray et al. 2002, Pearson et al. 2014; Purvis et al. 2000). In fact, Kindsvater et al. (2018) encourages the adoption of data of other closely related species when insufficient data on extinction vulnerability exist for a focal taxon. Knowing the general relationships between traits and extinction risk is important because these traits can serve as predictors of extinction risk for other species to guide conservation efforts in the local ecosystem (van Kleunen & Richardson 2007) as well as in similar ecosystems in other locations (Saar et al. 2012). Our study can shed light on other monkeyflower species which have trait variations including variation in flowering time, plant size, reproductive mechanism and growth rates in subpopulations that can result in different population growth rates in

subpopulations of the same species (Dickman et al. 2018, Hall & Willis 2006, Kooyers et al. 2015, van Kleunen 2007, Twyford et al. 2020). However, there are limitations in how far this inference extends, for population viability analyses at least. In this study, *E. cardinalis* and *E. guttata* had similar geographic distributions (Figure S1) while *E. cardinalis* and *E. lewisii* had greater similarity in life history traits (Figure 1, Table 3). However, the susceptibility of each species to each climate change scenario ranked differently (Figure 2) and *E. lewisii* and *E. guttata* showed greater vulnerability than *E. cardinalis* which mostly increased (Table 5). While past studies have used trait values to infer extinction risk (Chichorro et al. 2022, Pearson et al. 2014, Ribeiro et al. 2016, Rochet 2000), our study aligns with others (Buckley et al. 2010, Hoare et al. 2012) that show that such inferences may not be accurate when based on only a few measures of trait comparison.

This study has demonstrated the importance of exploring population viability at regional and local scales, reflecting the unique spatial and demographic contexts at those scales, and the consequences of climate and land-use change. In particular, this study has led to three main conclusions: 1. Habitat suitability was the limiting factor for *Erythranthe* species rather than their demography. The simulation results showed that the future population trajectories for the three species were generally tracking the change in habitat suitability. 2. *E. cardinalis* and *E. lewisii* subpopulations in different elevational ranges showed different patterns when the population projections were simulated at smaller scales. Results showed that, especially in *E. cardinalis* subpopulations, the demography plays a big role in its fate at the lower elevation which was not apparent in

the simulation for the whole population. 3. Small newly colonized habitat for *E. lewisii* populations were not always benefiting the overall population. Population oscillations due to very high growth rates in colonized small patches caused local extinctions which resulted in lower population sizes than scenarios without the small patches.

This study highlights the importance of spatial variability in vital rates and patch size in studies of vulnerability of plant populations to climate and land-use change. While many studies recognize the importance of temporal variability in vital rates in population models, explicit incorporation of spatial variability in average population growth rates is rare or absent. This study shows that more attention needs to be paid to spatial variability when constructing population models; not only will this lead to a more accurate characterization of species vulnerability to climate change, but it can also reveal novel conservation strategies and where they need to occur.

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Tables and Figures

Table 1. Population, location, elevation, and citation of matrix population models for each *Erythranthe* species

Species	Subpopulations	Location	Reference
<i>E. cardinalis</i>	Buck Meadows, Moore Creek	37.7770°N, 120.0635°W (830 m)	
	Rainbow Pool, South Fork Tuolumne River	37.8213°N, 120.0109°W (833 m)	
<i>E. cardinalis</i> & <i>E. lewisii</i>	Wawona, South Fork Merced River	37.5387°N, 119.6543°W (1,208 m)	Angert (2009) & personal communication
	Carlton, South Fork Tuolumne River	37.8152°N, 119.8657°W (1,320 m)	
<i>E. lewisii</i>	May Lake, Snow Creek	37.8365°N, 119.4944°W (2,690 m)	
	Warren Fork, Lee Vining River	37.9520°N, 119.2261°W (2,750 m)	
<i>E. guttata</i>	Eagle Meadows, Stanislaus National Forest	38.320°N, 119.920°W (2,046 m)	DeMarche et al. (2016)

Table 2. (a) Environmental predictors used to build the SDMs and (b) species location data and the list of individual SDM models included in the final ensemble model for each *Erythranthe* species.

(a) Environmental predictors used in SDMs		
Type	Predictors	Reference
hydrological and climatic predictors	climatic water deficit, actual evapotranspiration, minimum temperature of the coldest month, wet- and dry- season precipitation	Basin Characterization Model (BCM)
soil predictors	soil pH, available water holding capacity, soil depth, percent clay	Soil Survey Geographic Database (gNATSGO)
landscape positioning	landform types (15)	Theobald et al., 2015

(b) Species location data and type of SDM models used		
Species	Presences and absences	Models used in ensemble
<i>E. cardinalis</i>	Presence-only (135 presences, 132 pseudo-absences)	gbm, max
<i>E. lewisii</i>	Presence-only (102 presences, 102 pseudo-absences)	gam, gau, glm, max, net, raf, svm
<i>E. guttata</i>	Presence-absence (1167 presences, 10750 absences)	gam, gbm, glm, net, raf, svm

Table 3. Mean of all matrix projection models used for the population models in Q1. Zero values in cells of *Erythranthe cardinalis* and *E. lewisii* were not included when calculating averages. The life stages of the first two species are seeds, small nonreproductive plants, large nonreproductive plants, and reproductive plants and the life stages of *E. guttata* model are seeds, seedlings, and ramets.

