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Using mechanistic insights to predict the climate-induced expansion of a key aquatic predator

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Abstract

Ameliorating the impacts of climate change on communities requires understanding the mechanisms of change and applying them to predict future responses. One way to prioritize efforts is to identify biotic multipliers, which are species that are sensitive to climate change and disproportionately alter communities. We first evaluate the mechanisms underlying the occupancy dynamics of marbled salamanders, a key predator in temporary ponds in the eastern United States We use long-term data to evaluate four mechanistic hypotheses proposed to explain occupancy patterns, including autumn flooding, overwintering predation, freezing, and winterkill from oxygen depletion. Results suggest that winterkill and fall flooding best explain marbled salamander occupancy patterns. A field introduction experiment supports the importance of winterkill via hypoxia rather than freezing in determining overwinter survival and rejects dispersal limitation as a mechanism preventing establishment. We build climate-based correlative models that describe salamander occupancy across ponds and years at two latitudinally divergent sites, a southern and middle site, with and without field-collected habitat characteristics. Correlative models with climate and habitat variation described occupancy patterns better than climate-only models for each site, but poorly predicted occupancy patterns at the site not used for model development. We next built hybrid mechanistic metapopulation occupancy models that incorporated flooding and winterkill mechanisms. Although hybrid models did not describe observed site-specific occupancy dynamics better than correlative models, they better predicted the other site's dynamics, revealing a performance trade-off between model types. Under future climate scenarios, models predict an increased occupancy of marbled salamanders, especially at the middle site, and expansion at a northern site beyond the northern range boundary. Evidence for the climate sensitivity of marbled salamanders combined with their disproportionate ecological impacts suggests that they might act as biotic multipliers of climate change in temporary ponds. More generally, we predict that top aquatic vertebrate predators will expand into temperate-boreal lakes as climate change reduces winterkill worldwide. Predaceous species with life histories sensitive to winter temperatures provide good candidates for identifying additional biotic multipliers. Building models that include biological mechanisms for key species

such as biotic multipliers could better predict broad changes in communities and design effective conservation actions.

INTRODUCTION

Climate change is already altering the distribution and abundance of species worldwide and is expected to cause even greater impacts in the future, including extinctions, as the Earth warms (Cahill et al., 2012; Chen et al., 2011; Maclean & Wilson, 2011; Parmesan, 2006; Urban, 2015). These biodiversity changes could profoundly affect ecosystems as well as humans via the many services that biodiversity provides (IPCC, 2014; Scheffers et al., 2016; Steffen et al., 2015). To prevent the most damaging effects, we need to develop accurate predictions of climate change impacts to marshal limited conservation resources to protect biodiversity (Parmesan, 2006; Rockström et al., 2009; Urban et al., 2016).

Currently, conservation relies mainly on correlative models to predict climate change impacts. Correlative models are easily built and parameterized, but can perform poorly in extrapolation and over long time horizons (Buckley et al., 2010; Kearney & Porter, 2009; Petchey et al., 2015; Urban et al., 2016; Zurell et al., 2016) because they omit key components of species' biology including their demography, life history traits, dispersal, evolution, and species interactions (Araujo & Guisan, 2006; Buckley et al., 2010; Gilman et al., 2010; Kearney & Porter, 2009; Urban et al., 2013). Incorporating biological dynamics into climate-impact projections could improve predictions by grounding outcomes in causative mechanisms rather than statistical correlations (Buckley et al., 2010; Kearney & Porter, 2009; Schurr et al., 2012; Stanton et al., 2014; Zurell et al., 2016). Yet, more complicated mechanistic models require efforts that identify the important biological mechanisms underlying responses and collect the parameters needed by these data-intensive models (Urban et al., 2016). Collecting these data constitutes a challenge, considering the sheer number of species and our general ignorance of their biology. Therefore, both correlative and mechanistic models have their strengths and weaknesses, which are, in turn, mediated by the time horizon, the data quality, and the potential gain in accuracy from incorporating more information. Furthermore, limited resources and time require careful decisions about which species to study in detail to maximize the conservation value of research (Urban et al., 2017).

The biotic multiplier approach offers one way to prioritize limited research and conservation dollars. Biotic multipliers are defined as species with both high climate sensitivity and a disproportionate effect on community and ecosystem properties that can subsequently multiply the impacts of climate change on biological systems (Urban et al., 2017; Zarnetske et al., 2012). Climate sensitivity is determined by the degree to which a species' abundance, biomass, or distribution changes in response to environmental change (Voigt et al., 2003). The ecological impact is measured as the change in ecological properties relative to the change in the focal species' abundance, as proposed for keystone species (Morin et al., 1983; Power et al., 1996). Thus, high-priority species for further study are those that increase or decrease in abundance with climate variation and disproportionately affect their ecosystem. Theory and observations suggest that higher trophic levels might often be sensitive to climate change given the higher metabolic demands and larger body sizes of many consumers (Harley, 2011; Petchey et al., 1999; Post, 2013; Post & Forchhammer, 2008; Urban et al., 2017; Vasseur & McCann, 2005; Voigt et al., 2003; Zarnetske et al., 2012). Top consumers also often disproportionately affect communities and ecosystems via strong top-down effects, particularly in aquatic habitats (Brooks & Dodson, 1965; Estes et al., 2011; Hairston et al., 1960; Morin et al., 1983; Paine, 1966; Shurin et al., 2002). Thus, aquatic predators might frequently act as biotic multipliers of climate change, warranting attention in our early efforts to predict climate impacts on communities and ecosystems.

Here, we develop predictions of the future distribution with climate change of an important predator in temporary ponds, the marbled salamander (*Ambystoma opacum*). Prior work suggests that marbled salamanders disproportionately affect communities and ecosystems (Urban, 2007, 2013; Urban & Richardson, 2015), but we do not know what mechanisms determine their occupancy patterns and if they are sensitive to climate change. We focus on the effects of climate on recruitment and overwinter survival, which previous evidence suggests are the most sensitive demographic variables for this species (Gamble et al., 2009; Herstoff & Urban, 2014; Stenhouse, 1987; Walls et al., 2013).

We evaluate four mechanisms potentially underlying marbled salamander occupancy. We hypothesize that

marbled salamander distributions are affected by: (1) predation from overwintering newts (Hurst, 2007); (2) high autumn precipitation and pond filling prior to breeding, requiring adults to lay eggs above normal water levels where inundation cannot reach them and precipitate successful hatching (Gamble et al., 2007; Walls et al., 2013); (3) low survival when ponds freeze solid (Herstoff & Urban, 2014); and (4) winterkill via hypoxia (winterkill hereafter) (Table 1). We define winterkill via hypoxia as a mortality event caused when ice seals pond water from atmospheric oxygen, and decomposition consumes most oxygen, suffocating aquatic life (Greenbank, 1945). We test each of these hypotheses using marbled salamander occupancy patterns collected over 15–16 years at two field sites. Hereafter, we use site to indicate the regional location of a set of individual ponds and refer to each local habitat as a pond. Second, we use a manipulative experiment to evaluate the best supported hypothesis of winterkill by introducing marbled salamanders into ponds with low overwinter oxygen and measuring overwinter survival. Third, we evaluate the performance of three predictive models that fall along a gradient of increasing mechanistic sophistication to understand if incorporating important mechanisms into modeling efforts can improve predictions. Fourth, we use the best performing model to project marbled salamander occupancy under future climates.

MATERIALS AND METHODS

Natural history

Previous research has suggested that marbled salamander larvae are an important predator in northeastern United States temporary ponds, due to both their abundance and strong impacts on communities and ecosystems (Stenhouse, 1985; Stenhouse et al., 1983; Urban, 2007). Unlike most amphibians, marbled salamanders breed in early autumn in the dry basins of temporary ponds. Once

TABLE 1 Summary of predictions, standardized estimates for coefficients with 95% credible intervals, and best overall model for climate-only and climate–habitat models for the southern and middle sites.

Hypothesis and predicted coefficients	Southern site				Middle site			
	Coefficients for each hypothesis	Individual hypothesis ΔLOOIC[a]	Coefficients for best climate-only model	Coefficients for best climate–habitat model	Coefficients for each hypothesis	Hypothesis ΔLOOIC[a]	Coefficients for best climate-only model	Coefficients for best climate–habitat model
Best model ΔLOOIC		−29.3		−68.4			−4.0	−75.6
1. Winter predation		+0.7				+2.2		
−Newt density	−0.25 (−0.63, 0.10)				**+0.50 (0.01, 1.28)**			
2. Pond filling		−8.3				−1.0		
−SO rainfall								
+Rainfall²								
−SO well height	**−0.59 (−0.96, −0.23)**				**−0.49 (−0.92, −0.10)**		**−0.34 (−0.74, 10.03)**	**−0.66 (−1.36, −0.07)**
+Well height²								
3. Freezing		−5.2				−13.9		
+Water temperature	**−1.13 (−2.14, −0.28)**				**+1.04 (0.57, 1.56)**			**+1.22 (0.37, 2.34)**
−Water <0°C	**−1.11 (−1.81, −0.25)**			**−1.31 (−2.26, −0.64)**				
−Air <0°C	**−0.46 (−0.86, −0.07)**							
−Ice depth	**−0.53 (−0.99, −0.11)**							
4. Winterkill		−56.9				−64.7		
+Dissolved oxygen	**+0.66 (0.03, 1.32)**			**+1.46 (0.51, 2.77)**				
− Ice depth	**+0.58 (0.06, 1.17)**				**+0.96 (0.38, 2.12)**			+0.73 (−0.49, 2.21)
+Open water	**+1.48 (0.77, 2.30)**			**+2.02 (0.96, 3.53)**	**+5.41 (2.45, 9.55)**			**+3.87 (1.80, 6.52)**
+Snow	**+1.16 (0.58, 1.80)**		**+0.61 (0.17, 1.08)**	**+1.32 (0.65, 2.14)**				
+Snow²								
−Air <0°C	**−1.65 (−2.53, −0.91)**		**−0.78 (−1.38, −0.28)**	**−1.90 (−3.07, −1.03)**				
+Snow × cold air	**−1.06 (−1.81, −0.40)**		**−0.58 (−1.11, −0.08)**	**−1.25 (−2.19, −0.48)**				
+Ice × open water					**+3.62 (0.75, 7.75)**			**+3.31 (0.73, 6.24)**

Note: Bold indicates credible intervals that do not overlap with zero.

Abbreviation: SO, September–October.

[a]LOOIC of best model (southern = 244.5; middle = 217.9) minus intercept-only model LOOIC (southern = 312.9; middle = 296.5). More negative numbers indicate a better model.

temporary ponds refill in late autumn, the developing embryos hatch and aquatic larvae overwinter under ice in the northern parts of its range (Petranka, 1998). By breeding early and growing under ice cover, marbled salamander larvae reach sizes large enough to become one of the few early-season predators of the larvae of spring-breeding taxa. Other important predators in study ponds include *Dytiscus* diving beetle larvae, *Aeshna* dragonfly larvae, *Belostoma* water bugs, and red-spotted newt adults (*Notophthalmus viridescens*) (Urban, 2007). Newt adults are also present in ponds in early spring, but their gape size does not increase as fast as marbled salamanders, which prevents them from preying on prey species that grow rapidly (Urban, 2007, 2008). Observations suggest that higher-order predator species such as herons or water snakes are rare in this system and seldom prey on chemically defended marbled salamanders. Thus, marbled salamanders are key predators in this system, in terms of abundance, commonness, and impact.

