

RESEARCH ARTICLE

Cool microrefugia accumulate and conserve biodiversity under climate change

Christopher P. Nadeau¹  | Anjelica Giacomazzo¹ | Mark C. Urban^{1,2} 

¹Ecology and Evolutionary Biology Department, University of Connecticut, Storrs, Connecticut, USA

²Center for Biological Risk, University of Connecticut, Storrs, Connecticut, USA

Correspondence

Christopher P. Nadeau, University of Connecticut, Ecology and Evolutionary Biology Department, 75 North Eagleville Road, Storrs, CT 06269, USA.
Email: c.nadeau@northeastern.edu

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Abstract

A major challenge in climate change biology is to explain why the impacts of climate change vary around the globe. Microclimates could explain some of this variation, but climate change biologists often overlook microclimates because they are difficult to map. Here, we map microclimates in a freshwater rock pool ecosystem and evaluate how accounting for microclimates alters predictions of climate change impacts on aquatic invertebrates. We demonstrate that average maximum temperature during the growing season can differ by 9.9–11.6°C among microclimates less than a meter apart and this microclimate variation might increase by 21% in the future if deeper pools warm less than shallower pools. Accounting for this microclimate variation significantly alters predictions of climate change impacts on aquatic invertebrates. Predictions that exclude microclimates predict low future occupancy (0.08–0.32) and persistence probabilities (2%–73%) for cold-adapted taxa, and therefore predict decreases in gamma richness and a substantial shift toward warm-adapted taxa in local communities (i.e., thermophilization). However, predictions incorporating microclimates suggest cool locations will remain suitable for cold-adapted taxa in the future, no change in gamma richness, and 825% less thermophilization. Our models also suggest that cool locations will become suitable for warm-adapted taxa and will therefore accumulate biodiversity in the future, which makes cool locations essential for biodiversity conservation. Simulated protection of the 10 coolest microclimates (9% of locations on the landscape) results in a 100% chance of conserving all focal taxa in the future. In contrast, protecting the 10 currently most biodiverse locations, a commonly employed conservation strategy, results in a 3% chance of conserving all focal taxa in the future. Our study suggests that we must account for microclimates if we hope to understand the future impacts of climate change and design effective conservation strategies to limit biodiversity loss.

KEYWORDS

climate change adaptation, conservation, decoupling, freshwater rock pool, microclimate, thermophilization

1 | INTRODUCTION

Forty years ago, biologists predicted that human-induced climate change would have significant effects on biodiversity around the globe (McLean, 1978; Peters & Darling, 1985; Peters & Lovejoy, 1994; Urban, 2019). Since that time, the burgeoning field of climate

change biology has documented clear fingerprints of climate change on species including range shifts and in situ adaptations (Gardner et al., 2011; Nadeau & Urban, 2019; Parmesan & Yohe, 2003; Root et al., 2003; Scheffers et al., 2016). However, these fingerprints of climate change are not occurring homogeneously around the globe, and regional differences in temperature change explain only a

small proportion of variation in climate change responses (Chen et al., 2011; De Frenne et al., 2013; Gardner et al., 2011; Primack et al., 2009; Rafferty et al., 2020). Explaining why climate change responses vary among locations could improve future predictions of climate change impacts. Moreover, explaining variation in climate change responses could help determine where species will be less affected by climate change and therefore help prioritize areas for conservation. Hence, understanding spatial variation in climate change responses is a crucial goal of climate change biology.

Microclimates could explain substantial variation in climate change responses (Lenoir et al., 2017; Nadeau et al., 2017a). Microclimates are hypothesized to ameliorate the biological impacts of climate change in two key ways. First, microclimates can act as refugia where species can persist for many generations, despite unfavorable changes in macroclimates (de Lafontaine et al., 2014; Maclean et al., 2015; Patsiou et al., 2014; Rull, 2009). Second, species that occur in landscapes with high microclimate variation might need to move just a short distance to track suitable climates (i.e., reshuffling), therefore alleviating the need for in situ adaptation or longer-distance range shifts (Loarie et al., 2009; Scheffers et al., 2013). Refugia and reshuffling among microclimates might often buffer species and communities from the effects of regional climate change and cause unexpected species responses (De Frenne et al., 2013; Lenoir et al., 2017; Maclean et al., 2015; Patsiou et al., 2014; Suggitt et al., 2018; Virkkala et al., 2020). Moreover, the potential moderating effect of microclimates could make them an efficient means of conserving biodiversity in some areas (Groves et al., 2012; Nadeau & Fuller, 2016).

Despite their potential importance, the hypothesized effects of microclimates remain relatively untested in climate change biology for several reasons. Most studies in climate change biology overlook microclimates by using climate data with a coarse spatial resolution (Bütikofer et al., 2020; Nadeau et al., 2017b; Potter et al., 2013). The few studies that incorporate microclimates often focus on the effects of topography (e.g., elevation, slope, aspect) in terrestrial ecosystems (Lenoir et al., 2017). However, significant microclimate variation might also occur in other ecosystems (e.g., aquatic ecosystems) and many non-topographic factors (e.g., water depth, canopy density) can affect microclimates. Accounting for the non-topographic factors affecting microclimates is critical because, unlike topographic effects, many non-topographic effects might be altered by climate change and therefore alter future microclimate variation (Bramer et al., 2018; Davis et al., 2019; Lenoir et al., 2017; Zellweger et al., 2019, 2020). To fully evaluate the hypothesized effects of microclimates in climate change biology, it is therefore important to characterize microclimate variation and how that variation might change in the future in a variety of ecosystems.

In addition, we still have a limited understanding of how microclimates might mitigate the effects of climate change on regional biodiversity (De Frenne et al., 2021; Lembrechts et al., 2019; Lenoir et al., 2017; Zellweger et al., 2019). Microclimates might mitigate climate change effects because they are simply colder than the macroclimate (i.e., buffering) or because they warm less than the macroclimate

(i.e., decoupling) (Davis et al., 2019; De Frenne et al., 2021; Gollan et al., 2014; Lenoir et al., 2017). Few studies have accounted for the potential of decoupling, and only one simulation study has evaluated the relative benefits of decoupling and buffering effects on biodiversity under climate change (Lenoir et al., 2017). Understanding the relative influence of buffering and decoupling is critical to identifying microclimates for conservation (Gollan et al., 2014). In addition, many non-climatic factors (e.g., light, soil, or water chemistry) can affect the suitability of microsites and therefore constrain how species use future microclimates. However, few studies account for microgeographic variation in non-climatic factors. Last, protecting and restoring cool microclimates is commonly recommended as a climate change conservation strategy. However, this strategy has rarely been evaluated, especially in relation to other common conservation strategies. These key questions remain unaddressed due to their complexity and the detailed data required to model all the factors potentially affecting microclimates (Lenoir et al., 2017). Studying a system where we can accurately model microclimates, how microclimates might change over time, and how they alter the fingerprints of climate change could provide significant insight into the role of microclimate variation in climate change biology and conservation.