	Matrix projection model				λ
	<i>seeds</i>	<i>S. non-repro</i>	<i>l. non-repro</i>	<i>repro</i>	
<i>E. cardinalis</i>	0.2080	2166.02	7509.42	33657.61	1.2585
	$8.05 \cdot 10^{-5}$	0.07432	0.0283	0.02433	
	$4.89 \cdot 10^{-5}$	0.0951	0.3071	0.2374	
	$1.65 \cdot 10^{-6}$	0.0285	0.1150	0.5392	
<i>E. lewisii</i>	<i>seeds</i>	<i>S. non-repro</i>	<i>l. non-repro</i>	<i>repro</i>	1.4441
	0.0332	12344.04	16094.01	59977.45	
	$4.10 \cdot 10^{-5}$	0.1062	0.0347	0	
	$1.62 \cdot 10^{-5}$	0.1301	0.4655	0.1607	
	$2.64 \cdot 10^{-7}$	0.0783	0.1897	0.7229	
<i>E. guttata</i>	<i>seeds</i>	<i>seedlings</i>	<i>ramets</i>		1.7138
	0.284	0.142	0.142		
	0.25	0.125	0.125		
	0	1.564	1.564		

Table 4. Mean matrix projection models used in the (sub)population models for *E. cardinalis* and *E. lewisii* demarcated by elevational range. The elevational range of each subpopulation and the range of population growth rates of individual matrix models across all populations and years are provided with the mean matrix models of each subpopulation (Angert 2009).

Matrix projection model					λ
<i>E. cardinalis</i>					
Low	0.1971	232.18	674.27	3391.64	0.7846
elevation	0.0001	0.1026	0.0248	0.0287	(0.4724-
830-833m	$8.67 \cdot 10^{-5}$	0.1146	0.3188	0.2940	0.8874)
	$3.32 \cdot 10^{-6}$	0.0406	0.0859	0.4323	
High	0.2189	2869.25	14870.35	63923.57	1.1008
elevation	$3.50 \cdot 10^{-5}$	0.0531	0.0316	0.0154	(0.4370-
1280-1320m	$1.10 \cdot 10^{-5}$	0.0797	0.2955	0.1809	2.0479)
	$5.44 \cdot 10^{-7}$	0.0241	0.1464	0.6461	
<i>E. lewisii</i>					
Low	0.0367	30875.62	14729.89	36234.55	1.6552
elevation	$3.98 \cdot 10^{-5}$	0.1317	0.0332	0	(0.3333-
1208-1320m	$3.18 \cdot 10^{-5}$	0.1696	0.3690	0.1997	1.3129)
	$5.20 \cdot 10^{-7}$	0.1853	0.2021	0.6029	
High	0.0296	1225.10	17068.38	83720.35	1.0567
elevation	$3.24 \cdot 10^{-5}$	0.0852	0.0355	0	(0.8783-
2690-2750m	$2.89 \cdot 10^{-6}$	0.1088	0.5552	0.1273	1.9893)
	$7.12 \cdot 10^{-8}$	0.0141	0.1808	0.8430	

Table 5. Change in suitable habitat (as measured via carrying capacities of patches) and population trajectories of three *Erythranthe* species.

	CNRM-CM5 RCP 4.5	CNRM-CM5 RCP 8.5	HadGEM2-ES RCP 4.5	HadGEM2-ES RCP 8.5
		<i>E. cardinalis</i>		
Habitat (%)	116.91	137.64	99.49	122.95
Population (%)	117.40	135.57	100.80	115.04
		<i>E. lewisii</i>		
Habitat (%)	106.35	88.69	77.86	54.90
Population (%)	104.84	64.46	36.87	55.07
		<i>E. guttata</i>		
Habitat (%)	90.52	79.53	93.72	88.09
Population (%)	90.48	67.69	92.23	77.14

Table 6. Change in habitat (as measured via carrying capacities of patches) and population trajectories of subpopulations of *E. cardinalis* and *E. lewisii* in different elevational ranges.

