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# From models to management: Implementing the climate-change refugia conservation cycle in national parks of the northeastern United States

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## Abstract

Managing climate-change refugia is a commonly recommended strategy for conserving biodiversity. However, few efforts have moved beyond the modeling phase of refugia science to management. Here, we present two case studies that move beyond modeling to testing models and management. In the first case study, we model refugia for two plant species (three-toothed cinquefoil [*Sibbaldia tridentata*] and black crowberry [*Empetrum nigrum*]) in Acadia National Park, Maine, United States, and use greenhouse experiments, common-garden experiments, and participatory science to evaluate the output of those models. Our results suggest that three-toothed cinquefoil growth and survival are reduced under increased temperatures as models predict. However, other variables (e.g., soil moisture and salinity) might also be important to modeling and managing refugia for both species. National Park Service staff and partners have been directing restoration for both species to refugia, but are also exploring other adaptation strategies. In the second case study, we demonstrate that existing prioritization processes for habitat restoration in national parks of the northeastern United States rarely incorporate refugia for two indicator species: Jefferson salamander (*Ambystoma jeffersonianum*) and grasshopper sparrow (*Ammodramus savannarum*). Our work demonstrates that moving beyond modeling can improve models and lead to new management insights.

KEYWORDS

Acadia National Park, adaptation, black crowberry, grasshopper sparrow, Jefferson salamander, restoration, species distribution models, three-toothed cinquefoil

## 1 | INTRODUCTION

Climate change is fundamentally changing the goals for biodiversity conservation as species redistribute to track suitable climates. Conservation practitioners are having to make difficult decisions about whether to resist species redistributions to maintain current biodiversity in situ, accept changes to biodiversity as species shift in response to climate change, or direct change toward a desired future state (Lynch et al., 2021; Schuurman et al., 2020, 2022; Thompson et al., 2021). Whatever their goals, conservation practitioners have to choose among dozens of climate-change adaptation strategies ranging from conventional approaches to novel (e.g., assisted gene flow), and often untested strategies (Hansen et al., 2023; McLaughlin et al., 2022).

A commonly recommended climate-change adaptation strategy is to identify and manage climate-change refugia (Bringer et al., 2003; McLaughlin et al., 2022; Morelli et al. 2026; Stein et al., 2014). Climate-change refugia are areas relatively buffered from contemporary climate change over time that enable persistence of valued physical, ecological, and socio-cultural resources (Morelli et al., 2016). Climate-change refugia can be managed in a diversity of ways, but often practitioners hope to resist change in refugia and conserve biodiversity in situ using traditional conservation approaches (Keppel et al., 2024). Low-risk climate-adaptation strategies are a very attractive option for conservation practitioners (Barr et al., 2023). Consequently, refugia science has proliferated in recent years (Morelli et al. 2026). However, effectively incorporating refugia science into management requires coproduction of research between scientists and conservation practitioners (Morelli et al. 2026).

The Climate-Change Refugia Conservation Cycle (CCRCC; Figure 1) is a coproduction process developed to ensure that refugia research is guided by and informs conservation priorities (Morelli et al., 2016). The CCRCC is similar to multiple other climate-change adaptation processes (e.g., Climate-Smart Conservation Cycle, Adaptation for Conservation Targets) that use an iterative approach to identify management objectives, assess climate-change vulnerabilities, identify management actions, and evaluate management effectiveness (Abrahms et al., 2017; Cross et al., 2012; Stein et al., 2014). Specifically, the CCRCC includes steps to identify management priorities and climate-change vulnerabilities (Steps 1–3, Figure 1), model refugia (Step 4a), test model results with independent data (Step 4b), identify priority management actions (e.g., protection, restoration) in refugia (Steps 5–6), and monitor the effectiveness of those actions (Step 7). Most refugia conservation efforts to date focus on identifying refugia (Steps 1–4a), but do not test model results or move beyond modeling to management action and effectiveness monitoring (Morelli et al. 2026). Without these steps, it is difficult to know if refugia research and management are effectively addressing biodiversity conservation goals (Barrows et al., 2020; Hansen et al., 2023).

Here we—a team of scientists and natural resource managers—present two case studies that have gone through much of the CCRCC to connect refugia modeling to management through coproduction in the northeastern United States. Both case studies involve iterative coproduction between a diverse group of scientists and managers beyond the authors of this paper, as described in the methods. In Case Study 1, we present a local refugia modeling effort in Acadia National Park, Maine, where we address all seven steps of the CCRCC (Figure 1). In Case Study 2, we present a regional refugia modeling effort and demonstrate how these results could be incorporated into a regional restoration project using two indicator species (Figure 1). In both case studies, managers hope to maintain focal species in predicted refugia (i.e., resist change) and improve site conditions through restoration of native plants and the removal of invasive species. We share lessons learned from each step of the CCRCC from these two case studies to inform future refugia science and management.

## 2 | METHODS

All analyses were performed in the R statistical software environment version 3.6.0 (R Core Team, 2021).

### 2.1 | Case Study 1: Implementing the CCRCC in Acadia National Park

Acadia National Park (hereafter Acadia) includes over 20,000 ha along the Atlantic coastline of Maine, United States (Figure 2). Acadia is near the southern distribution of many boreal and arctic species and habitats, and therefore many species could be vulnerable to climate change in Acadia. However, many of the physical characteristics that tend to create terrestrial climate-change refugia, such as high spatial heterogeneity in topography and proximity to large water bodies (Ashcroft, 2010; Dobrowski, 2011; Morelli et al., 2016), are present in Acadia. For these reasons, identifying refugia is a research priority for guiding management in Acadia (Roman & Babson, 2013).

Starting in 2018, we followed the CCRCC (Figure 1) to identify and manage refugia in Acadia. We first briefly describe our process for objective setting and modeling (CCRCC Steps 1–4a), including results for two priority plant species in Acadia: three-toothed cinquefoil