Given the marbled salamander's need to overwinter under ice cover in temporary ponds, they are likely to be highly sensitive to winter conditions. Previous research has demonstrated that marbled salamanders had higher survival in ponds with warmer water, but the mechanism underlying this relationship could not be determined (Herstoff & Urban, 2014). Alternatively, winter predation or autumn precipitation might also affect recruitment and survival (Gamble et al., 2009; Herstoff & Urban, 2014).

Study sites

We studied three metapopulations found ~80 km apart along a latitudinal gradient from coastal Connecticut to southern New Hampshire, USA. Specifically, these metapopulations occur at a coastal site in Northford, Connecticut; a middle site in Union, Connecticut; and a northern site in Chesterfield, New Hampshire, which is situated ~10 km beyond the northernmost boundary of the marbled salamander's range (see Figure 1; Appendix S1: Table S1). Hereafter, we refer to these sites as the southern, middle, and northern sites. Since 2002 we have surveyed marbled salamander populations in 12–14 temporary ponds at each of the two southern sites and confirmed that no marbled salamanders occupy the northern site. Each site encompasses a 2 km^2 area of mixed deciduous forest at similar elevations (180–280 m). At the southern site, marbled salamanders occur on average in 79% of ponds at a density of 0.61 larvae per m^2. At the middle site, marbled salamanders occur on average in 38% of ponds at a density of 0.17 larvae per m^2. Marbled salamanders do not occur at the northern site.

Future climates

Annual temperatures have risen 1.7°C since 1895 in the northeastern USA, with the largest increases in winter (NOAA, 2023; Seth et al., 2019). Average temperatures are expected to rise another 3–4°C or 5–6°C by 2100 for the SSP2–4.5 and SSP5–8.5 scenarios, respectively, with greater increases expected in winter (Masson-Delmotte et al., 2021). In addition to temperature changes, the Northeast has experienced a 10%–20% increase in overall precipitation, with most of the increase happening in the autumn (NOAA, 2023; Seth et al., 2019). Precipitation is expected to increase another 5%–15%, depending on the model and scenario (Masson-Delmotte et al., 2021).

Data collection

To parameterize models, we collected data on marbled salamander occupancy, pond characteristics, and climate at each of our sites. We performed annual area-standardized dip net surveys for 15–16 years, depending on the site (see Appendix S1: Table S2 for details) to estimate marbled salamander occupancy (presence or absence). We focused on occupancy rather than density because densities can fluctuate daily depending on precipitation and drying. Usually, we perform two surveys each year. The first survey corresponds to just after the ice-off and the subsequent breeding of spring amphibians, which happens from mid-March to late April depending on the weather. The second survey corresponds to the hatching of spring-breeding amphibians, generally 5 weeks after the first survey. During each survey, we used 22 × 28 cm dip nets to make 0.8-m long sweeps of every 2 m^2 of wetland area, such that we took more samples in larger ponds (Skelly & Richardson, 2009; Urban, 2007). We recorded the number of dipnet sweeps in each survey to estimate the sampling effort. We also used these surveys to estimate the density of the marbled salamanders' only overwintering predator, red-spotted newt (*N. viridescens*) adults.

We deployed HOBO Pendant loggers (Onset, Bourne, MA) to record hourly temperature on pond bottoms at maximum depth from December until April. From these data, we calculated the number of days with temperatures <0°C. In midwinter (late January–early February), we augured through the ice at each pond's maximum depth and recorded ice depth. We then used a Hydrolab MS5 multiparameter sonde (OTT Hydromet, Loveland, CO) to sample dissolved oxygen at the center of the water column. We also recorded if ponds had open water anywhere in the pond, usually where springs or streams entered the pond. Even on the coldest days, some ponds still retain open water produced by warmer, spring-fed water.
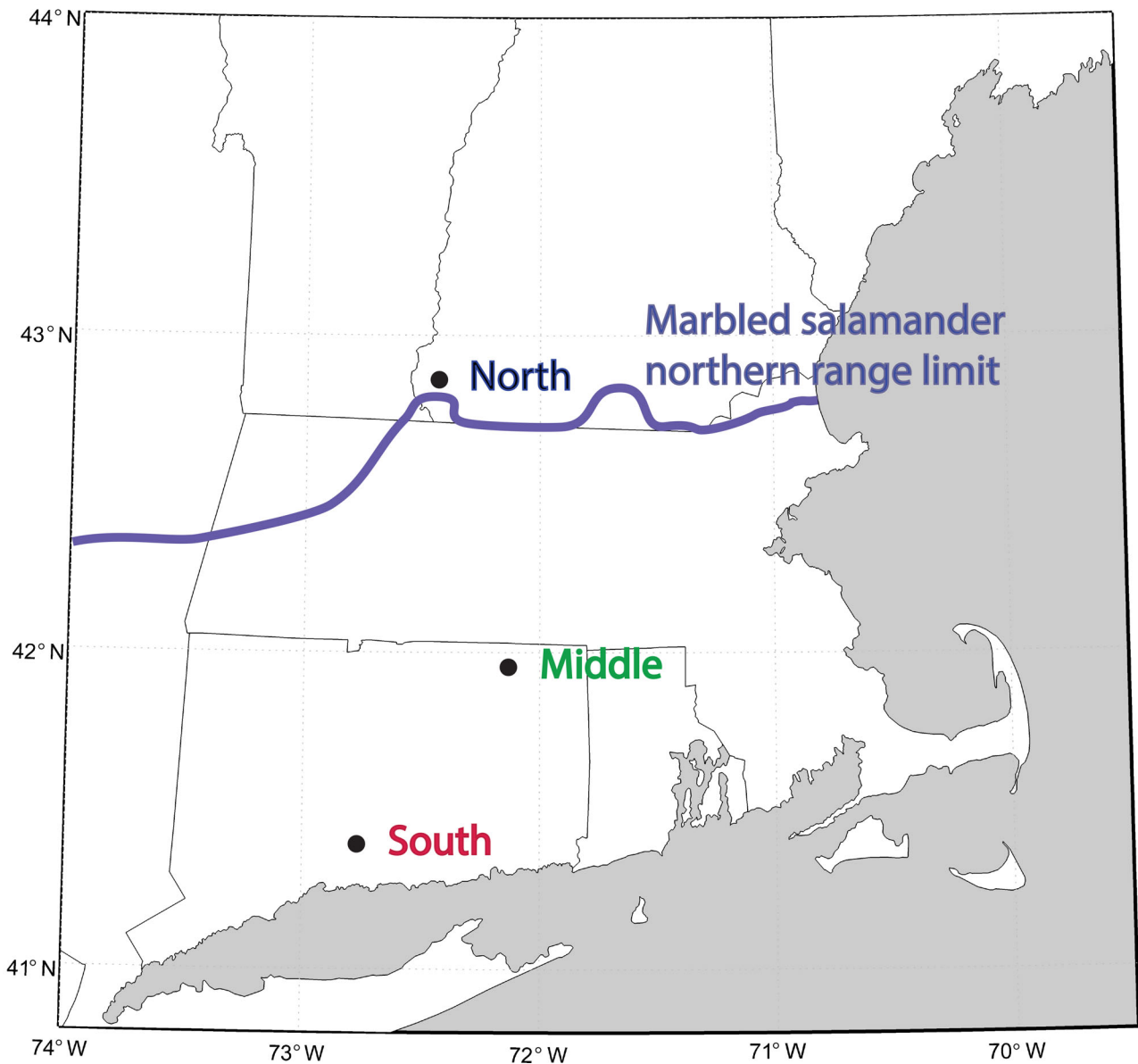
FIGURE 1 We studied 12–14 temporary ponds at each of three sites along a latitudinal gradient separated by ~80 km: South (Northford, CT, USA), Middle (Union, CT, USA), and North (Chesterfield, NH, USA). The current northern range limit of marbled salamanders in New England occurs just south of the northern study site.

We collected information on autumn (September–October) precipitation during marbled salamander breeding (Petranka, 1998), cumulative days below freezing to measure cumulative ice cover for both the freezing and winterkill hypotheses, and annual snowfall, which can maintain ice by insulating it (Vavrus et al., 1996) (Appendix S1: Table S2) (Urban et al., 2023). For the southern site, we obtained climate data from the Meriden, CT weather station 14 km northwest of the site. Because this weather station did not record snowfall, we used data from the closest weather station with snowfall (Sikorsky Airport, Bridgeport, CT; 38 km west of the site). For the middle site,

we obtained climate data from Storrs, CT, 17 km southwest of the site and used data from Staffordville, CT (12 km west of the site) to fill a few data gaps ($n = 8$, <0.5%). Predicting ice cover in one of the more mechanistic models also required climate variables unavailable from local weather stations (see Appendix S1: Table S2). We thus extracted site-specific weather data from the 1970 to 2020 NCEP North American Regional Re-analysis (Mesinger et al., 2006; NCEP, 2022). We downloaded shallow well depth data from two USGS continuously monitored well gauging stations in Marlborough, CT and Mansfield, CT near the southern and middle sites, respectively.

General modeling approach

Across all approaches, we applied Bayesian occupancy models (MacKenzie, 2006), which include linked submodels for observation and occupancy processes and then used approximate Bayesian leave-one-out cross-validation (hereafter LOOIC) for model selection (Vehtari et al., 2017). We independently developed models for each site to allow for spatial cross-validation and comparison in later stages. We first chose the best-fitting observation model for each site, excluding environmental factors, and used each of these site-specific observation models for subsequent analyses. We expected higher detection probability with greater sampling effort (net sweeps), smaller pond area, and early-season samples when metamorphosis had not yet occurred. At the southern site, the best observation model included sampling effort and indicated that at the median sampling intensity of 75 dip nets, the probability of detecting marbled salamanders reached 96% (Appendix S1: Figure S1). At the middle site, detection probabilities decreased with pond size (Appendix S1: Figure S2). At a median pond size of 585 m^2, the detection probability reached 85%.

We fit all models using the R2Jags package in R (version 3.6.2) with weakly informative priors for coefficients (mean = 0, variance = 100) and variances (gamma [0.001, 0.001]). All data were centered and standardized before using them in models. Generally, we ran three chains for 4.5e+5 samples with a burn-in of 4e+5 and a thinning rate of 10. We assessed interchain convergence using the Gelman–Rubin diagnostic and increased burn-in time if models did not converge. In a few cases, we increased burn-in times to 5.5e+5 to reach convergence. We were missing a few data points for well depth (1 year for the middle site), ice depth (1 year for the southern site), pond- and year-specific newt density (8% of surveys missing for the middle site). We estimated these few missing data points by specifying weakly informed priors (mean = 0, variance = 100) on the covariates using standard Bayesian methods (Fouley, 2013). We did not directly model year or pond effects because models with these random effects failed to converge.