Here, we evaluate microclimate variation at a sub-meter horizontal resolution in a tractable model system: the freshwater rock pool ecosystem. The simplicity of this ecosystem allows us to accurately model current and future microclimates, measure important non-climate environmental factors at microsites, and use multiple approaches to evaluate how microclimate variation could alter the impacts of climate change on the biodiversity of aquatic invertebrates. Specifically, we address four key questions to further our understanding of how microclimates affect the impacts of climate change on biodiversity:

1. How much microclimate variation in temperature currently exists among freshwater rock pools?
2. How will microclimate variation change in the future under climate change, and what is the relative importance of buffering and decoupling?
3. How does microclimate variation, buffering, and decoupling influence the effects of climate change on biodiversity?
4. How valuable are microclimates to the conservation of biodiversity relative to another commonly suggested conservation strategy?

2 | METHODS

2.1 | Study system

Freshwater rock pools are small depressions in bedrock that fill with rainwater (Brendonck et al., 2010; Jocque et al., 2010). We focus on 149 freshwater rock pools in a 1.9 ha study area between the intertidal zone and forest edge on Schoodic Point in Acadia National Park, Maine, USA (Figure 1a; Lat: 44.334, Long: -68.064). The focal

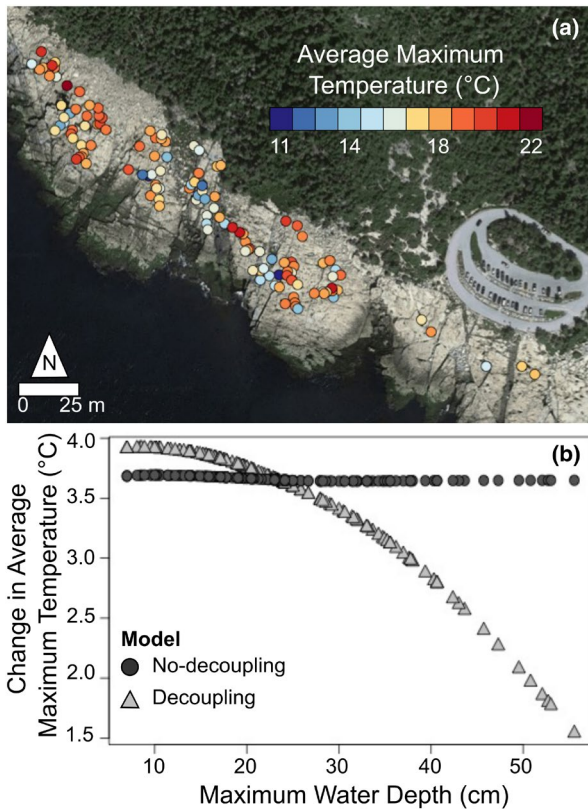


FIGURE 1 (a) The location and current water temperature of 149 freshwater rock pools on Schoodic Point, Maine, USA (Lat: 44.334, Long: -68.064) and (b) the predicted effects of climate change on the average maximum water temperature during the growing season (April–November) in each pool based on weather data from the Australian Community Climate and Earth System Simulator coupled model (Bi et al., 2013) forced with the RCP 8.5 scenario. (a) Each point represents a pool and the color represents the average daily maximum temperature during the growing season as predicted from a water-temperature model for the current period (1989–2018). (b) The change in average maximum temperature in each pool between the current and future period (2071–2100) as predicted by two water-temperature models: (1) a model where deep pools warm less than shallow pools because the effect of air temperature depends on water depth (i.e., decoupling) and (2) a model where all pools warm equally (i.e., no-decoupling) [Colour figure can be viewed at wileyonlinelibrary.com]

pools are part of a dense cluster of pools along a continuous section of coastline (Figure 1a) and unstudied rock pools occur on either side of our study area. The pools host a community of freshwater invertebrates that are active between approximately April and November (hereafter the growing season) when the pools are not frozen. Invertebrates persist through the winter in a resting stage (e.g., ephippia) or recolonize the pools in the spring.

Our focal pools range in size from 0.07 to 71.52 m² (median = 1.03 m²) and vary between 7.0 and 55.5 cm in maximum depth (median = 22.9 cm). Despite being small and shallow, most pools stay inundated throughout the growing season and temperature is often homogenous throughout the water column within a pool because coastal winds regularly mix the water. Despite the near absence of

terrestrial vegetation (Figure 1a), water temperatures in rock pools less than a meter apart can differ substantially due to differences in water depth and micro-topographic effects on solar exposure (e.g., boulders, crevices). Shallow and unshaded pools track daily air temperatures more closely and therefore experience lower daily minimum and higher daily maximum temperatures than deeper pools. However, climate change could reduce this microclimate variation in temperature if changes in air temperature, precipitation, humidity, and wind reduce water depths and cause the temperatures in deeper pools to track air temperatures more closely.

2.2 | Overall approach

To address the four questions detailed above, we compare a suite of predictions that make different assumptions about microclimate variation and how that variation responds to warming. We first develop three linked models to predict (1) water depth, (2) water temperature given water depth, and (3) species occupancy given the water temperature in each focal rock pool (Figure 2a). We develop two versions of the water-temperature model: one with and one without the potential for decoupling (Figure 2a). We use a suite of independent data to evaluate each model (Figure 2a). Second, we use the water-depth model and the two water-temperature models to predict current and future water temperature (Figure 2b), which allows us to address the degree of microclimate variation (Question 1) and how that variation might change in the future (Question 2). Third, we generate three sets of species-occupancy predictions using macroclimate temperatures and microclimate temperatures from the two water-temperature models (Figure 2b) to evaluate how microclimate variation and changes in that variation affect the biological impacts of climate change (Question 3). Last, we use the species-occupancy predictions to assess the conservation value of microclimates (Question 4).