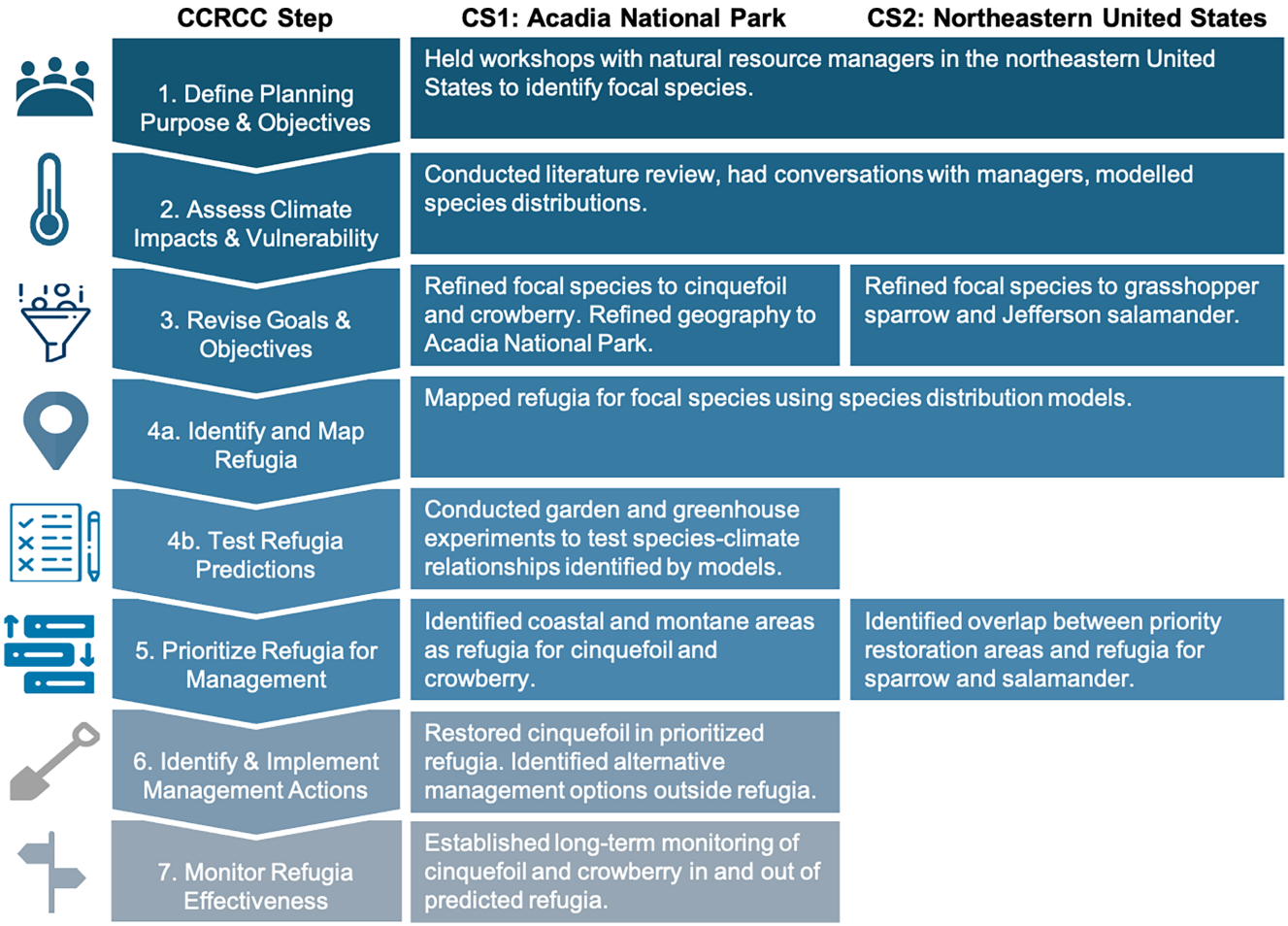


**FIGURE 1** The Climate-Change Refugia Conservation Cycle (CCRCC) and how we addressed each step of the cycle for the two case studies (CS) presented. The CCRCC, despite being a cycle, is represented linearly here to show how we addressed the steps of the cycle in the two case studies.

(*Sibbaldia tridentata*; hereafter cinquefoil) and black crowberry (*Empetrum nigrum*; hereafter crowberry). We then present how we continued through CCRCC Steps 4b–7, focusing on those species.

### 2.1.1 | CCRCC Steps 1–4a: Objectives and modeling

Following Step 1 of the CCRCC and a knowledge coproduction approach (Meadow et al., 2015), we held a meeting at Acadia with managers from Acadia and 11 organizations (e.g., local land trusts, state and federal agencies) to refine project objectives and identify focal species for analysis. The group identified a broad list of focal species for the project. Following Steps 2–3 of the CCRCC, we refined the list to 10 species vulnerable to climate change and of conservation and/or cultural interest (Smetzer & Morelli, 2019). Here, we focus on two plant species in Acadia: cinquefoil and crowberry.

Cinquefoil is a creeping evergreen subshrub found throughout southern Greenland and most of Canada, with southern disjunct populations in the northeastern United States (including Acadia) on rare coastal bluffs and rocky bald mountain summits (Bresowar & Walker, 2011). In Acadia, cinquefoil could be an important species for reducing soil erosion on mountain summits and coastal headlands (Olfelt et al., 2009). Crowberry is a small low-growing, woody shrub with a circumpolar distribution. In North America, it is found on coastal bluffs and exposed sea cliffs, and in sphagnum bogs, muskegs, open conifer woodlands, and open tundra and rock fields (Robin, 1992). On the Atlantic shores of North America, such as Acadia, crowberry plays an important role on coastal heads by reducing erosion, maintaining shrub habitats through allelopathic interference, and as the host for the endemic crowberry blue butterfly (*Plebejus idas empetri*). Acadia may have important climate-change refugia for both species on cool coastal heads and rocky bald mountain summits.