	CNRM-CM5 RCP 4.5	CNRM-CM5 RCP 8.5	HadGEM2-ES RCP 4.5	HadGEM2-ES RCP 8.5
<i>E. cardinalis (high elevation)</i>				
Habitat (%)	113.56	137.88	97.62	124.54
Population (%)	107.72	124.36	97.36	103.28
<i>E. lewisii (high elevation)</i>				
Habitat (%)	108.63	92.31	79.74	57.40
Population (%)	105.92	79.33	50.48	39.34
<i>E. lewisii (low elevation)</i>				
Habitat (%)	62.27	19.53	37.99	5.57
Population (%)	66.45	22.78	39.60	7.85

Table 7. Change in population in *E. lewisii* models with different sizes of patches omitted. Number represents the carrying capacity of the omitted patches.

	CNRM-CM5 RCP 4.5	CNRM-CM5 RCP 8.5	HadGEM2-ES RCP 4.5	HadGEM2-ES RCP 8.5
		Patches < 150 removed		
Population (%)	92.01	59.11	35.61	39.28
		Patches < 250 removed		
Population (%)	104.84	64.46	36.87	55.07
		Patches < 500 removed		
Population (%)	85.61	88.24	60.69	38.81
		Patches < 750 removed		
Population (%)	85.59	88.14	75.06	54.60

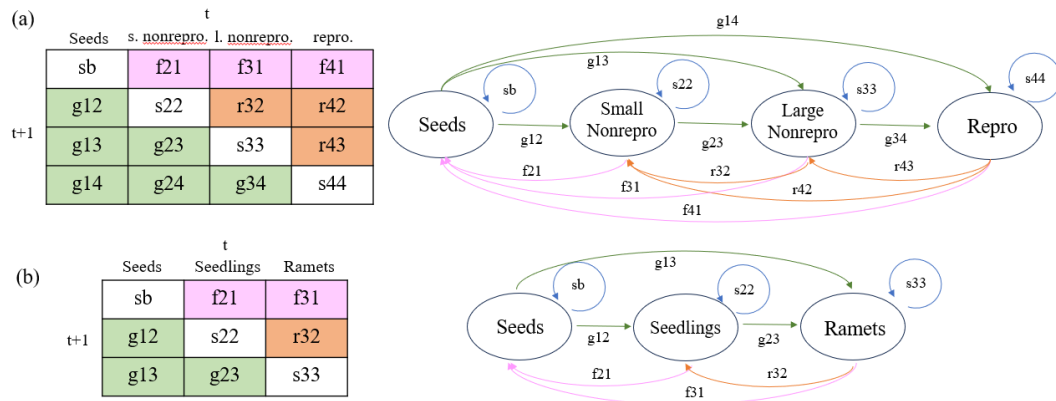


Figure 1. Matrix population model structure and life history diagrams for (a) *E. cardinalis* and *E. lewisii*, and (b) *E. guttata*. Each column and row of the matrix projection models represents a life stage of the respective *Erythranthe* species: (a) Seeds, small nonreproductive plants, large nonreproductive plants, and reproductive plants, for *E. cardinalis* and *lewisii* and (b) seeds, seedlings, and ramets for *E. guttata*. Each cell represents the proportion of column stage at time t that transitions to the corresponding row stage at $t+1$, the next year in the model simulations. The variables in each cell of the matrices, and for each arrow of the life history diagrams, can be interpreted as the type of transition (sb = seed bank, g = growth, r = retrogression, s = stasis, f = fecundity), from starting stage to ending stage. For example, g12 represents the proportion of plants in stage 1 that survive and grow into stage 2 in the next time step.