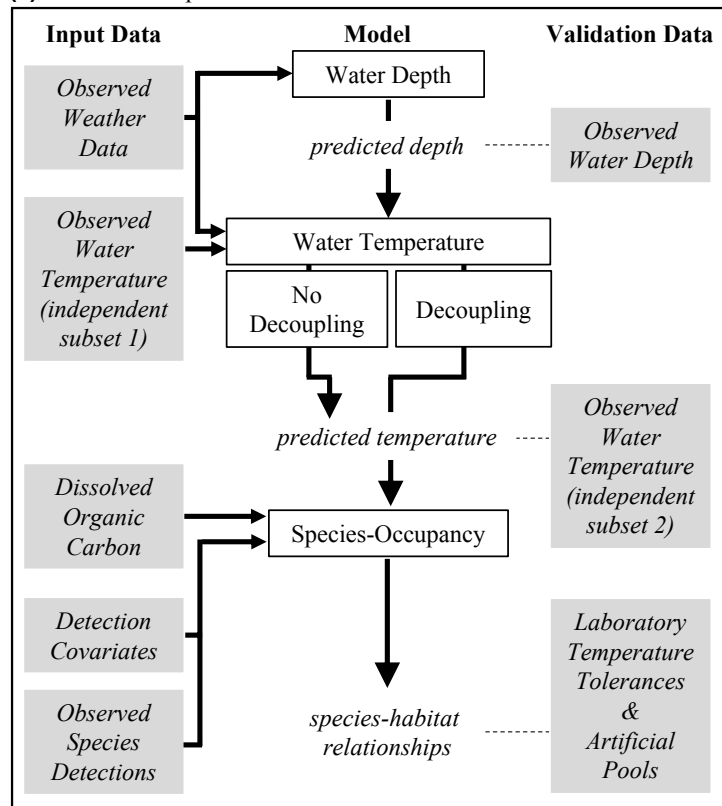
We focus on maximum temperature throughout the paper because previous studies suggest maximum temperature is a more relevant predictor of species occurrence than mean temperature in freshwater rock pools (Vanschoenwinkel et al., 2007). Moreover, we wanted to compare maximum daily water temperatures to measures of thermal tolerance for our focal taxa as a way of evaluating our species-occupancy predictions (Figure 2a, Supplemental Material S8). We note, however, that many measures of temperature are correlated and, as is often the case (Körner & Hiltbrunner, 2018), it is not clear which aspects of temperature aquatic invertebrates are sensitive to.

2.3 | Model development and evaluation

2.3.1 | Water-depth model

Water depth can be modeled accurately in freshwater rock pools with a simple water-balance model due to a lack of vegetation and groundwater influences (Tuytens et al., 2014; Vanschoenwinkel et al., 2009). Here, we modified the water-balance model described

(a) Model Development



(b) Predictions

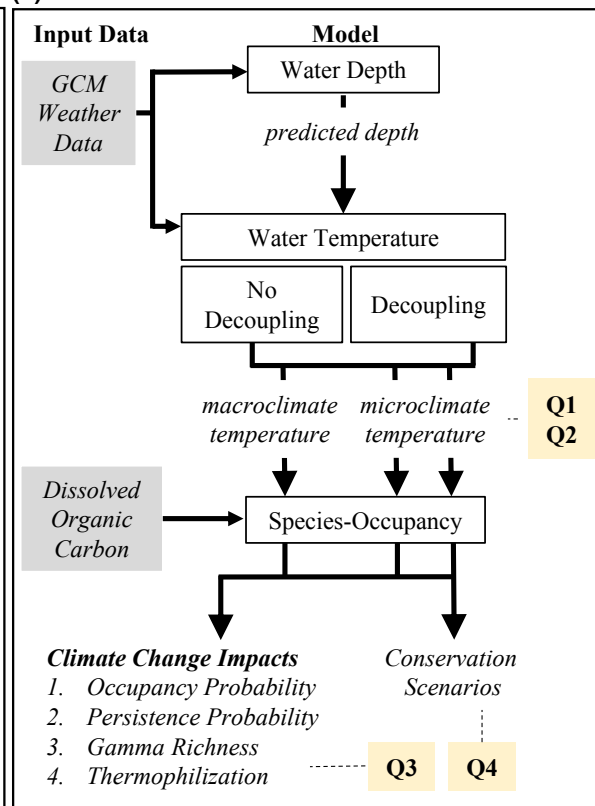


FIGURE 2 A conceptual diagram of our approach to evaluate the following: (Q1) How much microclimate variation in temperature currently exists among freshwater rock pools? (Q2) How will microclimate variation change in the future under climate change, including the importance of buffering and decoupling? (Q3) How does microclimate variation, buffering, and decoupling influence the effects of climate change on invertebrate biodiversity? (Q4) How valuable are microclimates to the conservation of biodiversity relative to another commonly suggested conservation strategy? [Colour figure can be viewed at wileyonlinelibrary.com]

by Vanschoenwinkel et al. (2009) to predict daily water depth in each rock pool (Supplemental Material S2) using daily data on average wind speed, total precipitation, minimum and maximum temperature, and minimum and maximum humidity. We evaluated the model by comparing predictions generated from weather data recorded 250 m from our study site to 1848 measurements of maximum daily water depth from water-depth data loggers (model: Onset Hobo U20L, accuracy = 40 mm) deployed in 13 pools in 2017 and 2018. We evaluate model bias using the mean error (i.e., predicted minus observed depth) and accuracy using the root-mean-squared error.

2.3.2 | Water-temperature model

We developed two water-temperature models to predict maximum daily water temperature in the 149 focal pools given predictions of water depth. In the first model (hereafter the no-decoupling model), water temperature is cooler (i.e., buffered from air temperature) in deep and shaded pools, but all pools respond similarly to warming air temperatures under climate change (i.e., no decoupling). In the second model (hereafter the decoupling model), deeper pools are less affected by warming than shallower pools (i.e., deeper pools are more decoupled from air temperature) in addition to the buffering

effects in the first model. Deeper pools might warm less for a variety of reasons. For example, deeper pools are in deeper rock crevices and are, therefore, more exposed to deep, cold bedrock that might track changing air temperatures more slowly than the surface bedrock. Making water-temperature predictions with these two plausible models allowed us to evaluate the effects of decoupling on microclimate variation (Question 2) and biodiversity (Question 3).

We used generalized additive models in the R (version 3.6.0) package “mgcv” for both models. Generalized additive models allow for nonlinear relationships between predictor variables and water temperature. For example, other studies have identified an s-shaped relationship between air and water temperature due to the effects of evaporative cooling that could be especially important under climate change (Harvey et al., 2011; Mohseni et al., 1998; Morrill et al., 2005). We chose generalized additive models because they can perform better than other correlative water-temperature models (Laanaya et al., 2017) and they produced slightly better results than another widely used model (Supplemental Material S5). Both the no-decoupling and decoupling models modeled daily maximum water temperature using the following daily covariates: predicted water depth, average air temperature, total precipitation, and solar radiation (Supplemental Material S3). In the decoupling model, we included a depth by air-temperature interaction to allow the effect

of air temperature to differ depending on water depth. We included pool as a random effect in both models to account for the correlation among measurements within a pool.