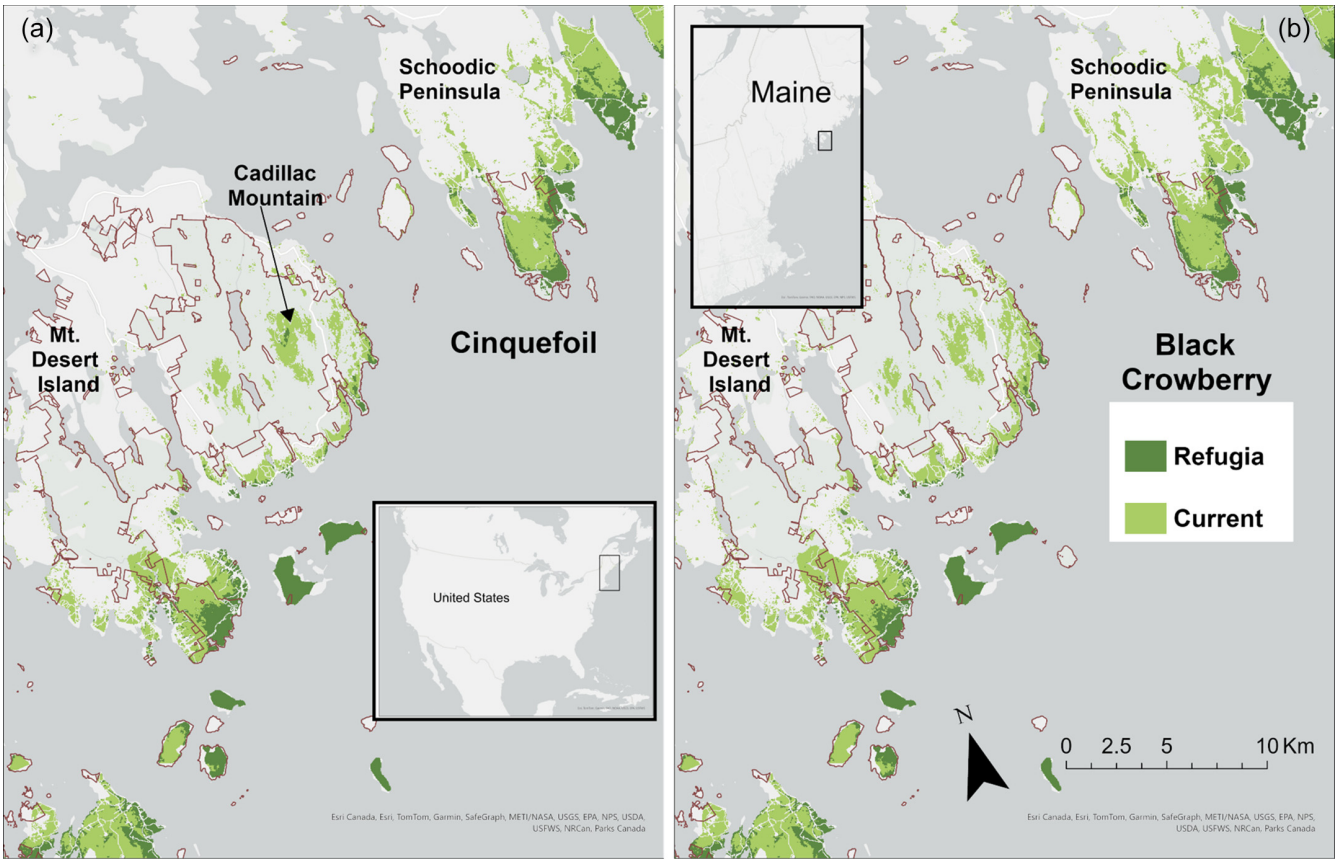


**FIGURE 2** Projected current occupancy of (a) three-toothed cinquefoil and (b) black crowberry in the Acadia National Park region, with putative refugia at late century under RCP4.5 overlaid. Areas without green are non-habitat, and the Acadia National Park boundary is outlined in brown. The insets show (a) the location of the northeastern United States in North America and (b) the location of Acadia National Park within the northeastern United States. The Schoodic Peninsula and Cadillac Mountain are noted for reference.

Following Step 4a of the CCRCC, we developed species distribution models to map refugia. Briefly, we used vetted occurrence records with sufficient positional accuracy to match the 800 m resolution of the climate data, including 81 occurrence records for cinquefoil and 36 for crowberry. We generated random background points within the spatial extent of occurrence records following best practices for reducing bias in presence-only data (Barbet-Massin et al., 2012; Hijmans, 2012). We used climate data developed by the Northeast Climate Adaptation Science Center (McGarigal et al., 2018) based on an ensemble average of 14 global climate model (GCM) projections from the Coupled Model Intercomparison Project Phase 5. Using an ensemble average does not capture as much of the potential future variability in climate as other methods that focus on capturing projection extremes, particularly in the near-term planning horizon (Lawrence et al., 2021). However, given our end-of-century time frame for projecting refugia and the decision context of the study, we deemed the ensemble approach acceptable. The data were spatially downscaled using the Bias Corrected Spatial Disaggregation method, and projected anomalies were subsequently resampled at 800 m resolution and combined with 30-year normal precipitation and temperature data from the PRISM Climate Group using the delta method. We chose these data as they were based on GCMs that best predicted historical climate within the northeast region and were downscaled to incorporate physiographic factors that can lead to climate-change refugia such as elevation, coastal proximity, aspect, topographic position, and orographic effects (McGarigal et al., 2018).

We used 30-year normals centered on 1995 (current period) to develop models, and 30-year normals centered on 2080 under Representative Concentration Pathways (RCP) 4.5 and 8.5 for future projections. We included soil data from the Natural Resources Conservation Service (2018) in models, and leveraged 30 m resolution elevation and canopy cover data from LANDFIRE (2013) to represent finer resolution refugial drivers. We used logistic regression to assess the relationship between occupancy and covariates, as this algorithm is less influenced by the choice of pseudo-absence points than others, particularly at the low sample sizes observed in our study (Barbet-

Massin et al., 2012). We retained 25% of the data for hold-out testing to calculate several performance metrics (Table S1). For each species and time period, we transformed predictions from the most well-supported model to binary suitable habitat output using the probability that maximized the sum of true-positive and true-negative rates. We defined refugia as areas that were considered suitable habitat in both the current and future periods. See Smetzer and Morelli (2019) for more information on the objectives and modeling methods.

### 2.1.2 | CCRCC Step 4b: Testing modeled species–climate relationships using external data for cinquefoil

Correlative models used to identify refugia need to be evaluated to ensure that the identified refugia meet the needs of the focal resource (Barrows et al., 2020; Morelli et al., 2016). In line with Step 4b of the CCRCC (Figure 1), we conducted two experiments to independently evaluate the prediction from refugia models that increased temperatures will reduce cinquefoil growth and survival: (1) a common garden experiment, and (2) a greenhouse experiment.

#### *Common garden experiment*

We grew cinquefoil in three 2.4 m × 3.7 m wooden boxes (hereafter gardens) to evaluate if increased temperatures reduced growth and survival. One garden was sited at the summit of Cadillac Mountain (465 m) in Acadia (Figure 2a) to represent current growing conditions for cinquefoil (hereafter control garden). A second garden was at the base of Cadillac Mountain with an average maximum summer temperature 2.2°C warmer than the control garden (hereafter warm garden). A third garden was on the Schoodic Peninsula in Acadia (Figure 2b) where the average maximum summer temperature is 2.9°C cooler than the control garden (hereafter cool garden). Other environmental variables also differed among the gardens (Section S3). Specifically, the cool garden was 20% and 33% wetter than the control and warm gardens, respectively, and the control garden received 51% and 36% more sunlight than the warm and cool gardens, respectively (Figure S3). If light and soil moisture affect the growth and survival of cinquefoil more than temperature, we expect different results than if warmer temperatures limit growth and survival (see below). Hence, this experiment is informative about the effects of temperature despite the other environmental differences among the gardens.