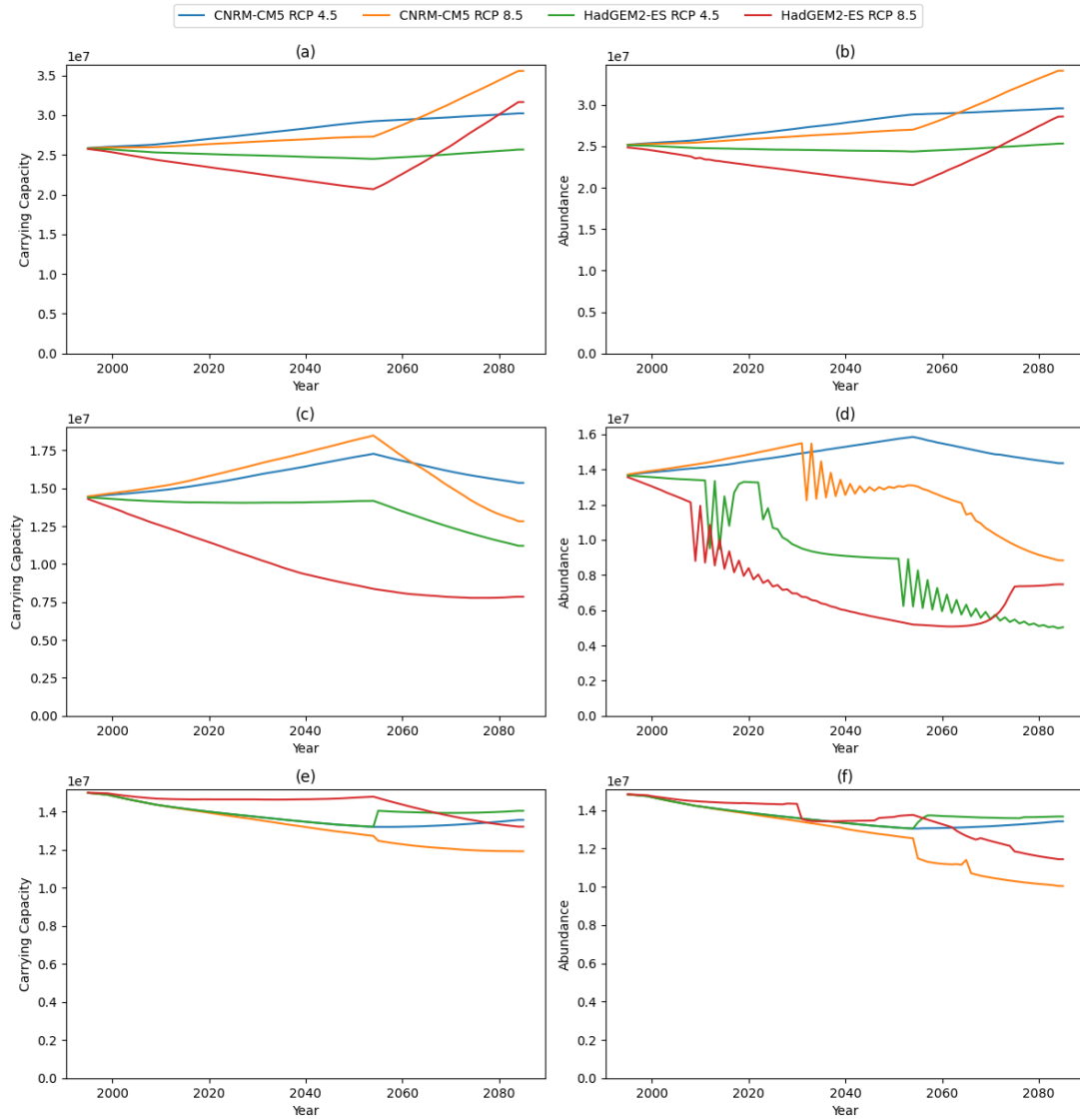


Figure 2. Habitat changes (as measured via carrying capacities of patches) and population trajectories of three *Erythranthe* species. (a) Habitat changes for *E. cardinalis*, (b) Population trajectories of *E. cardinalis*, (c) Habitat changes for *E. lewisii*, (d) Population trajectories of *E. lewisii*, (e) Habitat changes for *E. guttata*, and (f) Population trajectories of *E. guttata* under the combination of two climate models and two emissions scenarios.