For model development, we used observed air temperature and precipitation data from a weather station located 250 m from our study site as covariates (Figure 2a). We trained the generalized additive models using 5790 measurements of maximum daily water temperature recorded using temperature data loggers (models: HOBO Pendant UA-001-08 or Onset Hobo U20L, accuracy = 0.5°C) in 35 different pools between 2017 and 2018. We evaluated the models by comparing predictions of daily maximum water temperature to 2270 measurements of water temperature for a year (2016) and from 21 pools that were not included in the training data set. Moreover, 2016 had the hottest average air temperature of the 3 years with available water-temperature data, which provides a good test of how the models might perform in the future. We evaluate model bias using the mean error (i.e., predicted minus observed) and accuracy using the root-mean-squared error.

2.3.3 | Species-occupancy model

We developed a model to predict the occupancy of freshwater invertebrates in each pool given water temperature and other non-climate covariates. We developed the model using detection/non-detection data from 107 rock pools in the study area that we sampled in May and August of 2017 using either a dip net (in pools with a surface area <8 m²) or a plankton tow. We collected two samples from six pools in May and 12 pools in August to provide survey replication in addition to the replication between months, which we used to help estimate detection probability (see below). We also recorded the presence of taxa observed in the pool, but not captured during sampling. We emptied samples from nets into a white tub and recorded all taxa present to the taxonomic levels defined in Table S1. We then preserved the samples in 70% ethanol. We identified taxa using a microscope (Leica M125, Leica Microsystems, Germany) in the lab for 48 samples, which confirmed the accuracy of our field identifications and allowed us to detect microscopic taxa that we were unable to observe in the field (Table S1). We identified larval aquatic insects following Peckarsky et al. (1990) and all other taxa following Aliberti et al. (2013). We considered a species to have been detected in a pool if we observed the species using any of the methods described above.

We used a Bayesian multi-species occupancy model to estimate the habitat associations of each taxa. Our occupancy model estimates species-habitat relationships while using replicate survey data in each pool to account for the fact that some species may be present, but undetected, during sampling (Dorazio & Royle, 2005; Royle & Dorazio, 2009). Preliminary analyses demonstrated that habitat estimates were highly uncertain for taxa detected in fewer than 10 pools. We therefore restricted our data to include only taxa we observed in at least 10 pools during sampling, resulting in a total of 13 taxa included in the model. Initially, we included the following environmental variables in the model to explain occupancy of each taxa: dissolved

organic carbon (which affects species-occupancy through many mechanisms, for example, light availability, UV light filtration, toxin uptake), conductivity (i.e., a measure of salinity), pH, average maximum temperature during the growing season, and average maximum hydroperiod (i.e., the longest period of inundation within the growing season of each year). These variables are known to affect rock pool biodiversity in many other freshwater rock pool ecosystems, including a similar rock pool metacommunity on a nearby island (Jocque et al., 2010; Simonis & Ellis, 2014). We estimated average maximum hydroperiod and temperature in each pool using the water-depth and decoupling water-temperature models, including all available weather data (2013–2018) from the weather station located near our study site as inputs. We defined the annual hydroperiod as the maximum number of consecutive days during the growing season when the water depth was >25 mm in a pool. We used average pH and conductivity measurements taken in each pool in May and August 2017. We measured dissolved organic carbon from water samples collected in August 2017 using fluorometry. We also included a variable indicating whether we processed the sample with a microscope, the net-type (dip net or plankton tow), the sample volume (i.e., the length of the sample multiplied by the area of the net), and the month of the sample (May or August) as factors affecting the detection probability of each taxon. The 95% credible interval of the coefficient for conductivity, pH, hydroperiod, net type, and sample volume overlapped zero for all taxa. We, therefore, removed these variables and refit the final model.

We fit the model using Monte Carlo Markov chain (MCMC) estimation in JAGS using the "R2jags" package in R version 3.6.0. We used normal priors with a mean equal to 0 and precision equal to 0.001 for all mean hyperparameters, and a uniform distribution between 0 and 10 for the variance hyperparameters. We ran three chains for 75,000 iterations with a burn-in period of 15,000 and saved every fiftieth draw, resulting in 3600 posterior samples. All parameters had a Gelman–Rubin statistic <1.1, suggesting the chains converged (Gelman & Hill, 2006). We evaluated the model using area under the receiver operating characteristic curve (AUC) following methods described by Zipkin et al. (2012) for AUC estimation given imperfect detection. AUC values range between 0 and 1, and models with a value above 0.7 are considered to have decent predictive ability (Zipkin et al., 2012). Applying AUC to a multi-species occupancy model provides an overall estimate of the predictive ability across all taxa and estimates for each taxon. We also used results from lab measurements of species critical thermal maximum and a field experiment in artificial rock pools to evaluate the species-habitat models (Supplemental Materials S8 and S9).

2.4 | Current and future microclimate variation

We used our coupled water-depth and water-temperature models to predict daily water depth and temperature for each rock pool in a current (1989–2018) and future (2071–2100) period (Figure 2b). We used downscaled daily climate data from the Australian Community Climate and Earth System Simulator coupled model (Bi et al., 2013)

forced with the RCP 8.5 scenario as inputs (Supplemental Material S4). Our results were quantitatively similar when we used data from other earth systems models as inputs (Supplemental Material S4). We calculated the average maximum hydroperiod and water temperature for the current and future period as the variables of interest. Although hydroperiod was not an important predictor of species occupancy, significant decreases in hydroperiod could still affect the suitability of some pools. We therefore evaluated if hydroperiod decreased substantially in the future, but found only minor changes (Supplemental Material S6). Hence, we do not discuss hydroperiod further. We compare the range of temperatures among pools to explore the degree of microclimate variation in the current period (Question 1), how that variation might change in the future given changes in temperature, wind, humidity, precipitation, and water depth (Question 2), and compare the results from the no-decoupling and decoupling models to better understand how decoupling could alter microclimate variation (Question 2; Figure 2b).

2.5 | Current and future biodiversity predictions

We evaluate how microsite differences affect the impacts of climate change on biodiversity (i.e., Questions 3 and 4) using the species-occupancy model to generate posterior predictions of occupancy probability for each taxon in the current and future periods (Figure 2b). We make three sets of occupancy predictions (Figure 2b) for the current and future periods in 107 pools with available covariate data using estimates of average maximum temperature from (1) the decoupling model, (2) the no decoupling model, and (3) with all pools set to the average temperature from the decoupling model (i.e., macroclimate predictions without any microsite variation). In all models, we assume dissolved organic carbon does not change between the current and future period. Comparing predictions from the decoupling and no-decoupling models allowed us to evaluate the importance of decoupling. Comparing predictions from the decoupling model to predictions without any microclimate variation allowed us to evaluate the importance of microclimates.