Each garden was partitioned into 30 cells separated by tin walls lined with weed fabric to prevent plants from one cell spreading into an adjacent cell, which maintained independence among cells (Nadeau et al., 2024). We planted 10 populations of 20 individual cinquefoil plants in randomly selected cells in each garden (10 populations × 3 gardens = 30 total populations). We collected plants from Cadillac Mountain and planted two populations per week between May 23, 2021 and July 1, 2021. In August of 2021–2024, we removed any plants that were not cinquefoil and then took overhead photos of each population. We used ImageJ (Schneider et al., 2012) to estimate the percent cover of green cinquefoil in each population from the photos. If increased temperatures reduce cinquefoil growth and survival as refugia models predict, then we expected significantly lower percent cover of green cinquefoil in the warm garden. If differences in light among the gardens affected our results, then we expected lower percent cover due to light limitation in both the warm and cool gardens that have low light. Last, if differences in soil moisture among the gardens affected our results, then we expected the highest percent cover in the cool garden that has high soil moisture. We tested these predictions using linear mixed-effects models (Section S3).

#### *Greenhouse experiment*

In the summer of 2021, we observed that potted cinquefoil plants could survive extremely high maximum summer temperatures (>38°C) in a greenhouse with daily irrigation. This observation contradicts predictions from refugia models that increased maximum summer temperatures reduce cinquefoil growth and survival. We had two hypotheses to explain this observation: (H1) increased temperatures do not affect cinquefoil growth and survival as models predict, or (H2) daily irrigation was mitigating the negative impacts of high temperatures in the greenhouse, despite the fact that our models excluded variables associated with precipitation, soil moisture, or climatic water deficit. Although it is known that moisture can alter plant thermal tolerances (Cook et al., 2021; Ruehr et al., 2016), an experiment was necessary to differentiate H1 and H2. If H1 is true, then refugia models could be overestimating the vulnerability of cinquefoil to climate change and underestimating the amount of refugial area. If H2 is true, then managing soil water-holding capacity (e.g., by restoring mosses) could be an effective method for managing the long-term success of climate-change refugia during hot dry periods that are becoming more common under climate change (Climate Change Response Program, 2024).

To test the two competing hypotheses, we grew 408 cinquefoil plants in the greenhouse under one of two precipitation treatments: (1) daily irrigation of 0.8 cm/day, mimicking previous greenhouse observations, or

(2) twice-weekly irrigation of 0.8 cm/day, mimicking natural conditions on Cadillac Mountain in Acadia (hereafter the natural treatment, Section S4). We used plants collected in 2021 from 27 locations throughout New England and stored outside in seedling trays. We transplanted plants to 4-in. pots with commercial potting soil (Nature's Care Organic and Natural Potting Mix) on July 12–13, 2022 and allowed them to acclimate for 23 days with daily irrigation. On August 5, 2022 (Day 0 of the experiment), we randomly selected 204 plants to change to a natural irrigation regime. We counted the number of green leaves on each plant weekly until November 11, 2022. We considered a plant dead if it lost all its leaves and grew no new leaves over the course of the experiment.

We used generalized linear models to compare the following between the two irrigation treatments (Section S4): (1) the probability of survival on Day 48 of the experiment, and (2) the change in the number of green leaves between Day 0 and Day 48 of the experiment for plants that lived to Day 48. We focused on Day 48 because survival and the number of green leaves had remained similar for a few weeks, and plants had not yet begun to senesce. Choosing a different date did not alter our conclusions (Section S4). If increased maximum summer temperatures do not reduce cinquefoil growth and survival as the models predict, then we expected no difference in survival or change in the number of green leaves between the irrigation treatments. If irrigation frequency and amount mitigate the negative impacts of high temperatures, then we predicted lower survival or a larger loss of green leaves in the natural irrigation treatment.

### 2.1.3 | CCRCC Steps 5–6: Prioritizing management areas and identifying management actions

Areas identified as refugia in Acadia (the peak of Cadillac Mountain for cinquefoil and coastal areas for both species, Figure 2) are also among the most highly visited in the park, creating challenges for refugia management. Acadia attracts roughly 4 million visitors each year and nearly all of them visit coastal areas and most visit summits in the park. Repeated trampling has killed short-statured plants such as cinquefoil and crowberry, which has, in combination with increasingly intense rainfall events and coastal storms (Maine Climate Council, 2024), eroded soil and threatened the value of summits and coasts as refugia.

Park managers began active restoration of soil and native vegetation on Cadillac Mountain and other summits in Acadia in 2016, prior to receiving refugia modeling results (Lima et al., 2025). Cinquefoil is one of the most successful species in the restoration plots and likely serves the important function of reducing soil erosion. Restoring crowberry could also reduce soil erosion in coastal refugia in Acadia. However, before the refugia modeling project, park managers had no plans to actively restore crowberry. In Section 3, we describe how refugia models altered management plans for these species in Acadia.

### 2.1.4 | CCRCC Step 7: Monitoring refugia effectiveness using participatory science

Monitoring refugia is an essential step in understanding whether identified refugia continue to meet management objectives over time (Barrows et al., 2020; Morelli et al., 2016). However, long-term monitoring is often difficult to fund and maintain (Caughlan & Oakley, 2001; Vander Naald et al., 2019). To overcome these barriers and address Step 7 of the CCRCC, we developed a participatory science project to monitor the presence, health, and reproduction of cinquefoil and crowberry in and out of predicted refugia in partnership with Earthwatch Institute (hereafter Earthwatch). Earthwatch is a non-profit organization that engages people in participatory science projects, including field research projects.

We established 10 sites in the Acadia region to monitor both species: 6 sites in (refugia sites) and 4 sites out (non-refugia sites) of areas identified as refugia for cinquefoil, and 5 sites in and 5 sites out of refugia for crowberry. We chose sites where both species were either known to be present or were likely to be present based on the habitat. At each site, we overlaid a 20-$m^2$ grid and filtered out cells that did not include appropriate habitat for either species. Earthwatch teams (10–14 participants) surveyed a 5 m radius circle in the center of each grid cell for the focal species from June to September of 2023 and 2024. During surveys, small teams walked 5-m transects from the center of each grid cell following each cardinal and intercardinal direction while scanning for the two focal species. If a focal species was detected, they placed a 50-$cm^2$ quadrat divided into 25 equal cells with string over the closest section of the plant to the survey center point and counted the number of quadrat cells that (1) were occupied by the species, (2) contained flowers or flower buds, (3) contained fruits, and (4) showed brown leaves. The survey then continued until the other focal species was found and the same data were collected, or until we surveyed the entire circle without detecting the species. We predicted that both species would have lower reproduction or more brown

leaves in non-refugia sites than refugia sites if maximum summer temperatures have already warmed sufficiently to affect the plants. This prediction assumes that neither focal species induces flowering under stress (Takeno, 2016). We are unaware of any research on stress-induced flowering in our focal species. We used generalized linear mixed-effects models to test these predictions (Section S5). Note, our monitoring cannot inform what might happen in the future as climate continues to change but provides important baseline data and a useful comparison between refugia and non-refugia sites if the focal species are stressed by the recent climate change they have experienced.