Identifying the mechanisms of climate sensitivity

After selecting the best-fitting observation models, we evaluated each hypothesized mechanism explaining the relationship between climate and overwintering survival as outlined in Table 1: (1) overwintering predation; (2) pond filling; (3) pond freezing; and (4) winterkill. The overwintering-predation hypothesis predicts that higher newt densities will be associated with lower marbled

salamander occupancy. The pond-filling hypothesis predicts that higher rainfall and well height will be associated with lower occupancy by preventing recruitment. We also included a polynomial term in this analysis that, if positive, would indicate lower occupancy in drought years because of low water levels. The pond-freezing hypothesis predicts that colder water temperatures (measured as mean winter temperatures and days less than 0°C), thicker observed ice, and colder air temperatures (days less than 0°C) would be associated with lower occupancy because ponds freeze to the bottom and kill salamanders. The winterkill via hypoxia hypothesis predicts that thicker ice, less dissolved oxygen, less observed open water, and colder air temperatures would be associated with lower occupancy due to lethally low oxygen levels. We also expected that snow would affect survival through a hump-shaped relationship, estimated via linear and quadratic terms, whereby low snow levels promote thicker ice formation, intermediate snow levels insulate ice and reduce its potential depth, and high snow levels insulate ice but prolong its melting (Vavrus et al., 1996). We note that some variables inevitably overlap between the two ice-based hypotheses, but we evaluate the model performances separately and, in addition, use the results of the introduction experiment (see *Field experimental manipulative test of mechanisms*) to discriminate between them. We find the best model for each hypothesis using minimum LOOIC and compare models to a null intercept-only model to evaluate if they explain more variation than the model without environmental variables.

Field experimental manipulative test of mechanisms

We directly tested the winterkill hypothesis by introducing marbled salamanders into ponds without persistent natural populations. We then measured overwinter pond characteristics and salamander survival to evaluate alternative explanations for their absence in these ponds. We identified three ponds where marbled salamanders were historically absent or at low densities (hereafter low-density ponds) and three ponds with high densities of marbled salamanders (hereafter high-density ponds) to act as controls. We added marbled salamander larvae from neighboring ponds to each low-occupancy pond to reach a target regional fall density of 2 larvae per m^2. The final introduced autumn densities were 2.1 ± 0.5 (SD) larvae per m^2, which were not significantly different from the densities in high-occupancy, control ponds ($F_{1,4} = 0.43$; $p = 0.548$).

We sampled ponds after the autumn introduction and again in early spring and measured larval densities using

the methods described in "Survey data." We measured survival as the proportional change in density between autumn and spring. In one case, we set a survival estimate greater than 100% to 100%. We used a binomial generalized linear model and did not detect overdispersion. We also collected information on winter mean temperature and minimum water temperature from HOBO temperature loggers on pond bottoms and dissolved oxygen levels (mg/L) taken during midwinter (6 February 2013) immediately after drilling through the ice at the site of maximum depth. If introduced salamanders survived well in low-density introduction ponds, then their absence in these ponds might be explained by dispersal limitation, habitat choice, or an unknown mechanism. If survival was affected directly by ice formation (freezing hypothesis), then we would expect low survival in ponds that froze to the bottom as indicated by $<0°C$ bottom temperature recordings. If survival was affected by winterkill via hypoxia, then we expect low survival in ponds with low oxygen levels. We observed substantial differences in ice thickness and coverage among ponds within the same region due to differences in pond area, depth, and groundwater inflow.

Evaluating the performance of correlative and mechanistic models

After identifying the mechanisms affecting occupancy using the methods above, we evaluated the performance of three types of predictive models. In all cases, we modeled detection probability and chose the best suite of variables affecting occupancy using LOOIC, as described above. First, we assessed correlative, climate-only occupancy models that relied solely on easily accessible weather data (Appendix S1: Table S2) as is commonly done in climate-impact assessments. Second, we assessed climate–habitat occupancy models, including the same climate variables as above, but also long-term observations of habitat characteristics highlighted by the hydrological and winterkill hypotheses. Third, we developed and assessed a hybrid mechanistic model using a dynamic, metapopulation occupancy model which incorporated outputs from a physical lake ice model. All models incorporate stochasticity from parameter estimates obtained from Bayesian models and from stochastic runs of general circulation models during projections.

For the hybrid mechanistic model, we parameterized a dynamic metapopulation site-occupancy model (Kéry & Schaub, 2011; MacKenzie, 2006), which iterated marbled salamander occupancies in the spring for each pond at annual time steps. Each year, an empty habitat can be colonized as a function of well height to reflect its effects on autumn recruitment and maximum ice duration for its effects on overwinter survival. If a pond is colonized in the fall, but salamanders fail to survive the winter, we consider a pond

unoccupied. Each year, an occupied pond can become extirpated, also as a function of well height and winter ice duration. We initially explored separate functions for each of these variables for colonization and extirpation, but lacking model support, we simplified the model to assume the same relationships for both colonization and extirpation.

We also initially included adult immigration as the sum of the predicted number of immigrants from each occupied pond to a focal pond, subject to an exponential decay function. We explored two exponential decay functions that reflected the dispersal kernel estimated by Gamble et al. (2007) and a less restricted one (exponents = 0.007, 0.010, respectively). Including either dispersal submodel did not improve the model, and therefore we excluded it from future models.

To model ice duration, we developed three parameterized models of lake ice thickness that varied in complexity and mechanistic details: a degree-day model, freeze–thaw model, and a fully mechanistic ice model called FLake (Kirillin et al., 2011). We applied Approximate Bayesian Computation (Sunnåker et al., 2013) in the R package *abc* (Csilléry et al., 2012) to estimate unknown parameters in the ice models by using a dataset of ice cover based on photos from automatic field cameras and in-person observations for validation parameters (Appendix S1: Figure S3). See Appendix S1: Section S2 for more detailed information on these models and their parameterization. We tested how well these parameterized ice models could predict marbled salamander occupancy and determined that the FLake ice model performed best (Appendix S1: Section S2), and thus we used this model to predict winter maximum ice duration for the hybrid mechanistic model. Correlative and semimechanistic codes are available here: Urban et al. (2023).

We compared models based on four criteria: (1) *internal description*: the ability to predict current observations accurately; (2) *transferability*: the ability to predict out-of-sample data that are distant in time or space; (3) *parsimony*: only as complex as needed to satisfy (2); and (4) *realism*: models should be based on the first principles of natural history and biology when possible (Urban, 2019). We assessed model performance on the training data for each site, which we refer to as internal description, and the ability to predict occupancy patterns at the alternative site, which we refer to as transferability. To assess internal description, we use the difference in LOOIC values from the model of interest and the intercept-only model from each site, such that more negative values indicate a better description of held-out data. We used the area under the curve (AUC) calculated from predicted presences and root mean squared error (RMSE) calculated from estimated occupancy probabilities to assess internal description and transferability. The AUC measures how well model predictions classify two groups, without assuming a specific threshold, and thus

assays discrimination ability but not necessarily accuracy. The RMSE, conversely, directly measures how accurately predictions match observations. We counted the number of estimated parameters to assess parsimony.

Future projections

We evaluated climate projections from two scenarios: SSP2-4.5, a mid-level projection with an average global warming peak of 2.7°C, and the worst-case SSP5-8.5, which projects an average warming of 5.0°C. We do not endorse a given trajectory of worldwide emissions, but rather provide a range of estimates based on these possibilities. We selected three general circulation models that reliably represented historical North American temperature and precipitation patterns (Agel & Barlow, 2020; Almazroui et al., 2021): GFDL-CM4, BCC-CSM2-MR, and CESM2-WACCM from the CMIP6 database (Danabasoglu, 2019; Guo et al., 2018; Wu et al., 2018; Xin et al., 2019), while also demonstrating climate sensitivities (Zelinka et al., 2020) within the range of greatest confidence (2.3–4.7 K) (Sherwood et al., 2020). We downscaled climate model data to the NCEP NARR dataset (NCEP, 2022) using the *qmap* package for postprocessing climate model output.

We also developed a model for local well depth based on past and future precipitation patterns. We used a moving window approach, iteratively assessing how the cumulative precipitation starting from the beginning of the year until the end of October described observed September–October well heights for the period of record using a simple regression and R^2 as our optimization parameter. The best models aggregated precipitation data from 21 July (southern) and 1 June (middle).

We created projections for each of the three general circulation models and then averaged results to create an ensemble prediction. We also created a secondary ensemble of the predictions generated by both the southern and middle models to project marbled salamander colonization and occupancy at the northern site, which currently lies beyond the species' northern range boundary. Thus, we assumed that models from the two sites were equally likely to predict the northern site.

RESULTS

Identifying the mechanisms of climate sensitivity

Southern site

The model for the winterkill hypothesis garnered the most support (Table 1; ΔLOOIC = −56.9 = intercept-only

model minus test model, where negative values indicate greater model support), which included strong effects of higher dissolved oxygen (β_{DO} = +0.66, 95% CI: 0.03, 1.32), more open water (β_{open} = +1.48, 95% CI: 0.77, 2.30), colder air temperatures (β_{air} = −1.65, 95% CI: −2.53, −0.91), more snowfall (β_{snow} = +1.16, 95% CI: 0.58, 1.80), and a negative interaction between cold air temperature and snowfall (β_{int} = −1.06, 95% CI: −1.81, −0.40). Contrary to predicted effects, deeper ice was associated with higher occupancy (β_{ice} = +0.58, 95% CI: 0.06, 1.17). Note that all data were centered and standardized such that β-values can be compared in effect size. The pond-freezing hypothesis had moderate support (ΔLOOIC = −5.2), and included negative effects of observed zero-degree water days and ice depth in ponds ($\beta_{waterDD}$ = −1.11, 95% CI: −1.99, −0.33; β_{ice} = −0.53, 95% CI: −0.99, −0.11) and zero-degree days of air temperature (β_{airDD} = −0.46, 95% CI: −0.86, −0.07). Contrary to predictions, higher mean water temperature was associated with lower occupancy ($\beta_{mnwater}$ = −1.13, 95% CI: −2.14, −0.28). We found similar support for the pond-filling hypothesis (ΔLOOIC = −8.3), which included a negative effect of well height (β_{well} = −0.59, 95% CI: −0.96, −0.23). We did not find support for the prediction that higher densities of predaceous newts decreased marbled salamander occupancy (i.e., the overwintering-predation hypothesis, ΔLOOIC = 0.7), which was also indicated by its 95% CIs overlapping zero (β_{newt} = −0.25, 95% CI: −0.63, 0.10).

Middle site

We found support for the same hypotheses at the middle site as at the southern site (Table 1). Winterkill via hypoxia was again the most supported hypothesis (LOOIC = −64.7), including a positive effect of open water (β_{open} = +5.41, 95% CI: 2.45, 9.55), an unexpected positive effect of ice depth (β_{ice} = +0.96, 95% CI: 0.38, 2.12), and a positive interaction between these two factors (β_{int} = +3.62, 95% CI: 0.75, 7.75). Data also supported the pond-freezing hypothesis (ΔLOOIC = −13.9), where ponds with warmer mean winter water temperatures supported higher occupancies ($\beta_{watertemp}$ = +1.04, 95% CI: 0.57, 1.56). We found moderate support (ΔLOOIC = −1.0) that high water levels during the fall breeding season decreased occupancy at this site (i.e., the pond-filling hypothesis; β_{well} = −0.49, 95% CI: −0.92, −0.10). Although the credible interval did not overlap zero for the model with newt density (β_{newt} = +0.50, 95% CI: 0.01, 1.28), the response was opposite in the direction expected if predation lowers survival, and the model was not supported by the ΔLOOIC (+2.2). Hence, we found no support for the overwintering-predation hypothesis.