We calculated four measures of climate change impacts from each set of predictions to provide a broad understanding of the importance of microsite differences (Figure 2b): (1) future occupancy probability of cold-adapted taxa, (2) persistence probability of cold-adapted taxa, (3) future gamma richness, and (4) thermophilization. We assumed taxa were cold adapted if their occupancy probability declined with increasing temperature (i.e., 97.5% quantile of their occupancy-temperature relationship from the species-occupancy model was less than 0). We estimated persistence probability as the proportion of posterior predictions that predicted the taxon was present in at least one pool in the study area. We estimated gamma richness as the total number of taxa estimated to be present in any pool in the study area. We considered a site occupied by a taxon if the estimated occupancy probability at a site was greater than or equal to the observed prevalence of that taxon (Jiménez-Valverde & Lobo, 2007; Liu et al., 2005). We calculated thermophilization as the change in the community

temperature index (CTI) between the current and future period (Devictor et al., 2008). We calculated the CTI as the weighted mean temperature preference of each taxon in the community as follows:

$$CTI = \frac{1}{13} \sum_{s=1}^{13} \Psi_s \times \beta_{temp,s}$$

where Ψ is the occupancy probability for taxon s in the community and β_{temp} is the occupancy-temperature relationship identified from the species-occupancy model for taxon s . Positive values of CTI suggest the community is dominated by taxa with a positive occupancy-temperature relationship and vice versa. Positive values of thermophilization suggest a predicted increase in warm-adapted taxa or a loss of cold-adapted taxa in the community in the future. Thermophilization is a common measure of climate change impacts, but also a method of estimating community change that incorporates uncertainty in the estimates of occupancy probability and does not require us to convert estimates of occupancy probability to presence/absence data using a somewhat arbitrary threshold.

2.6 | Comparing biodiversity conservation strategies

We used the posterior predictions of presence/absence from the species-occupancy model that included temperature from the decoupling model as an input to simulate and compare two commonly recommended conservation strategies: (1) conserving the 10 currently most biodiverse pools and (2) conserving the 10 pools with the coolest microclimates. Conserving the most diverse locations in a landscape is a common conservation strategy worldwide, and conserving cooler microclimates is increasingly recommended as a biodiversity conservation strategy under climate change. We used the probability of conserving all 13 taxa (i.e., the proportion of MCMC iterations that predicted all 13 taxa were present in the focal pools) as the outcome to compare the two conservation strategies, which assumes the conservation objective is to maintain current biodiversity. We also evaluated median alpha richness in the current and future period to further explain the results from each conservation strategy.

3 | RESULTS

3.1 | Model evaluation

The mean error of water-depth predictions (i.e., estimated minus observed depth) was 0.1 mm (SE = 0.7 mm) and the root-mean-squared error was 31.4 mm, which is within the typical error reported by the manufacturer for the water-depth data loggers (40 mm) and much less than the depth of most pools (i.e., most pools are >240 mm deep).

The mean errors from our water-temperature models were 0.10°C for the no-decoupling model and -0.05°C for the decoupling

model, suggesting the estimates of water temperature had little bias. The root-mean-squared error was 2.4°C for both the no-decoupling and decoupling models, which are similar to the accuracy reported in other studies predicting temperature in microclimates (Kearney et al., 2020; Maclean, 2020; Maclean et al., 2017; McCullough et al., 2016; Meineri & Hylander, 2017). The errors are also small relative to the variation within and among pools (water temperature can range 19°C in a day and 30°C in a year within a pool and can also differ by as much as 15°C among pools within a day; Figure 1a) and are less than the range of uncertainty in temperature change projections among climate models (Supplemental Material S4).

The median overall AUC value for our occupancy model was 0.78, suggesting the model had acceptable predictive ability on average. Only one species, *D. magna*, had an AUC value lower than 0.7 (AUC = 0.65), suggesting the model performed well for most taxa. Lab measurements of critical thermal maximum and experiments in artificial pools further supported the accuracy of our species-habitat models (Supplemental Materials S8 and S9).

3.2 | Current and future microclimate variation

Predicted water temperatures differed substantially among pools due to differences in depth and solar exposure. In the current period, the decoupling model predicted a microclimate range of 11.6°C (i.e., the difference in temperature between the warmest and coolest pools; Figure 1a). In the future, the decoupling model predicted an average temperature increase of 3.5°C across pools. However, warming was substantially less in deeper pools (Figure 1b). The shallowest pool is predicted to warm 2.4°C more than the deepest pool in our study area (Figure 1b). This differential warming among pools due to decoupling increased the microclimate range by 21% to 14.0°C in the future period.

Without decoupling (i.e., without the effect of air temperature depending on water depth), the microclimate range was lower in both the current and future periods. The no-decoupling model predicted a microclimate range of 9.9°C in the current period, which is 15% less than the decoupling model. The no-decoupling model predicted a similar average temperature increase across pools as the decoupling model (3.7°C; Figure 1b). However, as expected, the no-decoupling model predicted similar warming among pools (Figure 1b), and therefore no change to the microclimate range. With a smaller microclimate range in the current period, and no change in the future period, the no-decoupling model predicts a 29% lower microclimate range in the future relative to the decoupling model.

3.3 | Habitat associations of focal taxa

The species-occupancy model identified two taxa with a negative occupancy-temperature relationship (amphipods [Order: *Amphipoda*] and calanoid copepods; hereafter cold-adapted taxa)

and three taxa with a positive occupancy-temperature relationship (ostracods [Order: *Podocopida*], mosquito larvae [*Aedes* sp.], non-biting midges [Family: *Chironomidae*]; hereafter warm-adapted taxa; Supplemental Material S7). Six taxa also had a negative (amphipods, water boatman [*Trichocorixa verticalis*], and *Daphnia magna*) or positive (*Ceriodaphnia dubia*, *Chydorus sphaericus*, and mosquito larvae) occupancy relationship with dissolved organic carbon (Supplemental Material S7). Therefore, dissolved organic carbon could constrain how these taxa respond to temperature changes in the future.