## 2.2 | Case Study 2: Evaluating overlap between regional restoration priorities and refugia

The United States National Park Service recently started large-scale restoration of forest and grassland ecosystems in focal national parks in the northeastern United States. These focal locations have been degraded by historical land use changes, intense deer herbivory, and rapid spread of invasive plants (Miller et al., 2023). The restoration projects aim to reduce deer herbivory and invasive plant populations and enhance regeneration of native forest and grassland species. Here we evaluate how locations prioritized for these regional restoration projects overlap with refugia identified through a regional refugia modeling effort completed independently of planning for the restoration projects. We first briefly describe the overall process for objective setting and modeling (CCRCC Steps 1–4a), including results for a grassland and forest indicator species. We then present how we continued through CCRCC Step 5 to determine if priority restoration areas overlap with refugia.

### 2.2.1 | CCRCC Steps 1–4a: Objectives and modeling

Following the same knowledge coproduction process described above, we convened managers from federal, state, and non-profit agencies across the northeastern United States through a series of four virtual workshops to identify focal species for modeling. We initially identified 40 focal species but refined that list to 10 species that had not been the focus of previous refugia research in the region (see https://umassdsl.org/data/focal-species-models/ for previous refugia research). Here we present results for a grassland indicator species (grasshopper sparrow; *Ammodramus savannarum*) and an upland forest indicator species (Jefferson salamander; *Ambystoma jeffersonianum*) that can be used to understand if locations prioritized for regional restoration efforts in grasslands and forests overlap with refugia. Grasshopper sparrows are a grassland songbird species that breeds across southern Canada and much of the eastern United States (Vickery, 1996). They can be found in prairies and open fields with tall grasses and weeds and minimal shrub cover. Jefferson salamanders' range is limited to the eastern United States and southern Canada (DeGraaf & Rudis, 1986). They are found in undisturbed, well-drained upland forests that are within ~250 m of seasonal, semi-permanent, and fish-free permanent wetlands (Petranka, 1998).

We modeled refugia for the focal species using a similar process as described above for the first case study, including processes for occurrence record selection and background point generation, and the same climate and physiographic covariates, with some differences noted here. We used 129 occurrence records for grasshopper sparrow and 234 for Jefferson salamander. We first identified species–environment relationships using logistic regression and tested variables for collinearity. We used forward and backward stepwise selection on global models with different combinations of climate variables and relevant environmental predictors to identify the most parsimonious model for each species. Highly collinear variables were not included in the same global models. For final model covariate selection and species–habitat relationships, see Figures S1 and S2. To predict species distributions, we evaluated eight species distribution modeling methods, including a logistic regression, support vector machine, maxent, boosted regression trees, multivariate adaptive regression spline, bioclim, random forest, and maxlike models with bootstrapping, across 1000 replicates. We compared AUC values to determine the best model fit for each focal species (Araújo et al., 2005). Random forest was chosen as the final modeling approach as it had the highest AUC scores and has been shown to have higher predictive accuracy than ordinary decision trees (Cutler et al., 2007; Prasad et al., 2006). We transformed predictions from the most well-supported model to identify suitable habitat for each species and time period using the threshold that maximized the sum of sensitivity and specificity (Liu et al., 2015). See Wisner (2024) for more information on the coproduction and modeling methods.

### 2.2.2 | CCRCC Step 5: Overlap in projected refugia and restoration priorities

To assess Step 5 of the CCRCC, we evaluated the spatial overlap between projected climate-change refugia for our

two focal species and priority areas identified for grassland and forest restoration (Figure 1). Where refugia coincide with existing restoration priorities, this suggests that current planning—though not explicitly focused on climate resilience—may already support the conservation of key refugial habitats. In such cases, managers could refine restoration strategies, such as treatment timing or intensity, to better support species dependent on these refugia. Conversely, if refugia fall largely outside priority restoration zones, this could indicate gaps in existing prioritization processes or suggest that some refugial areas may not require restoration. In these instances, land managers may consider expanding or revising restoration priorities to include refugial areas, particularly where they provide critical habitat for climate-vulnerable species.

## 3 | RESULTS

### 3.1 | Case Study 1: Implementing the CCRCC in Acadia National Park

#### 3.1.1 | CCRCC Steps 1–4a: Objectives and modeling

Models had a strong predictive ability for both species (Table S1). Occurrence of cinquefoil was greatest at higher elevations ($\beta = 0.002$; $p < 0.001$), in areas with low canopy cover ($\beta = -0.035$; $p < 0.001$), and on dry soils ($\beta = -0.081$; $p < 0.001$) with high organic content ($\beta = 0.01$; $p = 0.01$). Cinquefoil occurrence was positively related to growing degree days ($\beta = 0.00003$; $p = 0.04$), but negatively related to maximum summer temperatures ($\beta = -0.017$; $p < 0.001$). Crowberry occurrence was greatest at lower elevations ($\beta = -0.0052$; $p = 0.01$), lower canopy cover ($\beta = -0.03$; $p < 0.001$), on dry soils ($\beta = -0.546$; $p = 0.03$), with low pH ($\beta = -2.084$; $p = 0.05$), and high organic content ($\beta = 0.051$; $p = 0.06$). Crowberry occurrence exhibited a negative relationship with maximum summer temperatures ($\beta = -0.011$; $p < 0.001$). Precipitation was not in the most supported model for either species.

Both species exhibited the highest probability of occupancy in coastal and montane areas at all time steps. Cinquefoil was predicted to exhibit a 93.6–98.5% decline in suitable habitat in Maine by late century under RCP4.5 and 8.5, respectively, and crowberry a 90.7–98.5% decline. Coastal and montane regions throughout Maine represented potential refugia for cinquefoil, and the eastern coast of Maine represented the only potential refugia for crowberry within the state by the end of the century. Despite the existence of 28 rocky-bald peaks in Acadia, the peak of the highest mountain (Cadillac Mountain; Figure 2a) was the only montane refugium for cinquefoil, whereas large parts of Acadia's coast were identified as refugia for both species (Figure 2).

#### 3.1.2 | CCRCC Step 4b: Testing modeled species–climate relationships using external data for cinquefoil

*Common garden experiment*

Percent cover in the control and cool gardens increased significantly from a low of 10.0% (SE = 3.03) and 11.8% (SE = 3.57) in 2021 to a high of 50.9% (SE = 15.31, $p < 0.001$) and 45.5% (SE = 13.70, $p = 0.001$) in 2023 (Figure 3). In contrast, percent cover in the warm garden decreased slightly from a high of 17.6% (SE = 5.33) in 2021 to a low of 6.2% (SE = 1.90, $p = 0.013$) in 2024. Percent cover declined in all gardens in 2024 for an unknown reason (Figure 3). Percent cover was similar between the control and cool gardens in all years (Figure 3), which suggests differences in soil moisture and light did not substantially affect our conclusions. These results support the hypothesis that higher temperatures negatively affect cinquefoil as refugia models predicted; however, more work would be needed to determine if maximum summer temperature or another aspect of temperature is most important.