Field experimental test of mechanisms

Despite adding enough marbled salamanders to three low-occupancy ponds to match regional densities, few survived the winter. The average overwintering survival in low-density introduction ponds was 0.004%, compared with 68% in high-density control ponds (Figure 2; $\chi^2 = 1559$, $p < 0.001$). The average temperature during the winter of the experiment was close to long-term averages ($-0.1°C$), and the site occupancy of marbled salamanders in unmanipulated ponds was high that year (0.79). This result suggests that pond-specific conditions, rather than dispersal, limit marbled salamanders.

We assessed if high-density and low-density introduction ponds differed in midwinter mean water temperature, minimum winter temperature, pH, or dissolved oxygen. The only characteristic that differed significantly between these two types of ponds was dissolved oxygen ($F_{1,4} = 7.8$, $p = 0.049$). Low-density ponds had dissolved oxygen levels

2.9 mg/L lower than high-density ponds. Also, minimum bottom water temperatures were somewhat higher in low-density ponds relative to high-density ponds, contrary to expectations that ice depth or chronic cold determined survival. These results support the hypothesis that winterkill linked to hypoxia limits the occupancy of marbled salamanders at study sites.

Evaluating the performance of correlative and mechanistic models

Best climate-only models

Southern site
The best climate-only model included positive effects of snowfall (Table 1; $\beta_{snow} = +0.61$, 95% CI: 0.17, 1.08), negative effects of air temperature ($\beta_{airDD} = -0.78$, 95% CI: -1.38, -0.28), and negative interaction between snowfall and air temperature ($\beta_{int} = -0.58$, 95% CI: -1.11, -0.08). This model was characterized by a lower ΔLOOIC (-29.3), but unimpressive AUC = 0.66 and RMSE = 0.43 (Table 2). This poor performance was not just because it ignored spatial habitat variation: the model only explained 14% of temporal variation.

Middle site
The best climate-only model only included a negative effect of well height ($\beta_{well} = -0.34$, 95% CI: -0.74, -0.03) on occupancy. This model performed marginally better at describing occupancy patterns than an intercept-only model (ΔLOOIC = -4.0) and was characterized by internal description (AUC = 0.59; RMSE = 0.49) not much better than a random or invariant model.

Transferability
Predictions generated by the southern model for middle site occupancy demonstrated even poorer performance than observed for describing local patterns

FIGURE 2 Marbled salamander survival when introduced into low-density ponds characterized by limited midwinter dissolved oxygen is low compared with natural survival in high-density ponds. Error bars indicate SEM.

TABLE 2 Summary of model performance.

Model	Site	No. parameters	Internal description (AUC/RMSE)	Internal cross-validation (ΔLOOIC)	External validation (AUC/RMSE)
Correlative climate-only	Southern	**3**	0.66/0.43	-29.3	0.56/0.67
Correlative climate + habitat	Southern	7	**0.87/0.35**	**-68.4**	0.75/0.56
Hybrid mechanistic	Southern	4	0.80/0.38	-61.5	**0.77/0.48**
Correlative climate-only	Middle	**2**	0.59/0.49	-4.0	**0.69**/0.52
Correlative climate + habitat	Middle	6	**0.88/0.39**	**-75.6**	0.61/0.66
Hybrid mechanistic	Middle	3	0.84/0.42	-35.3	**0.69/0.44**

Note: Best site-specific performance indicated by bold text.
Abbreviations: AUC, area under the curve; LOOIC, Bayesian leave-one-out cross-validation; RMSE, root mean squared error.

(AUC = 0.56; RSEM = 0.67; Table 2; Appendix S1: Figure S4). Predictions generated by the middle model for southern site occupancy performed similarly to its internal descriptive performance with a higher AUC (0.69), but worse RMSE (0.52) (Appendix S1: Figure S5).

Best climate–habitat models

Overall, integrated climate–habitat models described observed data better than the climate-only model and better than any model of an individual mechanism (Tables 1 and 2).

Southern site

The best climate–habitat model included the negative effects of colder temperatures (β_{air} = −1.90, 95% CI: −3.07, −1.03) and positive effects of snow (β_{snow} = +1.32, 95% CI: 0.65, 2.14) as well as a negative interaction between these two factors (β_{int} = −1.25, 95% CI: −2.19,

−0.48). High-occupancy ponds had higher dissolved oxygen (β_{DO} = +1.46, 95% CI: 0.51, 2.77), more open water (β_{open} = +2.02, 95% CI: 0.96, 3.53), and warmer water temperatures ($\beta_{waterDD}$ = −1.31, 95% CI: −2.26, −0.64), matching initial predictions. Including the previous year's occupancy reduced model performance (ΔLOOIC = +3.1; β_{pre} = 0.41, 95% CI: −0.82, 1.62) relative to the best model without temporal autocorrelation. Overall, the model explained observed occupancy levels well (internal description; ΔLOOIC = −68.4; AUC = 0.87), over both time and space (Figure 3; Appendix S1: Figure S6), and had the best accuracy of the three model types (RSME = 0.35; Table 2).

Middle site

Ponds occupied more often were characterized by more open (β_{open} = +3.87, 95% CI: 1.80, 6.52) and warmer water ($\beta_{meanwater}$ = +1.22, 95% CI: 0.37, 2.34). The model included a positive effect of ice depth (β_{ice} = +0.73, 95% CI: −0.49, 2.21), but the credible interval overlapped
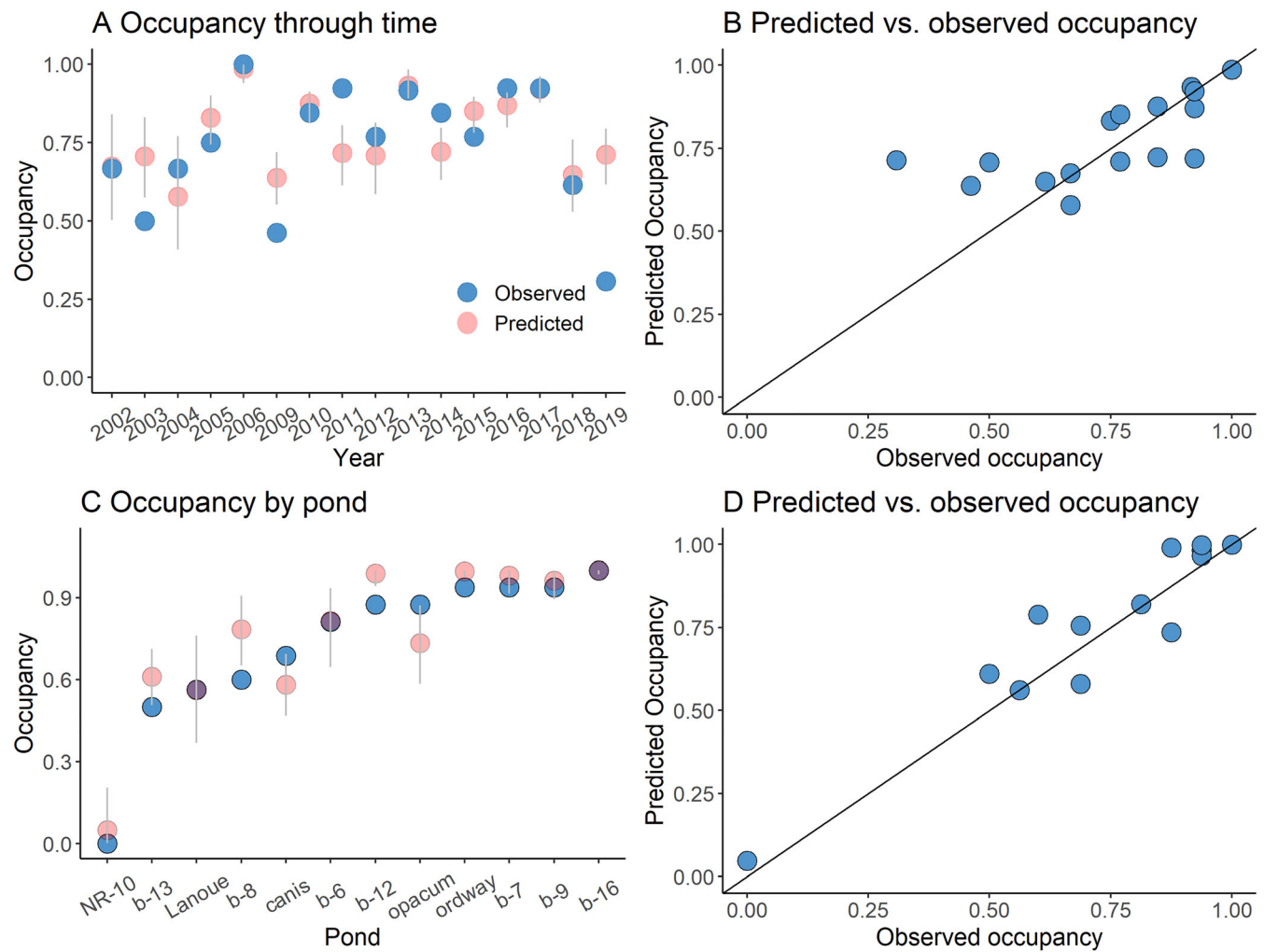

FIGURE 3 Southern site, climate–habitat model: Marbled salamander observed (blue) and predicted (red) occupancy (A) through time and (C) across ponds (median ± 95% confidence intervals) based on the correlative model. Also, the predicted versus observed occupancy is plotted in time (B) and space (D); diagonal line indicates 1:1 relationship.

zero. The model also included negative effects of well height (β_{well} = −0.66, 95% CI: −1.36, −0.07) and a positive interaction between ice thickness and open water (β_{int} = +3.31, 95% CI: 0.73, 6.24). A temporal autocorrelation term did not affect occupancy (β_{pre} = 1.19, 95% CI: −0.41, 3.95) or improve model performance (ΔLOOIC = +3.1) relative to the model without it. Of the three model types, this model was best at describing observed occupancies (internal description; Table 2: ΔLOOIC = −75.6, AUC = 0.88, and RMSE = 0.39), although it tended to over-predict occupancy in some low-occupancy years (Figure 4; Appendix S1: Figure S7).

Transferability

Using the southern climate–habitat model to predict middle site occupancies resulted in a somewhat lower AUC (0.75) and much lower accuracy (RSME = 0.56) (Table 2). The model explained 35% of the temporal variance and 32% of the spatial variance (Figure 5). The model overpredicted some middle-site ponds that never host marbled salamanders (e.g., Erica Shrub and X-8). Using the middle climate–habitat model to predict southern site occupancies resulted in poor performance as measured by AUC (0.61) and RSME (0.66). Although the model explained 39% of the temporal variance, it largely underpredicted southern occupancy patterns (Figure 6A,B). Across ponds, the model explained 14% of the variance and again overpredicted occupancy substantially (Figure 6C,D).