3.4 | Current and future biodiversity predictions

Accounting for decoupled microclimates significantly altered predictions of climate change impacts relative to predictions that used the same temperature for every pool (Figure 3). When we predicted species occupancy using decoupled water temperature, the maximum probabilities of occupancy for the two cold-adapted taxa (i.e., amphipods and calanoid copepods) were 0.97 and 0.98, respectively (Figure 3a). Both cold-adapted taxa were predicted to persist in the study area and gamma richness remained at 13 species (Figure 3b,c). However, when we excluded microclimates by making predictions using the average temperature for every pool, the maximum probabilities of occupancy were reduced by 91% and 68% to 0.08 and 0.32 for amphipods and calanoid copepods, respectively (Figure 3a). Consequently, the predicted probabilities of future persistence were reduced by 98% and 27% to 0.02 and 0.73 for amphipods and calanoid copepods, respectively (Figure 3b) and median gamma richness dropped to 12 taxa (Figure 3c). Thermophilization also increased 825% in predictions that excluded microclimates because of decreases in the occupancy probability of cold-adapted taxa and increases in the occupancy probability of warm-adapted taxa (Figure 3d).

Cool microclimates decreased the impacts of climate change through both buffering and decoupling. However, most of the effect of microclimates (i.e., the difference between the decoupling and no microclimate predictions) was due to buffering rather than decoupling. When we predicted species occupancy using temperatures from the no-decoupling model, predicted maximum occupancy for amphipods and calanoid copepods decreased by 31% and 15% to 0.67 and 0.84 relative to predictions incorporating decoupling (Figure 3a). Decoupling accounted for 34% and 23% of the overall microclimate effect on maximum occupancy probabilities for amphipods and calanoid copepods, respectively (i.e., the difference between the predicted maximum occupancy with and without decoupling was 34% and 23% of the difference between predicted maximum occupancy using decoupled microclimates and no microclimates). Not including decoupling increased thermophilization by 271% and accounted for 33% of the overall microclimate effect on thermophilization (Figure 3d). There were no differences in the persistence probabilities of either cold-adapted taxa or gamma richness between the predictions made with and without decoupling (Figure 3b,c).

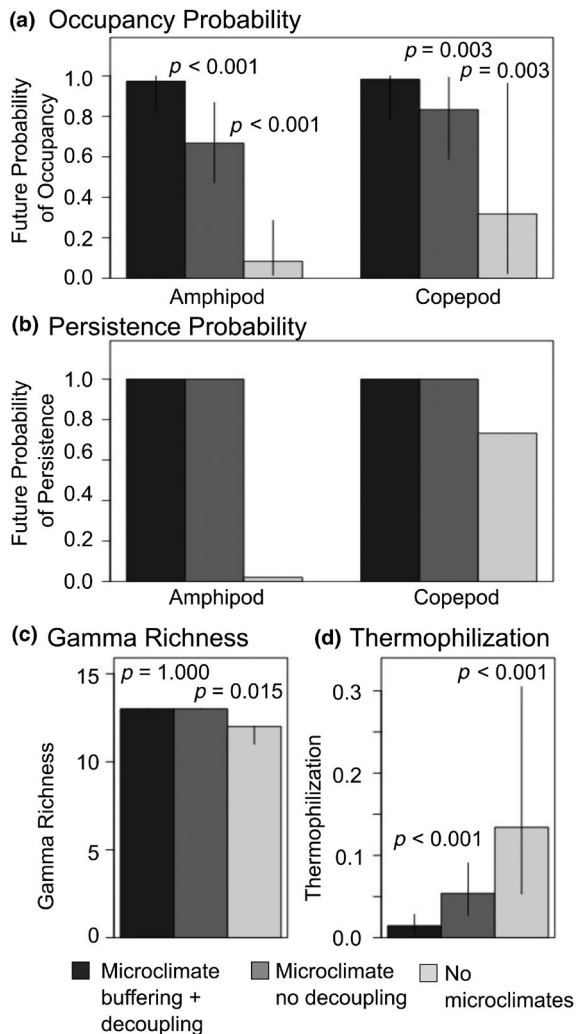


FIGURE 3 Differences in site-level impacts of climate change on biodiversity as predicted from (left bar) microclimate temperatures including decoupling (i.e., differential warming among pools), (middle bar), microclimate temperatures excluding decoupling, and (right bar) no microclimate variation (i.e., all pools set to the average temperature). We include predictions of the following climate change impacts from a multi-species occupancy model that identified occupancy–habitat relationships for 13 taxa: (a) estimates of occupancy probability for two cold-adapted taxa, (b) estimates of persistence probability based on estimated presence/absence data for two cold-adapted taxa, (c) estimates of gamma richness (maximum = 13), and (d) estimates of thermophilization (see Section 2). Bars are medians and error bars are 95% credible intervals. p -values are the proportion of posterior predictions that predicted no difference or a difference opposite of that predicted between the microclimate predictions with and without decoupling (left), and the predictions with decoupled or no microclimates (right)

3.5 | Comparing biodiversity conservation strategies

The best microclimate conservation strategy differs with and without climate change because taxa are predicted to reshuffle among the pools as climates change. Without climate change, conserving the 10 currently most biodiverse pools (often moderate-temperature

pools, Figure 4) results in a 99% probability of conserving all 13 taxa (Figure 5). However, the probability of conserving all 13 taxa decreases to only 3% under climate change (Figure 5) because moderate-temperature pools become unsuitable for cold-adapted taxa (Figure 4). In contrast, cool pools currently lack warm-adapted taxa (Figure 4) and, therefore, protecting the 10 coolest pools results in only a 33% probability of conserving all taxa without climate change (Figure 5). However, under climate change, cool pools both preserve cold-adapted taxa and gain warm-adapted taxa (Figure 4). Hence, cool pools often transition from the pools with the least taxa to the most taxa (Figure 4). Therefore, protecting the 10 coolest pools results in a 100% probability of conserving all 13 taxa under climate change (Figure 5). Note, however, that many of the coolest pools are unlikely to contain all 13 taxa because dissolved organic carbon constrains reshuffling, despite temperatures being suitable for all taxa in the future (Figure 4b). Protecting the 10 coolest pools conserves all 13 taxa because the 10 coolest pools also have a wide range of dissolved organic carbon values. The coefficient of variation for dissolved organic carbon is 1.3 for the 10 coolest pools and 1.2 across all the pools.

4 | DISCUSSION

Most studies evaluating the effect of microclimates in climate change biology focus on terrestrial landscapes that are either mountainous or forested. Our results extend these studies by demonstrating that aquatic ecosystems surrounded by little terrestrial vegetation could experience moderating effects due to microclimates. We demonstrate that aquatic microclimates just meters apart can differ by 9.9–11.6°C due to microtopographic effects. For reference, the differences in temperature that we observed over less than a meter are similar to changes in air temperature that would occur over a 150-km change in latitude or 1350-m change in elevation in our study region. The temperature differences we observed due to variation in microtopographic effects among pools are greater than many of the temperature differences observed due to factors more typically included in microclimate studies (reviewed by Dobrowski, 2011; Lenoir et al., 2017). Moreover, unlike most studies, we evaluate how this microclimate variation might change in the future due to climate change by modeling potential changes in water depth and the potential for decoupling. We predict little change in water depth in the future. However, if our decoupling model is accurate, we predict a 21% increase in the microclimate range because deeper pools will warm less than shallow pools (i.e., higher decoupling).