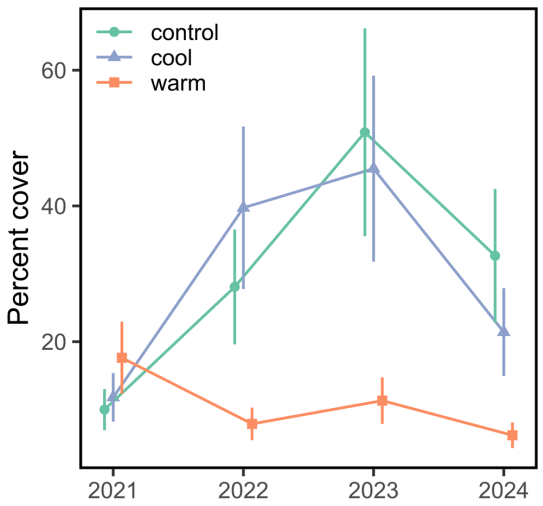


**FIGURE 3** Percent cover of 10 three-toothed cinquefoil populations growing in each of three common gardens: (control) the summit of Cadillac Mountain where cinquefoil is common, (warm) the base of Cadillac Mountain, which is 2.2°C warmer than the summit, and (cool) a location 2.9°C cooler than the summit site. Results are estimated marginal means (±1 SE) from a linear mixed-effects model (Section S3).

*Greenhouse experiment*

The average daily maximum temperature in the greenhouse between Days 0 and 48 of the experiment was 30.4°C (max = 39.9°C, SD = 13.5°C), which is much higher than temperatures throughout much of cinquefoil's current range. Survival probability was 19.0% lower in the natural irrigation treatment ($p = 0.001$; Figure 4a). Plants in both treatments lost green leaves between Days 0 and 48 of the experiment, and the change in the number of green leaves did not differ between the treatments ($p = 0.228$; Figure 4b). The results suggest increased temperatures will reduce cinquefoil growth and survival as refugia models predict, but that irrigation can mitigate the negative impacts of high temperatures. These results likely explain the high survival observed in the greenhouse in previous years, but contradict the finding that precipitation was not an important covariate in refugia modeling. Considering how increased temperatures, precipitation, and soil water-holding capacity interact could therefore improve refugia models and management in the future.

### 3.1.3 | CCRCC Steps 5–6: Prioritizing management areas and identifying management actions

Once locations on the summit of Cadillac Mountain were identified as the only montane refugia for cinquefoil (Figure 2a), park managers adjusted management to prioritize cinquefoil in restoration areas. Specifically, new restoration sites established in 2024 on Cadillac Mountain were located in areas identified as refugia, and managers continued to seed cinquefoil in those areas. Managers and scientists are also testing other strategies to improve the climate resilience of cinquefoil on mountain summits not identified as refugia. Specifically, they are evaluating whether increasing genetic diversity or planting cinquefoil from warmer areas might benefit cinquefoil restoration outside of refugia in Acadia using a common garden experiment (Nadeau et al., 2024). There might also be restoration opportunities in suitable microclimates, which were not included in the refugia models due to the resolution of the climate data. More work is needed to identify such microclimates.

Managers at Acadia are entering the planning stages of the restoration of coastal vegetation in areas eroded by trampling and extreme storms. In part because of the refugia modeling, managers are considering crowberry and other species that will likely benefit from and depend on climate-change refugia as a part of these restoration projects, particularly given the species' ability to reduce erosion and maintain shrub habitats through allelopathic interference.

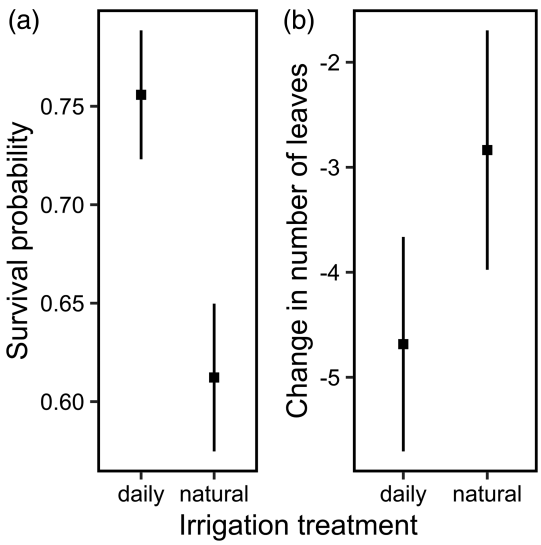


**FIGURE 4** (a) Survival probability (±1 SE) on Day 48 of the experiment, and (b) mean change in the number of green leaves (±1 SE) between Days 0 and 48 of the experiment under two irrigation treatments. Means and SE are estimated marginal means and SE from linear regression models (Section S4).

### 3.1.4 | CCRCC Step 7: Monitoring refugia effectiveness using participatory science

The proportion of quadrat cells with brown cinquefoil leaves, cinquefoil flowers, and brown crowberry leaves did not differ between refugia and non-refugia sites ($p = 0.881$, 0.092, and 0.131, respectively; Figure 5). The proportion of cells with crowberry fruits was lower in refugia than in non-refugia sites ($p < 0.001$). These

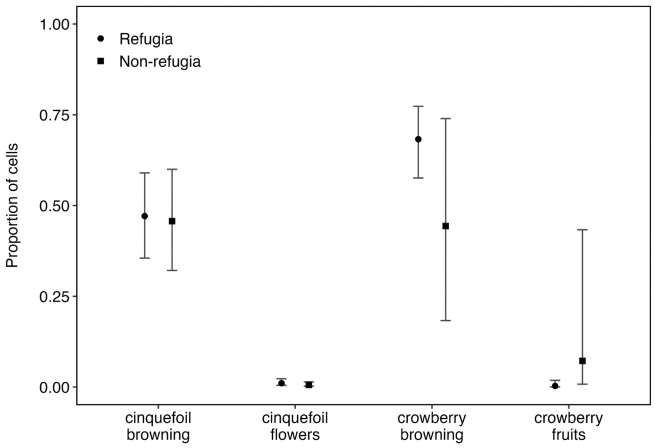


**FIGURE 5** Proportions of occupied quadrat cells that contained browning leaves and flowers or fruits for black crowberry and three-toothed cinquefoil, in refugia and non-refugia.

results do not support our prediction that both species would have more brown leaves or less reproductive effort in non-refugia sites. In fact, we observed the opposite pattern as we predicted for crowberry fruits, suggesting a factor other than temperature might be affecting crowberry in refugia sites or that crowberry exhibits stress-induced flowering (Takeno, 2016). Note, however, that we might need to experience more climate change to observe the predicted results. Continued monitoring at these sites is therefore necessary to evaluate how both species perform in and out of refugia over time as climates continue to change.