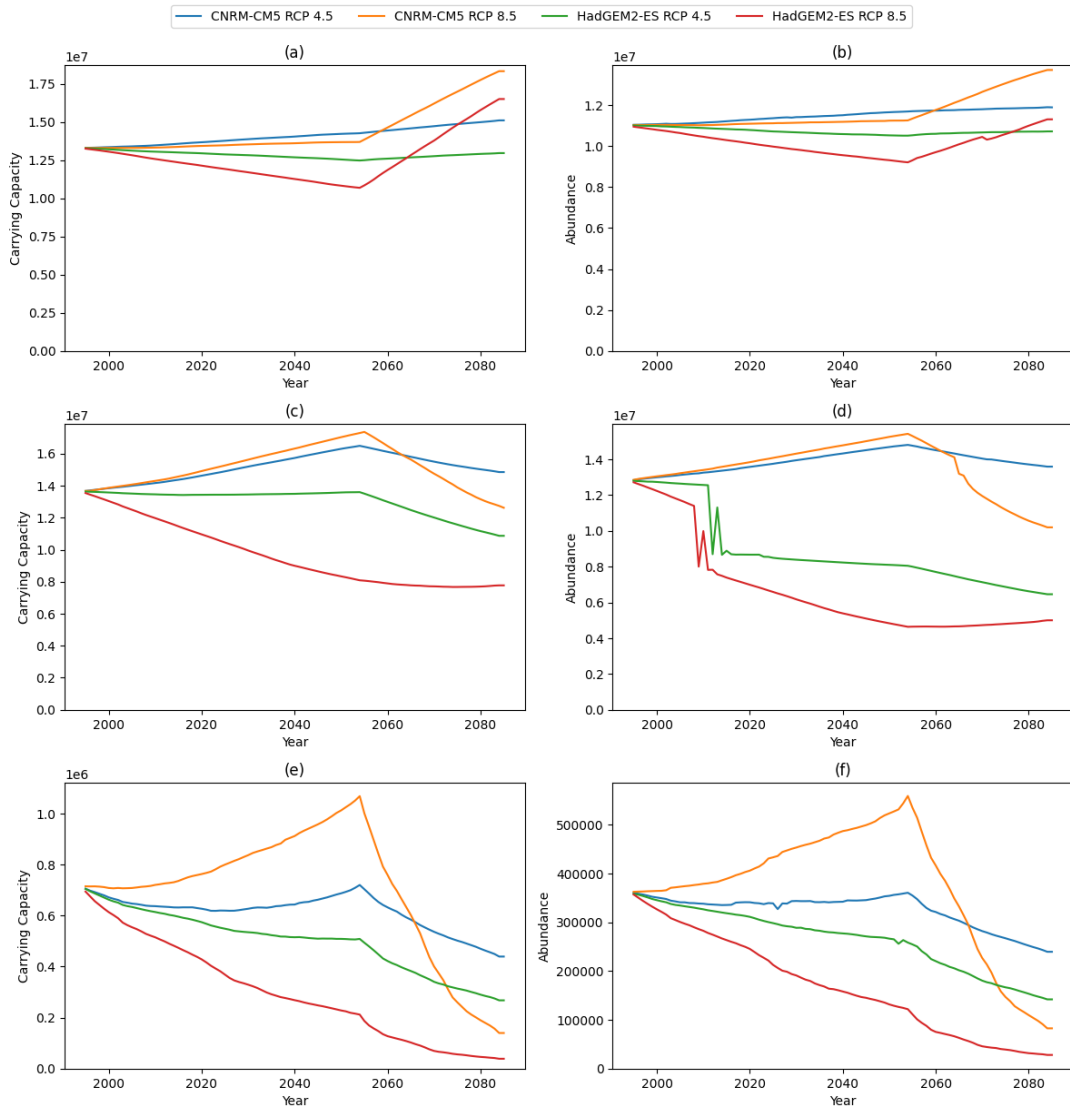


Figure 3. Habitat changes (as measured via carrying capacities of patches) and population trajectories of subpopulations of *E. cardinalis* and *E. lewisii* in different elevational ranges under the combination of two climate models and two emissions scenarios. (a) Habitat changes of *E. cardinalis* subpopulations at high elevation, (b) Population trajectories of *E. cardinalis* subpopulations in high elevation, (c) Habitat changes of *E. lewisii* subpopulation in high elevation, (d) Population trajectories of *E. lewisii* subpopulation in high elevation, (e) Habitat changes of *E. lewisii* subpopulations in low elevation, (f) Population trajectories of *E. lewisii* subpopulations in low elevation.