Hybrid mechanistic metapopulation model

Southern site

A metapopulation occupancy model based on FLake maximum ice duration (β_{icedur} = −0.50, 95% CI: −0.96, −0.06) and groundwater height (β_{well} = −0.71, 95% CI: −1.20, −0.23) was selected as the best performing model (Figure 7;
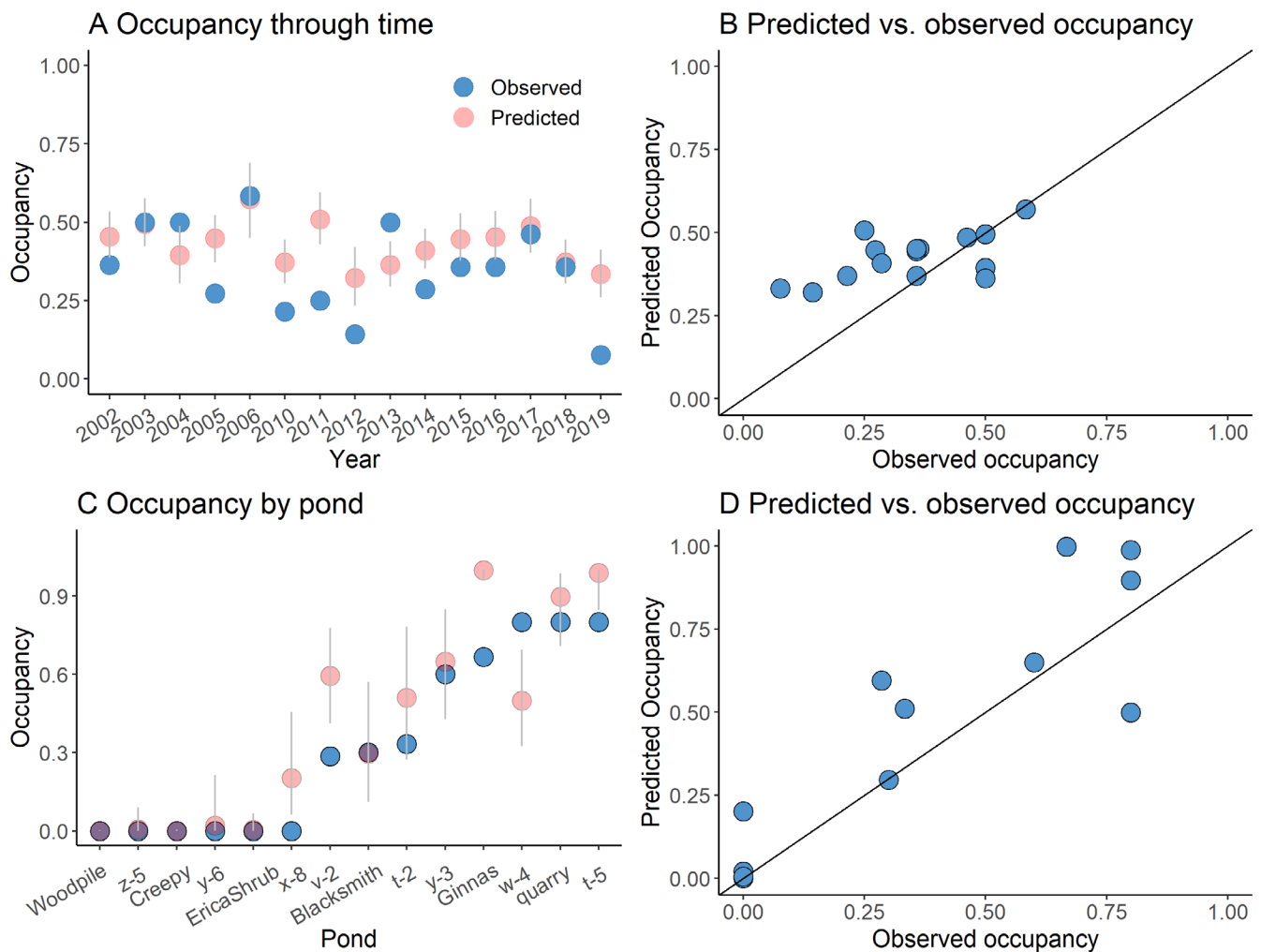

FIGURE 4 Middle site, climate–habitat model: Marbled salamander observed (blue) and predicted (red) occupancy (A) through time and (C) across ponds (median ± 95% confidence intervals) based on the correlative model. Also, the predicted versus observed occupancy is plotted in time (B) and space (D); diagonal line indicates 1:1 relationship.
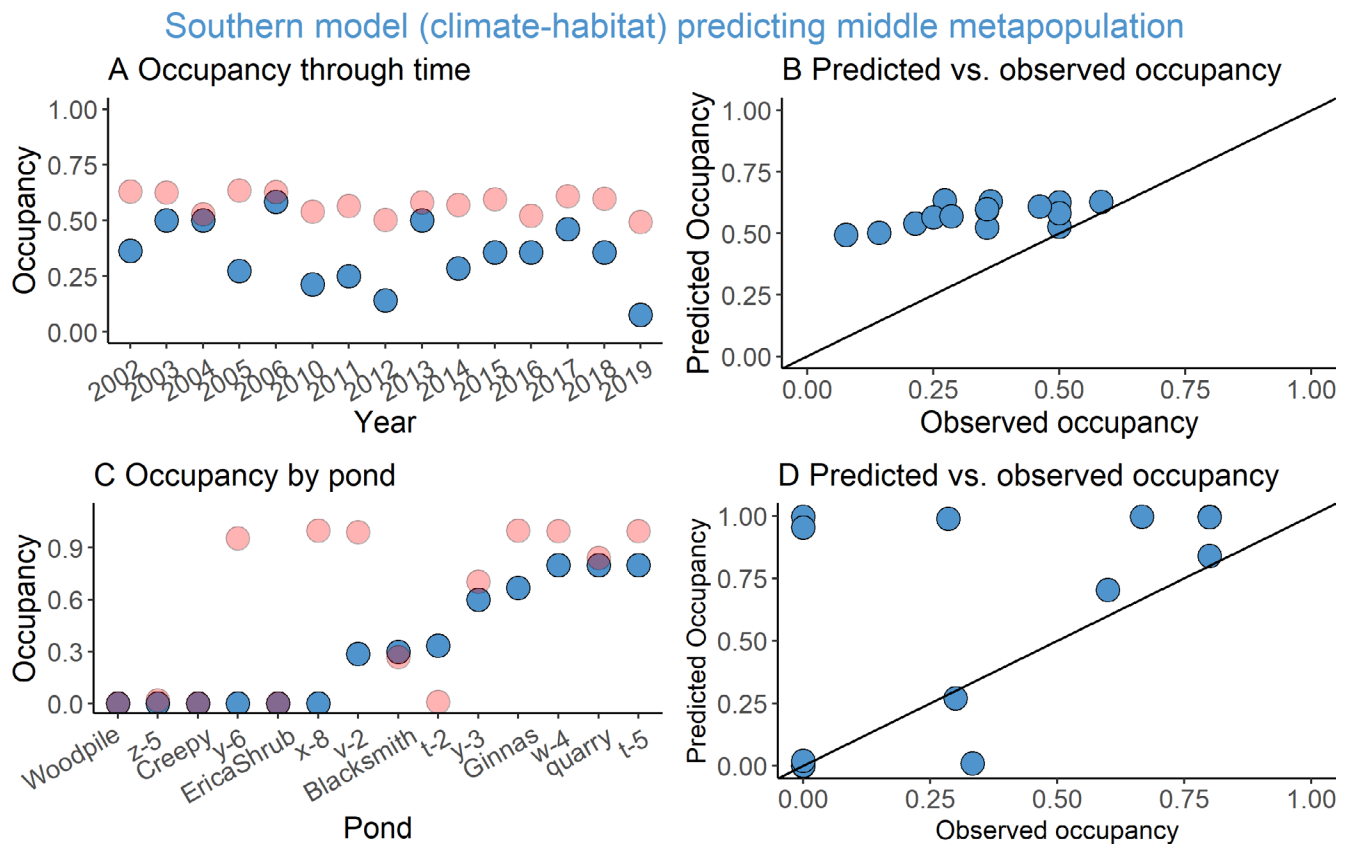
FIGURE 5 Southern model poorly predicts middle metapopulation occupancy: Marbled salamander observed (blue) and predicted (red) occupancy through time (A) and (D) across ponds. The predicted versus observed occupancy is plotted in time (B) and space (D); diagonal line indicates 1:1 relationship.

Appendix S1: Figure S8; Table 3) with a delta LOOIC = −15.4 over the intercept-only model, which included metapopulation colonization-extinction dynamics without weather contributions. The probability of local colonization was high at 0.56 (95% CIs: 0.37, 0.74), while the probability of local extirpation was estimated at 0.13 (95% CIs: 0.07, 0.20) at average weather conditions (all factors are mean centered), suggesting an expanding metapopulation. The model performed moderately well at describing local occupancy patterns according to AUC (0.80) and RMSE (0.38), better than the climate-only model but not quite as well as the climate–habitat model for this site.

Middle site
The best metapopulation model (ΔLOOIC = −13.9) included FLake maximum ice duration only (β_{icedur} = −1.34, 95% CI: −3.27, −0.55) (Figure 8; Appendix S1: Figure S9; Table 3). The probability of local colonization was estimated at 0.13 (95% CIs: 0.02, 0.27), and the probability of local extirpation also was estimated at 0.13 (95% CIs: 0.00, 0.43), suggesting a stable metapopulation under average weather conditions. The model performed moderately well according to AUC (0.84) and RSME

(0.42), but again not quite as well as the climate–habitat model.

Transferability
The southern model predicted middle metapopulation occupancies moderately well, as measured by moderate AUC (0.77) and RSME (0.48), which was better than the other models. The model explained 58% of the among-pond variation, but generally overpredicted occupancies in uninhabited ponds (Figure 9C,D). For instance, the model predicted between 0.36 and 0.66 probability of occupancy for the six ponds that never hosted marbled salamanders. The model poorly predicted occupancy in earlier years, with better predictions of occupancies post-2011, but again suffering from over-prediction.