### 3.2 | Case Study 2: Evaluating overlap between regional restoration priorities and refugia

#### 3.2.1 | CCRCC Steps 1–4a: Objectives and modeling

Models had a strong predictive ability for both species (Table S1). Occurrence of grasshopper sparrow was highest in areas of low canopy cover, moderate precipitation (~100 mm per year), a mean maximum summer temperature of approximately 24–29°C, and mean minimum winter temperature of approximately −4°C (Figure S1). Occurrence for Jefferson salamander was highest with cumulative growing degree days of approximately 2000, low precipitation (~800–1000 mm per year), and mean minimum winter temperatures of approximately −4°C to −5°C (Figure S2). Projected refugia occur in only 2.3% and 5.5% of the northeastern United States for grasshopper sparrow (refugia are predominately small and only a few pixels in size; hence, we do not provide a map for grasshopper sparrow) and Jefferson salamander, respectively (Figure 6).

#### 3.2.2 | CCRCC Step 5: Overlap in projected refugia and restoration priorities

Five of 112 grassland restoration priority areas (4.5%) contained some climate-change refugia for grasshopper sparrow, and several of these restoration areas were entirely refugia. There was no overlap with Jefferson salamander refugia in any of the 42 forest restoration priority areas, though several restoration areas were located in close proximity to refugia (Figure 6). These results suggest that existing prioritization methods for regional restoration may miss key climate-change refugia. In the short term, managers might consider on an ad hoc basis whether specific refugial areas require restoration and, if so, whether they should be prioritized given their status as refugia for key species. In the longer term, managers might consider whether prioritization processes could be adjusted to better target climate-change refugia and support focal species resilience.

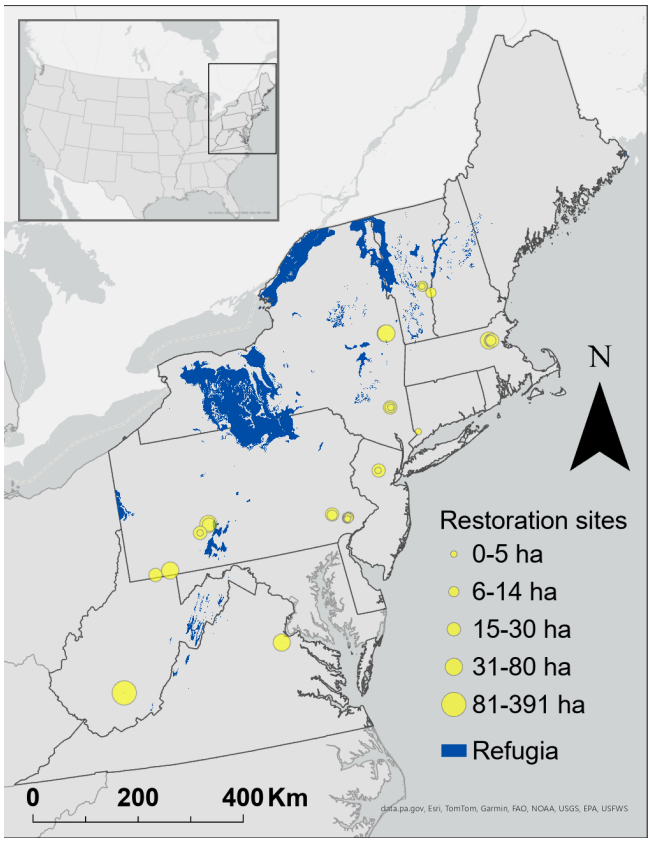


**FIGURE 6** Projected climate-change refugia across the northeastern United States for Jefferson salamander, an upland forest salamander. Yellow points show proposed National Park Service forest restoration sites scaled by the size of the restoration site in hectares. Climate-change refugia for grasshopper sparrows are too small to be visible at the regional scale, but five of the NPS grassland restoration sites include grasshopper sparrow refugia.

## 4 | DISCUSSION

Our research indicates the value of following the CCRCC to incorporate refugia science into management. In the first case study, model projections for focal species in Acadia suggested 90.7–98.5% declines in suitable habitat in Maine, but refugia will likely remain in montane and coastal areas, including within Acadia. Independent experiments suggested the species–climate relationships identified by the models, specifically the negative effects of increased temperature, are likely accurate. However, other variables related to precipitation and/or soil water-holding capacity might also be important to both

modeling refugia and management. With some confidence in the models, National Park Service staff and partners have been directing restoration efforts for both species to refugia areas where we can resist change and exploring novel management approaches in areas where the species are most vulnerable (see below). Finally, we have used a novel participatory science method for effectiveness monitoring that will allow us to understand the long-term value of refugia for both species. This method is already suggesting that factors other than temperature might threaten the long-term success of refugia.

Our second case study demonstrates the value of the CCRCC for incorporating refugia science into regional management. However, existing prioritization processes that do not incorporate refugia predictions might not incorporate refugia for indicator species. Opportunities in the regional effort exist to ground truth refugia models, incorporate refugia into regional restoration plans, test strategies to enhance the resilience of target species in restoration areas outside of refugia, and monitor the performance of restoration and refugia sites.

Throughout these two case studies, we have learned a number of important lessons about implementing the CCRCC that can inform future efforts:

## 4.1 | Model validation and monitoring can improve refugia models and lead to new management insights

Recent research calls for more testing of refugia models with independent data and efforts to monitor the effectiveness of refugia as a climate-change adaptation strategy (Barrows et al., 2020; Hansen et al., 2023; Nadeau et al., 2024; Prober et al., 2019). We echo these previous calls. Without such tests and monitoring, refugia models could misguide conservation efforts. Further, our work highlights how validation and monitoring can identify gaps in refugia models and improve management in several ways.

First, our greenhouse experiment suggests that temperature and precipitation interact to affect cinquefoil growth and survival. Incorporating this important relationship into models through a temperature–precipitation interaction, or by including variables such as soil water-holding capacity or climatic water deficit in models could result in more accurate refugia predictions. Moreover, managing refugia areas to increase water-holding capacity, such as restoring mosses (Berdugo et al., 2022), could improve the effectiveness of the refugia during hot and dry periods that are increasing under climate change in Acadia (Climate Change Response Program, 2024).