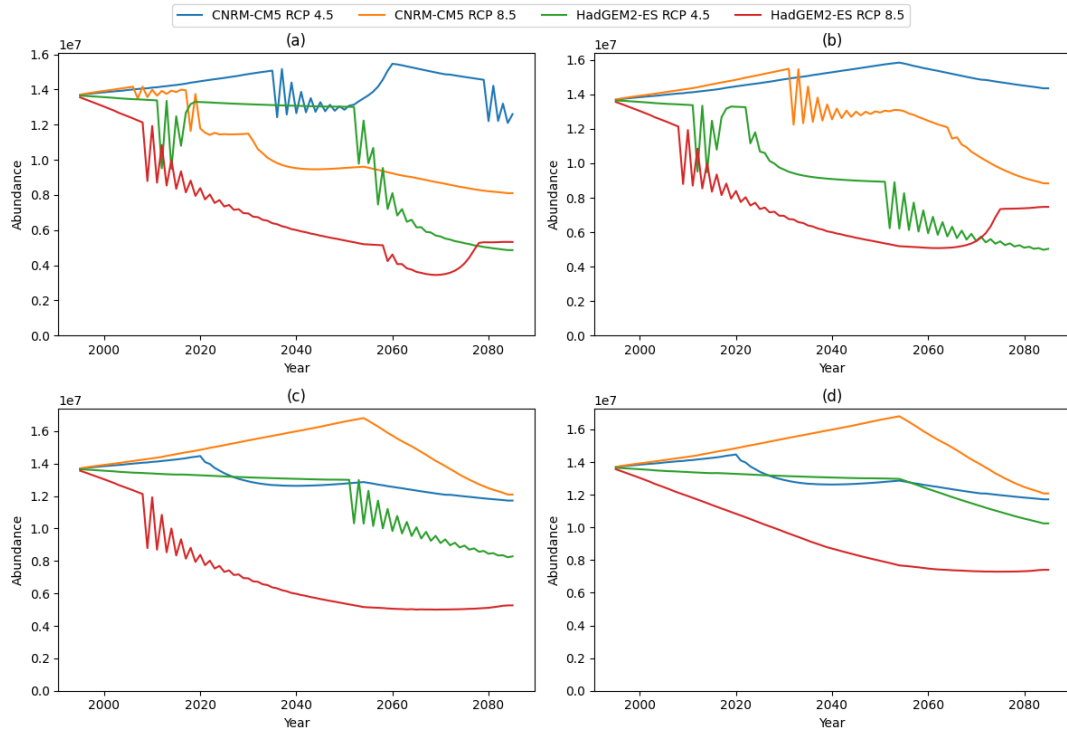


Figure 4. Population abundances of *E. lewisii* with different sized patches omitted (K = Carrying capacity): (a) patches with $K < 150$ individuals omitted, (b) patches with $K < 250$ omitted, (c) patches with $K < 500$ omitted, (d) patches with $K < 750$ omitted.

Appendix

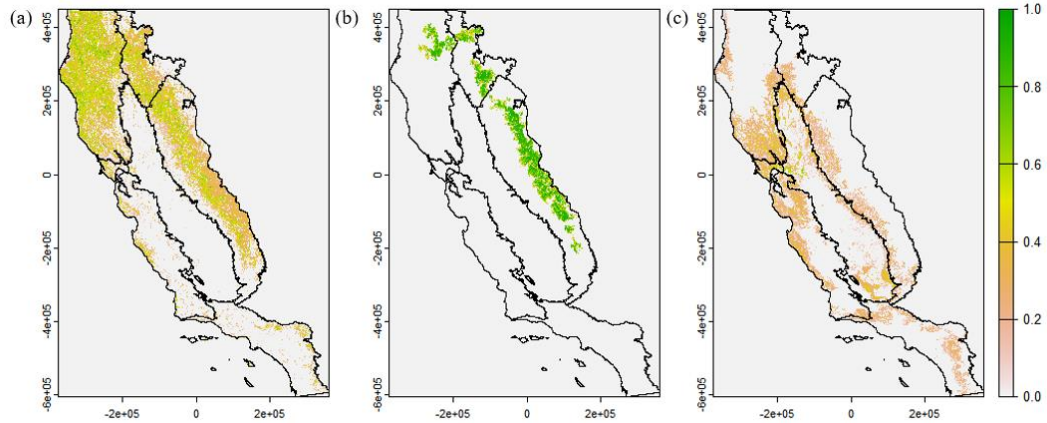


Figure S1. Habitat suitability of three *Erythranthe* species at initial time step, year 1995, limited by the current occurrence data: (a) *Erythranthe cardinalis*, (b) *Erythranthe lewisii*, (c) *Erythranthe guttata*

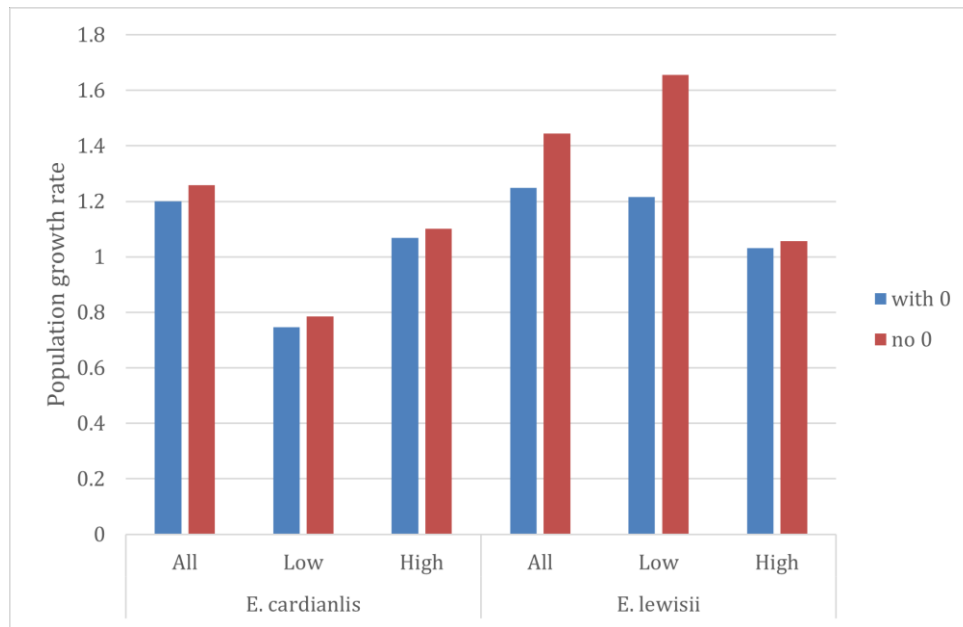


Figure S2. Comparison of average population growth rates of *E. cardinalis* and *E. lewisii* species across the entire species' ranges and restricted to subpopulations at low and high elevations using the data from Angert pers. comm.. Blue bars represent the population growth rates of the average matrix calculated by including all zero values across all subpopulations in the range of interest. Orange bars represent the population growth rates of the average matrix that omitted values of zero in the calculation (with the exception of “structural” zero values where a transition was never observed in any subpopulation) across all subpopulations in the range of interest.