The microclimate variation we observed significantly altered our predictions of climate change impacts on biodiversity. Predictions excluding microclimates for our study site are consistent with typical fingerprints of climate change: low occupancy and persistence probabilities result in the predicted loss of cold-adapted taxa, and therefore a decrease in gamma richness and a shift towards warm-adapted taxa in the community (i.e., thermophilization). However, predictions

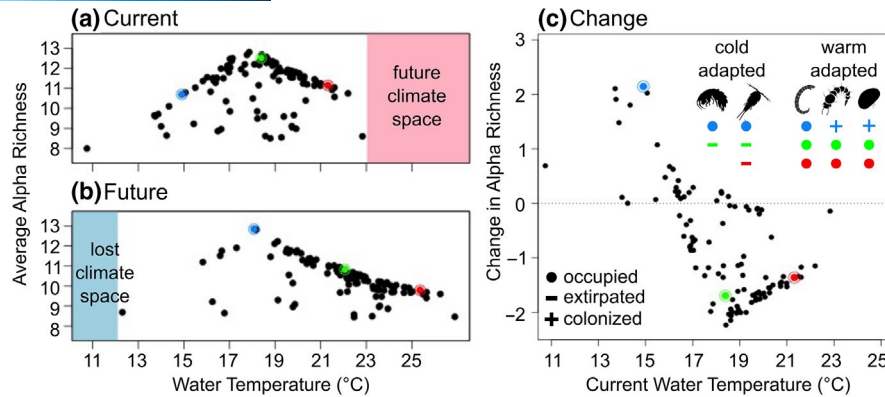


FIGURE 4 Average alpha richness in 107 freshwater rock pools with different microclimates as predicted by a multi-species occupancy model in (a) the current period (1989–2018) and (b) a future period (2071–2100). (c) The change in average alpha richness between the current and future period. In all three panels water temperature is the average daily maximum temperature throughout the growing season (April–November). Three pools are highlighted to demonstrate how average alpha richness is predicted to change in cool (blue point), moderate-temperature (green point), and warm microclimates (red point). Predicted changes in community composition are shown in the upper right of panel (c). Taxa include (from left to right): amphipod, calanoid copepod, mosquito larvae, chironomid, and ostracod. Circles represent presence in both periods, + signs represent gain of the taxon in the future, – signs represent loss of the taxon in the future, and no symbol represents absence of the taxon in both periods. The color of the symbols matches the highlighted pools in all three panels [Colour figure can be viewed at wileyonlinelibrary.com]

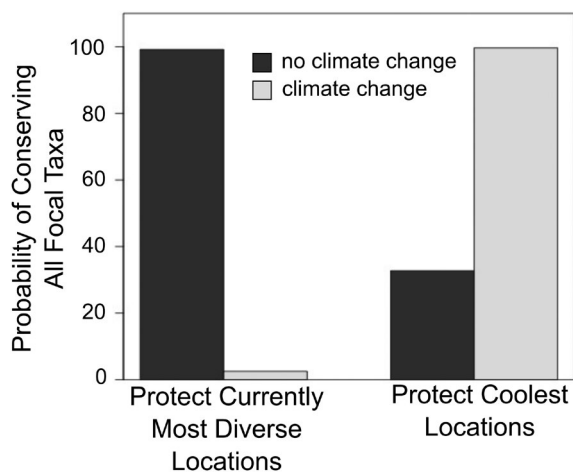


FIGURE 5 The probability of conserving all 13 taxa (i.e., the proportion of MCMC iterations where all 13 taxa were present in the focal pools) using two different conservation strategies: conserving the 10 currently most diverse pools, and conserving the 10 coolest pools. The dark gray bars are predictions assuming climates remain as they are in the current period (i.e., no climate change) and the light gray bars assume climate change

incorporating microclimates suggest cold-adapted taxa could persist in cool microclimates, and therefore all 13 taxa are likely to persist in the study area, reducing thermophilization substantially. We observed these results despite identifying only two cold-adapted and three warm-adapted taxa. Thus, in systems with more temperature-sensitive taxa, we expect microclimates to have a larger effect on climate change impacts. Indeed, a growing number of studies are demonstrating that microclimates can reduce the observed (Maclean et al., 2015; Suggitt et al., 2018; Virkkala et al., 2020) and predicted impacts of climate change (reviewed in Lembrechts et al., 2019; Lenoir et al., 2017). For instance, all studies that compared

predictions of species persistence under climate change using microclimate (<30 m resolution) and macroclimate (>1 km resolution) data have shown increased persistence in models accounting for microclimates (Lenoir et al., 2017). Community-level impacts of climate change, such as thermophilization, are also reduced in cool microclimates (De Frenne et al., 2013; Duque et al., 2015). Significant microclimate variation has been observed in many seemingly homogenous landscapes like our study area, including peat bogs (van der Molen & Wijmstra, 1994; Turlure et al., 2010), talus fields (Varner & Dearing, 2014), and grasslands (Thomas et al., 2009). Hence, the moderating effects of microclimates might be much more widespread than previously assumed. We therefore recommend extending microclimate research to an array of systems to better understand where microclimates will provide value in the future.

Freshwater rock pools in our study area are not currently a conservation concern. However, studying this tractable system allowed us to provide a detailed evaluation of the value of microclimates that would be difficult in many other systems. Our results demonstrate how reshuffling of taxa among the pools under climate change could make cool locations particularly valuable as a conservation tool. Cool microclimates are clearly valuable for conserving cold-adapted taxa. However, because we also predict cool microclimates will become suitable for warm-adapted taxa under climate change, protecting just a small number of cool microclimates also becomes an efficient means of conserving all focal taxa in our study area. Furthermore, protecting cool microclimates is a significantly better long-term strategy in our system than conserving current biodiversity hot spots, which is a commonly utilized strategy worldwide (Myers et al., 2000). Our results, therefore, suggest conserving landscapes with high microclimate variation, which should support biodiversity now and into the future.

Our results also demonstrate that non-climate microsite factors can constrain reshuffling in the future. Dissolved organic carbon limited the suitability of some cool pools in our study area in the future.

Thus, it is important to consider non-climate microsite factors when evaluating the effects of microclimates on future biodiversity. It might also be important to account for potential changes in non-climate microsite factors. We assumed dissolved organic carbon will remain the same in the future. However, changes in terrestrial runoff could alter the amount of dissolved organic carbon in some pools, which could alter our results. Without knowing how non-climate microsite factors might change in the future, conserving microsites with a diversity of climate and non-climate environments will likely be the best conservation strategy.