Second, lower reproduction for crowberry in refugia compared to non-refugia suggests stressors not captured in the model might be impacting crowberry in coastal refugia sites. We suspect increased salt spray and saltwater inundation from coastal storms and sea-level rise are contributing to these patterns (Du & Hesp, 2020). If true, then many coastal locations identified as refugia might not act as refugia for crowberry in the future. Without refugia monitoring, we would not have identified potential additional stressors, and may have proceeded with crowberry restoration in unsuitable locations. Indeed, managing multiple stressors, both climate and non-climate related, in potential refugia is important to effective management (Keppel et al., 2024).

Moreover, conserving refugia is only one approach in a manager's climate-change adaptation toolbox, and managers might need to implement multiple strategies to address management objectives (McLaughlin et al., 2022; Prober et al., 2019). For example, a common alternative approach to conserving refugia is "conserving the stage", where managers conserve geophysical settings that support biodiversity, even if the identity of species in the setting changes over time (Anderson & Ferree, 2010). Under the conserving the stage approach, conserving cool rocky coastlines and mountain summits in Acadia will likely result in the conservation of novel plant assemblages, even if these locations do not end up being climate-change refugia for current species. Alternatively, strategies such as assisted gene flow could help keep existing species present and ensure the long-term success of restoration efforts in and out of projected climate-change refugia. Scientists and managers at Acadia are exploring assisted gene flow as a management strategy with cinquefoil to hedge their bets in projected refugia and conserve cinquefoil outside of refugia (Nadeau et al., 2024).

## 4.2 | Implementing the CCRCC requires varied partners and is often opportunistic

Coproduction is critical to ensuring research can be incorporated into management (Beier et al., 2017) and is a critical component of the CCRCC (Morelli et al., 2016). Indeed, most on-the-ground adaptation action has involved coproduction (Halofsky et al., 2015). We were successful at completing the CCRCC for two reasons. First, partners with different expertise—modeling, experimental ecology, management, and participatory science—were involved throughout the coproduction process and led work at different steps of the CCRCC. Because one person or agency might rarely have such varied expertise, partnerships will benefit climate-change adaptation

processes like the CCRCC. Indeed, this iterative process of collaboration and the long-term relationship among scientists and managers is often necessary for successful coproduction (Beier et al., 2017; Nel et al., 2016; Reed et al., 2014).

Second, refugia modeling addressed species for which active management was already underway or was being planned. In the case of cinquefoil, this allowed managers to immediately incorporate refugia research into management. Refugia models for the other species have been beneficial in opportunistic, and often unanticipated, circumstances (e.g., restoration from coastal storms, new funding sources for regional planning). Managers may not utilize refugia models until an opportunity exists to apply the knowledge, and they combine the information with many other sources to make management decisions. This unpredictable nature of incorporating research into management often frustrates applied scientists (Beier et al., 2017), but solutions exist. Providing refugia model results and metadata in an easily accessible and usable format is critical to allow for their future use in such opportunistic applications. Personal relationships between scientists and managers developed through coproduction increase the likelihood that these resources will be used to improve management decisions.

### 4.3 | To complete the CCRCC, model outputs need to be tailored to specific management contexts

Many inherent factors can limit the utility of species distribution modeling in identifying refugia for management. Several of these key limitations were apparent in the case studies provided here. First, correlative models can fail to accurately predict a species' response to severe environmental conditions that are outside what the model is trained on (Soley-Guardia et al., 2024). Indeed, the limited range of climate conditions spanned by the cinquefoil occurrence records used in the Acadia modeling is likely partly responsible for the discord between the greenhouse experiments and model results. Second, different ecological conditions and processes can differentially influence species distributions at different scales, and consequently, there are often factors (e.g., adaptation, dispersal) that are latent, unmodeled, or poorly spatially resolved (Pearson & Dawson, 2003). For instance, as demonstrated in this study, citizen science efforts indicate that unmodeled factors could be impacting crowberry distribution and fitness within putative refugia areas at a finer spatial resolution than what was represented in the incorporated models. Third, the spatial scale at which these models are applied is of fundamental importance. The resolution of input variables and thus the resolution of model outputs can sometimes be too coarse to provide meaningful information at the level of individual management units (Chauvier et al., 2022; Seo et al., 2008). While resampling can help to address scale mismatches, it is imperative to think proactively about the spatial scale of model outputs to ensure that they reflect the scale of the management decisions that the model is intended to inform.

Despite these limitations, there are several practical strategies for using refugia model outputs in a way that can minimize uncertainty and align well with the decision context at hand. For one, managers can threshold (i.e., convert non-binary outputs from species distribution models to binary species distributions) based on whether there is greater risk in errors of commission or omission when applying refugia maps to the management question. Alternatively, managers can avoid thresholding entirely by using species distribution modeling outputs to highlight areas that are projected to experience the smallest amount of change into the future. Second, data from physiological experiments can validate species distribution models (as demonstrated in this study) and can prove invaluable for refining and complementing output from simple correlative models (Colado et al., 2022; Sánchez-Fernández et al., 2016) to better interpret where species may persist into the future.

### 4.4 | Participatory science is an efficient method to monitor refugia effectiveness

Long-term monitoring can be time-consuming and expensive (Caughlan & Oakley, 2001), which could explain why few attempts have been made to monitor the effectiveness of refugia. Participatory science can enable and enhance monitoring that would otherwise be unfeasible (McKinley et al., 2017). In addition to the example provided in this work, other national parks have also used participatory science for climate-change adaptation monitoring (Sweet et al., 2019). Our experience suggests that volunteers are excited by the relevance of monitoring in and out of refugia and motivated by the clarity of the scientific question. Our work was particularly successful because we are working with two easily identified species. Participatory monitoring also offers other benefits, such as improving attitudes about and engagement in conservation (Forrester et al., 2017; Toomey & Domroese, 2013). However, without extensive planning and training, caution is required in

situations where expertise is necessary to identify species or in habitats sensitive to human disturbance (McKinley et al., 2017).

## 5 | CONCLUSION

Climate-change refugia conservation is an attractive climate-change adaptation strategy for both managers and researchers because refugia offer hope in resisting change and can be identified relatively easily with existing statistical tools. Nonetheless, incorporating refugia modeling into management has been challenging. Here, we demonstrate how effective coproduction and completing all seven steps of the CCRCC can improve both refugia science and management at local and regional scales. More efforts to complete the CCRCC using diverse partnerships and coproduction can help inform biodiversity management under changing environmental conditions.

### AUTHOR CONTRIBUTIONS

All authors contributed to project design, implementation, and writing for this manuscript.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

### DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available at https://doi.org/10.5061/dryad.4qrfj6qqj

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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