The middle model did not predict southern metapopulation occupancies well (AUC = 0.69; RSME = 0.44), but did better than the other two models, especially when measured by accuracy. The model explained 76% of the among-pond variation, but overpredicted occupancies in low-occupancy ponds (Figure 10C,D), but this problem also plagued the other models as well. The model did more poorly at predicting temporal variation, especially in recent
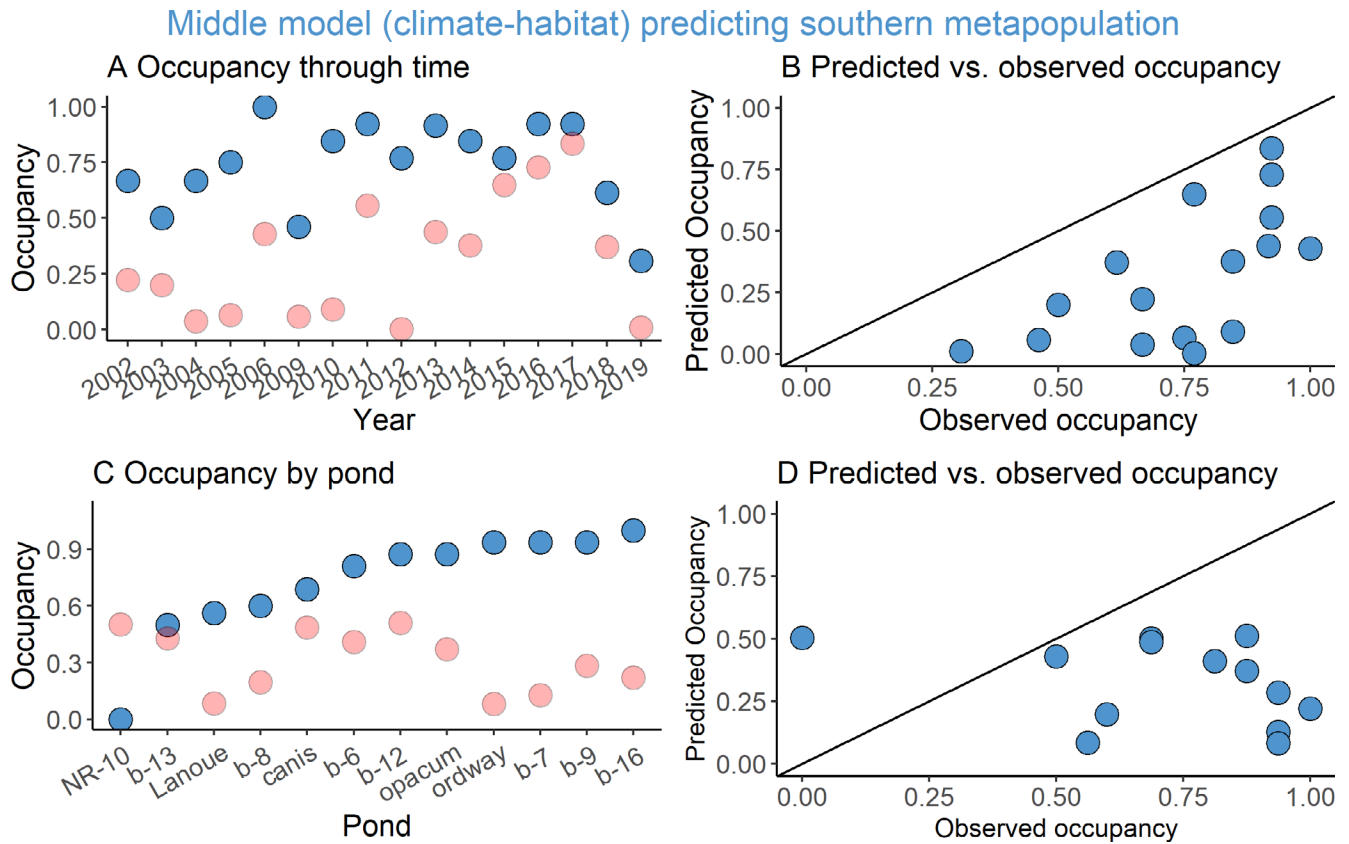
Middle model (climate-habitat) predicting southern metapopulation

FIGURE 6 Middle model poorly predicts southern metapopulation occupancy: Marbled salamander observed (blue) and predicted (red) occupancy through time (A) and (D) across ponds. The predicted versus observed occupancy is plotted in time (B) and space (D); diagonal line indicates 1:1 relationship.

years when early autumn pond-filling reduced occupancies to low levels (Figure 10A,B), which is not surprising given that this model did not include well height and maybe this should have been included.

Future projections

We applied hybrid mechanistic metapopulation models to generate future projections under climate change scenarios based on their performance in explaining out-of-sample data (transferability), our interest in projecting occupancy under extrapolated (future) conditions, and the inability to predict how some of the measured variables changed through time (e.g., open water, water temperature). However, we suggest alternative optimizations and ensembles in our discussion. Observed and predicted patterns are summarized in Figure 11.

Southern site

The mean maximum ice duration decreases under warmer climates to just a few days for the high-emissions scenario (Figure 12; Appendix S1: Figures S10–S12). Autumn well depth, however, is variable but the mean

remains consistent through time. Together, results suggest that marbled salamanders are already close to inhabiting all suitable ponds at the southern site and will likely not colonize the few remaining ponds with little groundwater contributions. Hindcasts along with observed patterns suggest that the site occupancy varied annually but without a strong directional bias from 1980 to 2020. Periodic high-precipitation or ice-duration years are likely to reset the metapopulation to lower levels with a rebound in subsequent years under favorable conditions. As winterkill conditions become weaker under future projected climates, these extirpations become less common. Patterns were essentially unchanged with the moderate-emissions scenario (Appendix S1: Figures S19 and S22–S24), which also suggested occupancy patterns were at their maximal extent.

Middle site

Ensemble projections suggest an impending increase in marbled salamander occupancy following a gradual rise from 25% to 40% during the last 40 years (Figure 13; Appendix S1: Figures S13–S15). Because well height was not included in this model, projections were less variable from year to year compared with the southern site, and
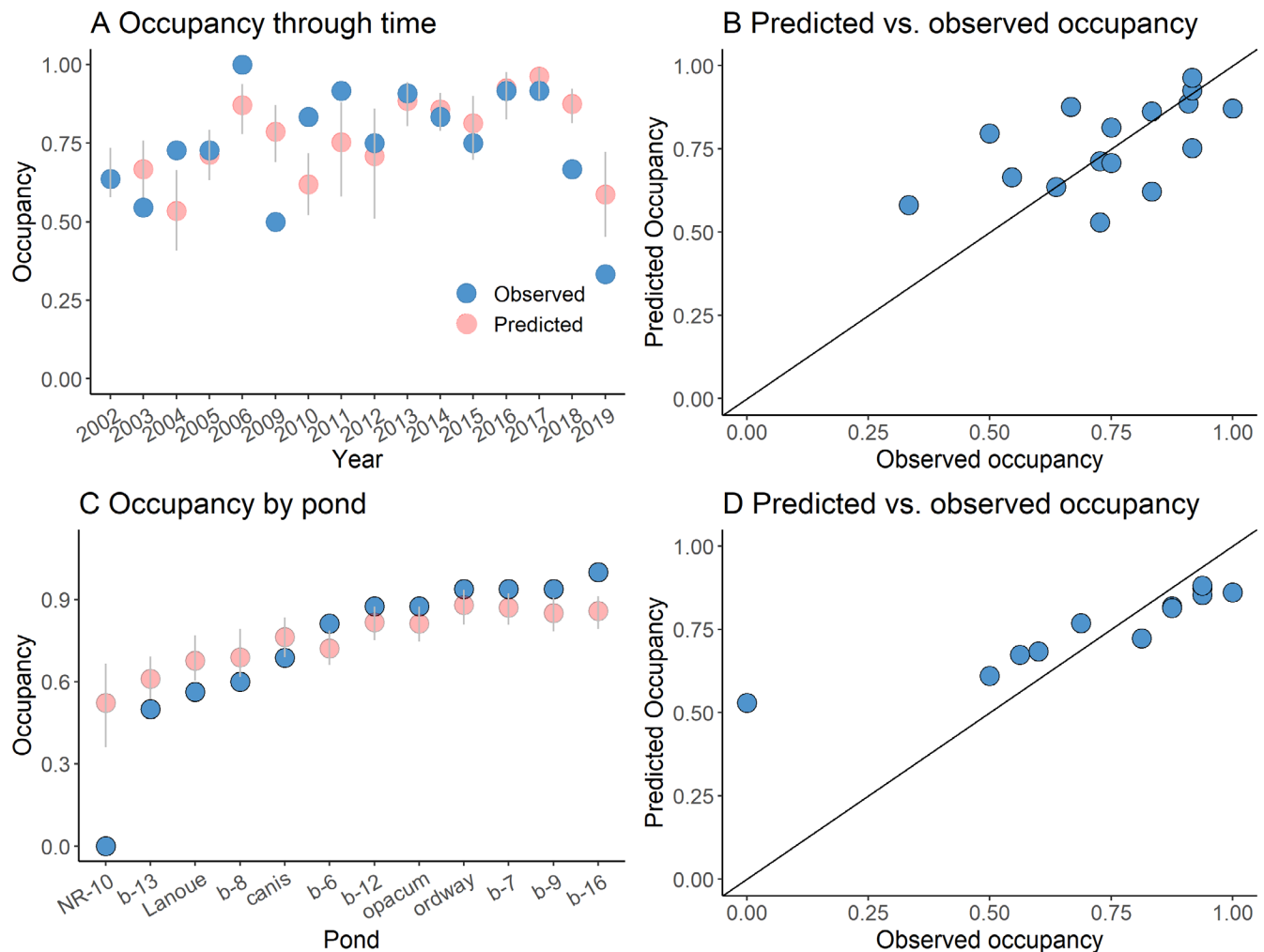
FIGURE 7 Southern site, hybrid mechanistic model: Marbled salamander observed (blue) and predicted (red) occupancy (A) through time and (C) across ponds (median ± 95% confidence intervals) based on the correlative model. Also, the predicted versus observed occupancy is plotted in time (B) and space (D); diagonal line indicates 1:1 relationship.

the model missed the observed low-occupancy years when flooding reduced occupancies below 20%. As ice durations decline from ~50 to 25 days or fewer by the 2030s, occupancy patterns after 2050 are projected to climb to ~100% in the high-emissions scenario and 75% in the moderate-emissions scenario (Appendix S1: Figures S20 and S25–S27).

Northern site
Current models estimate that maximum ice durations were generally >60 days from 1980 to 2020, more than enough to limit oxygen and prevent colonization by marbled salamanders (Figure 14; Appendix S1: Figures S16–S18). Future projections indicate that 20% of ponds could be colonized if introduced, assuming a similar distribution of groundwater influence as found at the other sites. Ice durations are predicted to decrease substantially within the next decade, while precipitation effects on pond refilling did not change substantially

(Figure 14, lower panel). Under the high-emissions scenario, the probability of marbled salamander occupancy increases to 30% by 2030 and up to 60% by 2100. Under the moderate-emissions scenario, occupancy is projected to reach 50% by 2100 (Appendix S1: Figures S21 and S28–S30).

DISCUSSION

Mechanisms of marbled salamander occupancy

We evaluated four hypotheses expected to affect marbled salamander occupancy in temporary ponds in New England: winter predation, pond filling, pond freezing, and winterkill via hypoxia. We found little support that winter predation affected marbled salamander occupancy. Pond filling improved model performance at both

TABLE 3 Summary of predictions, coefficients, and area under the curve (AUC).