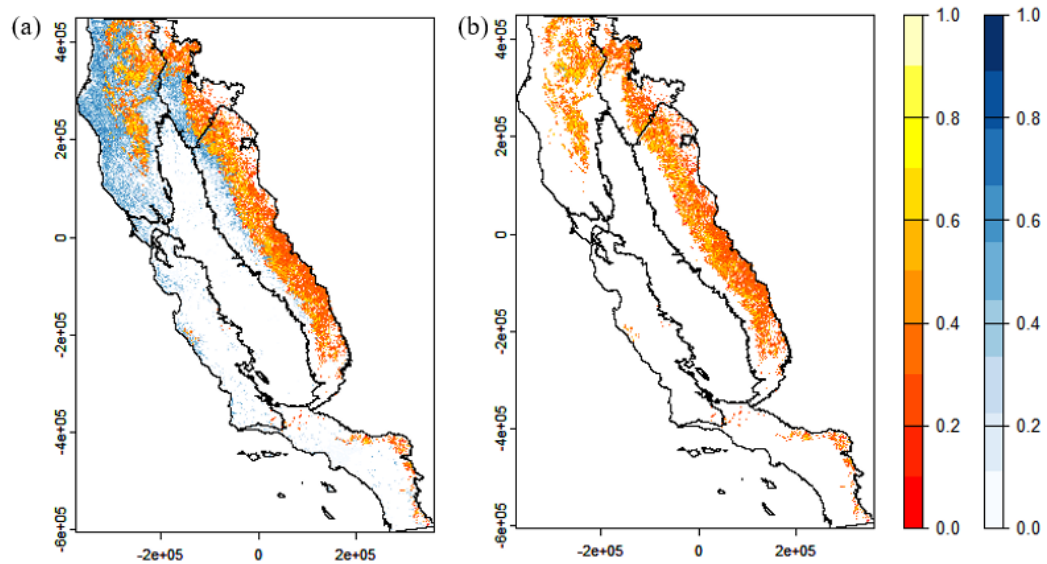


Figure S3. The geographical distinction between subpopulations of (a) *E. cardinalis* and (b) *E. lewisii* in higher elevation range and lower elevation range. The red color represents the habitat suitability at the high elevation range and the blue color represents the habitat suitability at the low elevation range. The maps are showing the habitat suitability at year 1995 limited by the current occurrence data.