Despite a strong influence of decoupling on current and future microclimate variation, our results suggest that the moderating effect of microclimates for biodiversity was primarily due to buffering and not decoupling. Other studies have also demonstrated that cool locations can be both buffered and decoupled from climate change (Gollan et al., 2014; Maclean et al., 2017; McCullough et al., 2016; Pepin et al., 2011). For example, Maclean et al. (2017) demonstrated that warming between 1979 and 2014 ranged between 0.87 and 1.16°C among locations on the Lizard Peninsula in the United Kingdom, but buffered locations on cool northeast facing slopes showed the lowest rates of warming (i.e., the most decoupling). However, these studies did not evaluate the relative benefits of buffering and decoupling for biodiversity. Moreover, not all buffered locations are decoupled from climate change and some buffered locations might warm more than warmer locations (Gillingham et al., 2012; Gollan et al., 2014). Consequently, understanding the relative value of buffering and decoupling has important implications for identifying the proper type of microclimates to protect as a conservation strategy (Gollan et al., 2014). Our results are similar to the only other study we are aware of to evaluate the relative value of buffering and decoupling. Lenoir et al. (2017) also demonstrated that decoupling increased the occupancy probability of a simulated species, but only 15% of the difference between predictions using macroclimate and microclimate data were due to decoupling. Protecting microclimates that provide both buffering and decoupling effects is likely the best conservation strategy, although these sites might be rare (Gollan et al., 2014). Our results suggest that protecting locations that are buffered from climate change might be sufficient to conserve biodiversity.

Like many attempts to predict the impacts of climate change on biodiversity, our results have some important caveats. Our statistical predictions of future water temperature should be interpreted with caution because we use a correlative model to extrapolate to locally novel conditions (Lembrechts et al., 2019; Lenoir et al., 2017). A mechanistic water-temperature model that captures all the important mechanisms controlling water temperature could be better for this reason. However, we are unaware of such a model for freshwater rock pools and we currently lack the data to parameterize mechanistic water-temperature models developed for other systems. Moreover, it is unclear from our model evaluation whether the no-decoupling model or the decoupling model is a better representation of reality in our system. Water temperature in deeper pools might be decoupled from long-term air temperature changes because they are more exposed to cool bedrock that will warm more

slowly or because pools in deep, shaded, rock crevices have their own microclimate. Identifying the exact mechanism for decoupling is beyond the scope of this study. As with most microclimate studies, we need a much longer temperature time-series to fully understand potential decoupling mechanisms and their importance to biodiversity under climate change.

There are also important biological uncertainties. We trained the species-occupancy model with data from a small portion of the geographical distribution of each focal taxa, which could affect the occupancy-habitat relationships we identified. We note, however, that laboratory measures of thermal tolerances (Supplemental Material S8) and field experiments in artificial pools (Supplemental Material S9) support some of our statistical results. In addition, if species are locally adapted, local models might perform better than models trained from data throughout a species range (Peterson et al., 2019; Hällfors et al., 2016). Nevertheless, the results of our comparison between predictions including or excluding microclimates might have differed if we trained the model excluding microclimates with macroclimate data from throughout the species distribution. Hence, our results highlight the importance of microclimates, but do not provide a strong comparison of species-occupancy models trained with micro- versus macroclimate data.

In addition, we do not consider metacommunity dynamics (e.g., dispersal, species interactions) or the potential for microgeographic adaptation that could have important effects on future occupancy. If species cannot access newly suitable microsites or coexist in those sites, then cool locations might not act as microrefugia. Similarly, if species that currently occur in cool sites are locally adapted to the temperature or temperature variation in those sites, then cool sites might not remain suitable for cold-adapted species in the future. Our artificial warming experiments provide some evidence that species can coexist and that species will be able to colonize newly suitable locations (Supplemental Material S9). Moreover, high dispersal among pools (as demonstrated by the quick colonization of our artificial pools, Supplemental Material S9), and therefore high gene flow, likely prevents microgeographic adaptation to temperature differences among pools in our system (Nadeau, 2020). However, this might not be true in other systems. Incorporating metacommunity dynamics, including stochastic extirpations, dispersal, genetic diversity, local adaptation, and biotic interactions is an important next step in climate change biology (Urban et al., 2012). Accounting for these important dynamics will help identify the number and spatial configuration of microsites needed to maintain sustainable metacommunities in the future.

We also do not incorporate the potential for novel species to colonize our study site in the future. Species with a higher temperature tolerance than any species currently in the community are likely to colonize warmer rock pools in the future. New species could increase gamma richness, alpha richness in warmer microclimates, and thermophilization. However, our primary conclusions would remain the same: cold-adapted taxa that currently occur at our study site could persist in cool microclimates, which would increase gamma richness and reduce thermophilization. In addition, protecting a diversity of

microclimates is the best strategy to achieve a diversity of near- and long-term conservation goals. Cool microclimates will conserve cold-adapted species now and into the future, warmer microclimates will help warm-adapted species persist now, and the hottest microclimates could facilitate range shifts of species that currently do not occur in the area (Hannah et al., 2014). Hence, protecting a diversity of microclimates will likely maximize biodiversity, while also conserving species that occur in the study region currently.

The fingerprints of climate change are clear, but variable around the globe. Explaining this variation is an important next step in climate change biology. A number of hypotheses might explain variation in climate change responses, but few have strong support on their own. For example, species traits explain only a small amount of variation in observed range shifts and phenological responses among species, especially outside marine environments (Angert et al., 2011; Buckley & Kingsolver, 2012; MacLean & Beissinger, 2017; Sunday et al., 2015). Microclimates are emerging as another compelling hypothesis that regularly explains variation in climate change impacts. Moreover, microclimates offer a potentially cost-efficient means of conserving species under climate change by targeting a small number of important locations. Hence, it is critical to move beyond macroclimate explanations for observed climate change responses, and start to incorporate microclimates into predictions in climate change biology if we hope to gain an accurate picture of climate change impacts worldwide. Determining the optimal spatial resolution to balance the sampling and computational costs of microclimate analyses and the biological realism necessary to make accurate future predictions is a necessary next step (Bennie et al., 2014; Bütikofer et al., 2020; De Frenne et al., 2021; Nadeau et al., 2017b; Potter et al., 2013).

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available on Dryad Digital Repository at <https://doi.org/10.5061/dryad.41ns1rng5>.

ORCID

Christopher P. Nadeau  <https://orcid.org/0000-0002-3568-0793>

Mark C. Urban  <https://orcid.org/0000-0003-3962-4091>

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