Factor	Predicted coefficients	Southern site Standardized estimates (95% CIs)	Middle site Standardized estimates (95% CIs)
Probability of local extirpation[a] (1 → 0)	0.10	**0.127 (0.073, 0.198)**	**0.133 (0.000, 0.426)**
Probability of local colonization[a,b] (0 → 1)	0.10	**0.558 (0.366, 0.739)**	**0.127 (0.016, 0.269)**
Ice duration estimated from FLake	− Ice duration	**−0.500 (−0.957, −0.060)**	−1.34 (−3.27, 0.55)
Fall groundwater level	− Water level	**−0.706 (−1.1988, −0.234)**	...
Interaction between ice duration and groundwater	− Interaction	...	...
Local immigration potential	+ Local immigration	...	...
Delta LOOIC from next model		−1.1 (next model includes dispersal and interaction)	−2.8 (next model includes flooding)
Delta LOOIC from metapopulation intercept-only model[c]		−15.4	−13.9
Delta LOOIC from best correlative model		+13.2	+43.2
Raw AUC[d]		0.80 (0.76, 0.82)	0.84 (0.79, 0.87)
Occupancy AUC[e]		0.81 (0.77, 0.84)	0.89 (0.80, 0.99)

Note: Bold indicates credible intervals that do not overlap with zero.

Abbreviations: AUC, area under the curve; LOOIC, Bayesian leave-one-out cross-validation; RMSE, root mean squared error.

[a]Assumes average ice duration and groundwater levels.

[b]Assumes zero local immigration potential (no nearby ponds within dispersal kernel with marbled salamanders).

[c]LOOIC of best model (southern: 251.4 and northern: 261.2) minus intercept-only model LOOIC. More negative numbers indicate better models.

[d]AUC calculated with observed presences of marbled salamanders.

[e]AUC with the occupancy of marbled salamanders estimated through modeling.

sites, albeit less so at the middle site. Aggregated rainfall during this period was similarly correlated with salamander occupancy but did not improve model performance as much as well height, likely to be because well height integrates hydrological dynamics over a longer period and is more indicative of groundwater contributions to the ponds. Marbled salamanders lay their eggs in the dry margins of temporary ponds, and these eggs hatch when inundated after autumn pond refilling (Petranka, 1998). If the pond is already filled when they arrive, adults can skip breeding or lay eggs too high on the banks to be inundated, resulting in death (Gamble et al., 2006). For example, the date of pond refilling relative to breeding explained much of the variability in recruitment in ponds in Massachusetts (Gamble et al., 2007). Complete cohort failure was observed for North Carolina populations after two hurricanes precipitated >0.5 m of rainfall in September (Wojnowski, 2000). We, too, have observed years when high rainfall in the late summer/early autumn fills temporary ponds early, and regional marbled salamander occupancy declines. We did not find the hypothesized hump-shaped relationship, however, in which drought years decreased recruitment. One

explanation is that late autumn rainfall is usually sufficient to refill ponds before winter.

The pond-freezing and winterkill hypotheses proposed that cold winter temperatures reduced marbled salamander occupancy either by freezing salamanders directly or indirectly by reducing oxygen via ice coverage. Although we found model support for both hypotheses, multiple lines of evidence suggest the importance of winterkill via hypoxia. First, observations indicate that few ponds freeze solid. Second, the winterkill model performed better than the freezing model (Table 1). Third, deeper ice was positively associated with marbled salamander occupancy at both sites, contrary to the prediction of the freezing hypothesis. Fourth, when we introduced marbled salamander larvae to uninhabited ponds in autumn, they survived poorly even though no ponds froze completely, and the only difference detected between low-density and high-density ponds was lower dissolved oxygen concentrations (Figure 2). Therefore, our analyses best support winterkill via hypoxia as the main determinant of marbled salamander occupancy.

During winter, full ice across a waterbody limits oxygen diffusion into water while decomposing organic material
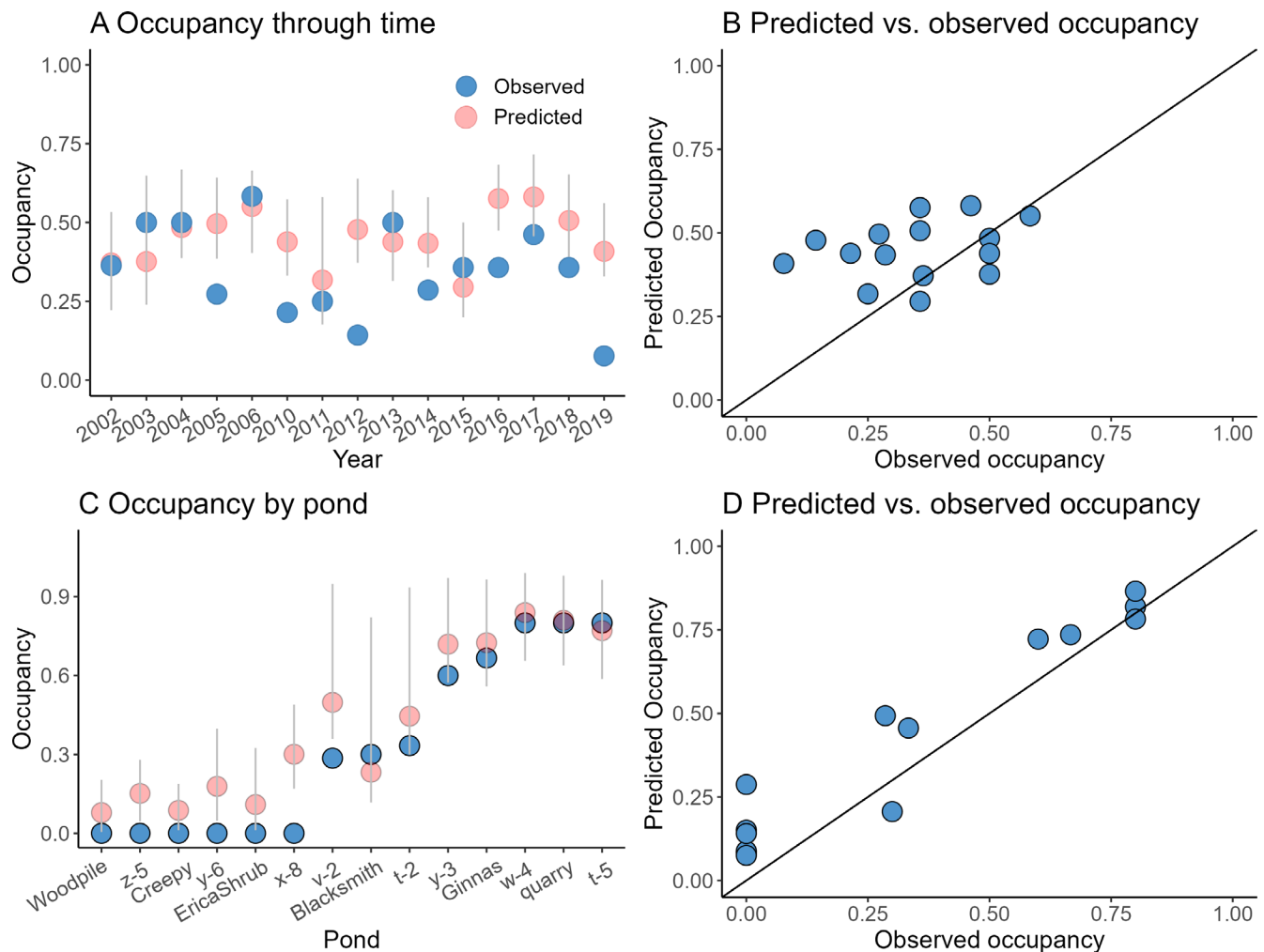
FIGURE 8   Middle site, hybrid mechanistic model: Marbled salamander observed (blue) and predicted (red) occupancy (A) through time and (C) across ponds (median ± 95% confidence intervals) based on the correlative model. Also, the predicted versus observed occupancy is plotted in time (B) and space (D); diagonal line indicates 1:1 relationship.

under ice absorbs the remaining oxygen. The resulting low oxygen levels under ice cover can kill overwintering species (Greenbank, 1945), a phenomenon widespread across temperate–polar regions (Heino et al., 2021; Leppi et al., 2016). Temporary ponds likely experience winterkill more often than most water bodies owing to low water volume-to-sediment ratios (McCord & Schladow, 2001). Winterkill does not affect overwintering species equally: the largest consumers require more oxygen and thus are more sensitive to hypoxia (Bradford, 1983; Carpenter et al., 1985). Therefore, winterkill via hypoxia determines the distributions of many large consumers in temperate climates, including fish and amphibians, which also disproportionately affect freshwater communities and ecosystems (Bradford, 1983; Greenbank, 1945; Herstoff & Urban, 2014; Tonn & Magnuson, 1982). Winters are warming more rapidly than other seasons throughout much of the world (Zhongming et al., 2021), such that top freshwater

consumers are predicted to expand northward and colonize new lakes as winterkill becomes less common (Fang & Stefan, 2000, 2009).

Winterkill in temporary ponds depends not just on water volume and decomposition levels, but also on groundwater flow. Indeed, observations of open water in winter were our best predictor of ponds that regularly hosted marbled salamanders. We observed these springs creating patches of open water in winter which facilitate atmospheric exchange of oxygen. We often observed marbled salamander larvae only in the vicinity of these open patches, either through behavioral choice or because they died in ice-covered parts of the pond. The importance of springs likely increases with latitude, potentially providing the only suitable habitat in colder parts of their range. Warmer winters could allow marbled salamanders to colonize ponds that lack springs and expand their range northward into groundwater-fed ponds.
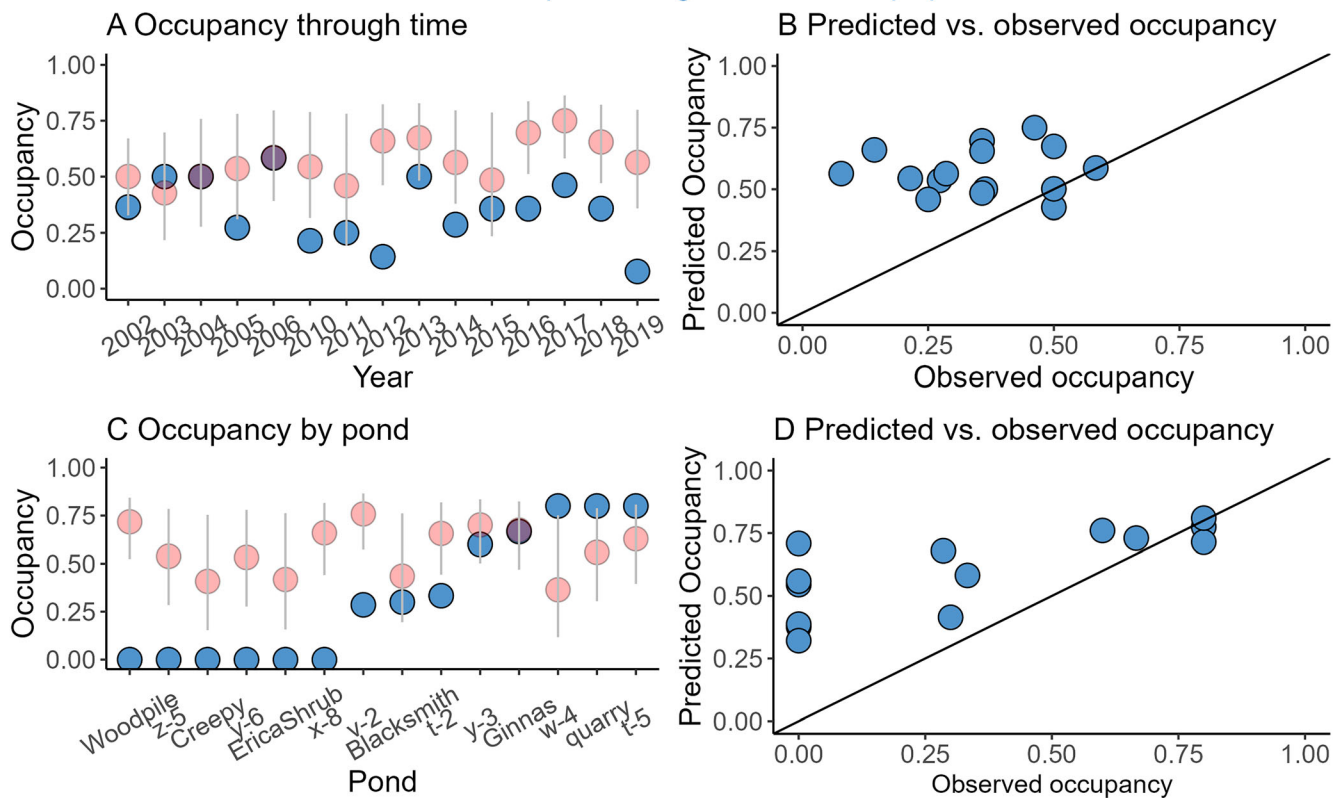
FIGURE 9 Southern model predicting middle metapopulation occupancy based on hybrid mechanistic model: Marbled salamander observed (blue) and predicted (red) occupancy through time (A) and (C) across ponds. The predicted versus observed occupancy is plotted in time (B) and space (D) where the diagonal line indicates a 1:1 relationship.