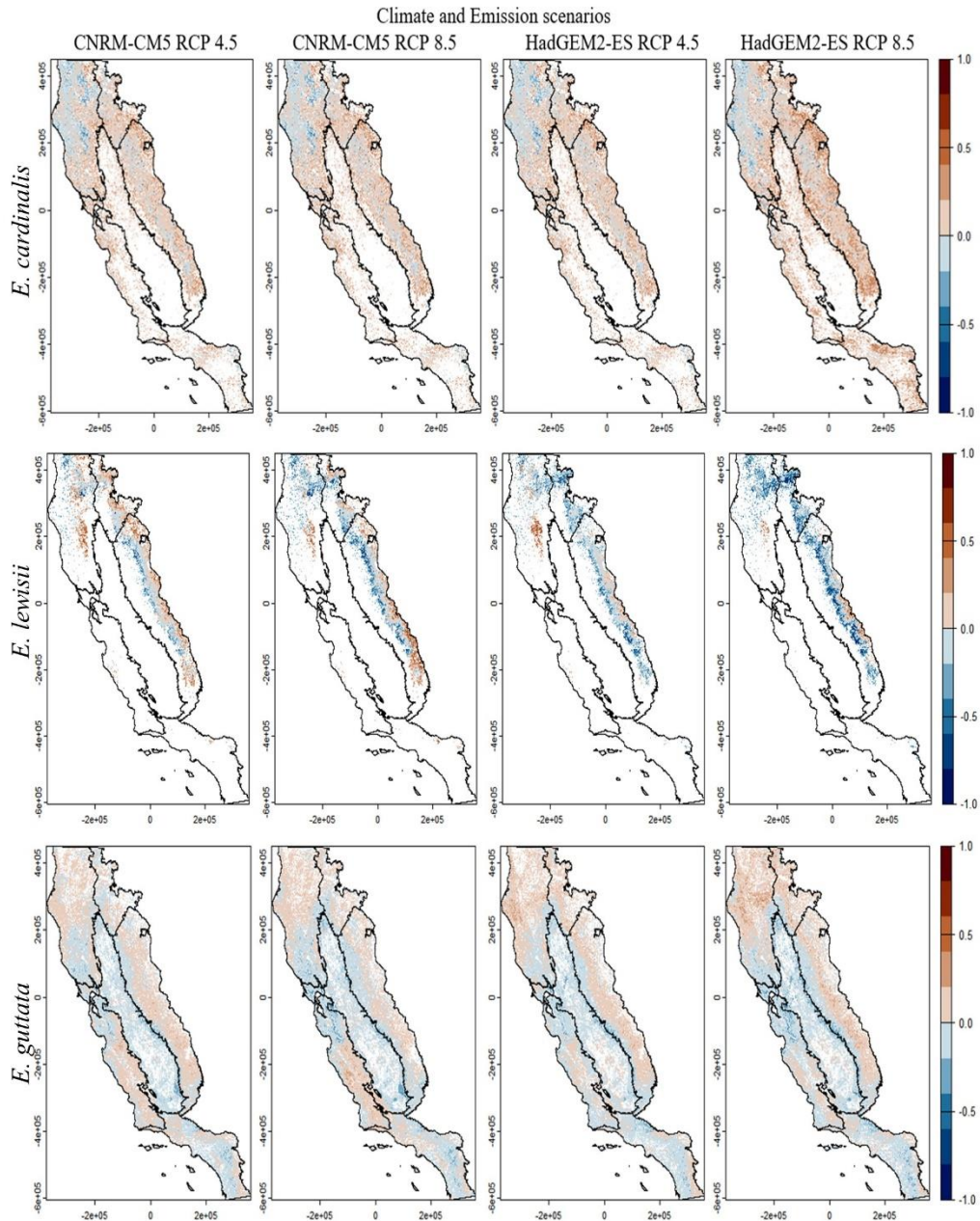


Figure S4. The difference in habitat suitability from year 1996 to 2085. Habitat suitability values at year 1996 were subtracted from the habitat suitability values at year 2085. Each column represents different climate change scenarios, and each row represents the three *Erythranthe* species in this study. The positive values indicate increased habitat suitability, and the negative values indicate decreased habitat suitability. The areas without the habitat suitability values and the areas that had no change of habitat suitability are not distinguished from each other in the maps.

Table S1. Number of habitat patches remaining in different size categories at $t = 0$ (year 1995) for *E. lewisii* when patches with carrying capacities of up to 150, 250, 500, and 750 are removed from the initial habitat map. The variable n represents the number of grid cells the patch is composed of, and each column shows the number of patches that fall into the patch size range.

Patch size	< 150 removed	< 250 removed	< 500 removed	< 750 removed
$n < 10$	35	1	0	0
$10 \leq n < 20$	266	86	0	0
$20 \leq n < 30$	78	76	10	0
$30 \leq n < 40$	51	51	39	1
$40 \leq n < 50$	21	21	21	11
$50 \leq n < 100$	49	49	49	48
$100 \leq n < 150$	12	12	12	12
$150 \leq n < 200$	4	4	4	4
$n \geq 200$	35	35	35	35

Among the simulation results of *Erythranthe* species for the first part of the experiment in this study, the population trajectories of *E. lewisii* species showed dampened oscillations and distinct population trends that did not track the habitat suitability trajectories (Figure 2c, d). Therefore, in order to examine the cause of these patterns, I ran simulations with habitat scenarios where small or low-quality patches (i.e. patches with low carrying capacity) were omitted from the habitat map at $t=0$. Scenarios included the omission of all patches with carrying capacities: $< 3 \times K$ ($K = 50$, the maximum carrying capacity of a single pixel), $< 5 \times K$, $< 10 \times K$, and $< 15 \times K$. The results showed that as more small patches were omitted the dampened population oscillations reduced and then disappeared. Patch size is calculated by the number of pixels (each of size $270 \text{ m} \times 270 \text{ m}$) in an aggregated “patch”. For example, the column “ $n < 10$ ” represents the number of patches that are composed of less than 10 pixels. Table S3 shows a high number of small patches remaining even when patches with carrying capacities less than 150 individuals are removed. When patches with carrying capacities less than 750 individuals are omitted (the habitat scenario that removes population oscillations across all climate scenarios) only 111 patches remain from a total of 551 patches under the < 150 population size omission scenario. Even with this dramatically reduced number of patches, and therefore total habitat area, all but the CNRM-CM5 RCP 4.5 climate scenario resulted in final population abundances that were greater than under the < 150 patch removal scenario, indicating that small patch sizes are driving the oscillations.