A biotic multiplier of climate change in temporary ponds

Our results suggest that marbled salamanders act as biotic multipliers of climate change on temporary pond communities because they are disproportionately sensitive to climate change and have strong impacts on communities. Previous studies suggest that marbled salamanders disproportionately affect other species and ecosystem properties such as primary productivity (Urban, 2013). In experiments, marbled salamander larvae reduced prey diversity and biomass by 40% and 75%, respectively, and doubled primary production (Urban, 2013). In the field, marbled salamanders can extirpate prey species and decrease prey densities by orders of magnitude (Petranka, 1998; Stenhouse, 1985; Urban, 2007). In this study, we validated the second requirement that marbled salamanders are sensitive to climate change. Their dependence on oxygenated underwater habitat during winter makes them sensitive to changes in winter ice cover. As such, winterkill is likely to determine their ability to expand northward with climate change (Urban, 2020; Urban et al., 2019). Thus, a state change from ice to water could also cause a state change

in temporary pond ecosystems by facilitating the colonization of a large, vertebrate predator (Urban, 2007). More generally, ecologists looking for biotic multipliers might focus on those most affected by winter conditions (Urban et al., 2017).

Correlative modeling

To reflect the more common situation, we first developed climate-only models as if we only had access to climate data and lacked long-term habitat variation data. Models for both sites performed poorly, with the middle site model performing no better than an intercept-only model. This poor performance does not indicate that climate is unimportant, but rather that climate interacts with habitat-specific variation, which can decouple local from regional climate impacts (Lenoir et al., 2017; Zellweger et al., 2020). For example, a particularly cold winter probably does not affect a groundwater-fed pond in the same way that it does a precipitation-fed pond.

Models that included habitat variation, especially open water observations, performed better at describing marbled
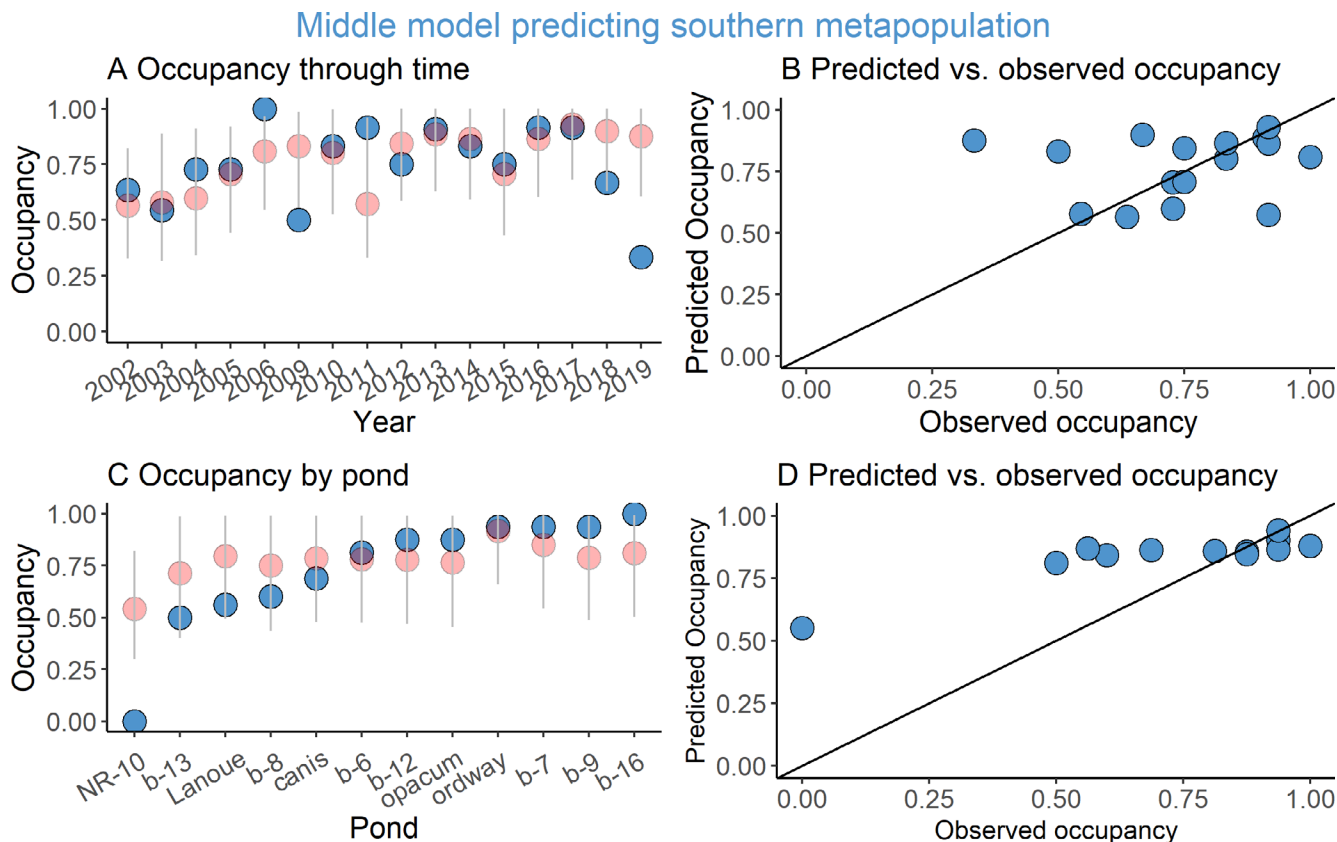
Middle model predicting southern metapopulation

FIGURE 10   Middle model predicting southern metapopulation occupancy based on hybrid mechanistic model: Marbled salamander observed (blue) and predicted (red) occupancy through time (A) and (C) across ponds. The predicted versus observed occupancy is plotted in time (B) and space (D) where the diagonal line indicates a 1:1 relationship.
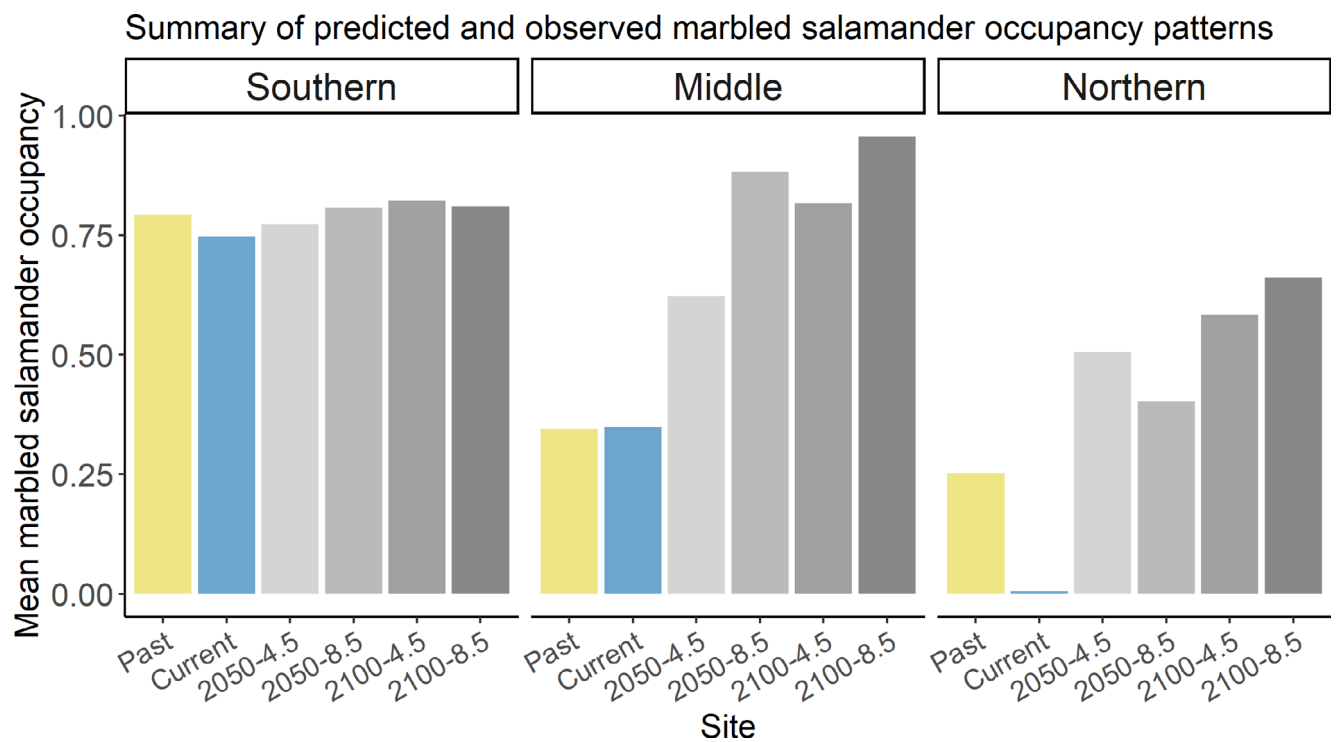

FIGURE 11   Summary of hindcasted (1980–2001; yellow), observed (2002–2021; blue), and predicted (gray) marbled salamander occupancy patterns, projected for 2050 and 2100 with the SSP4–4.5 and SSP5–8.5 climate scenarios, organized by site.
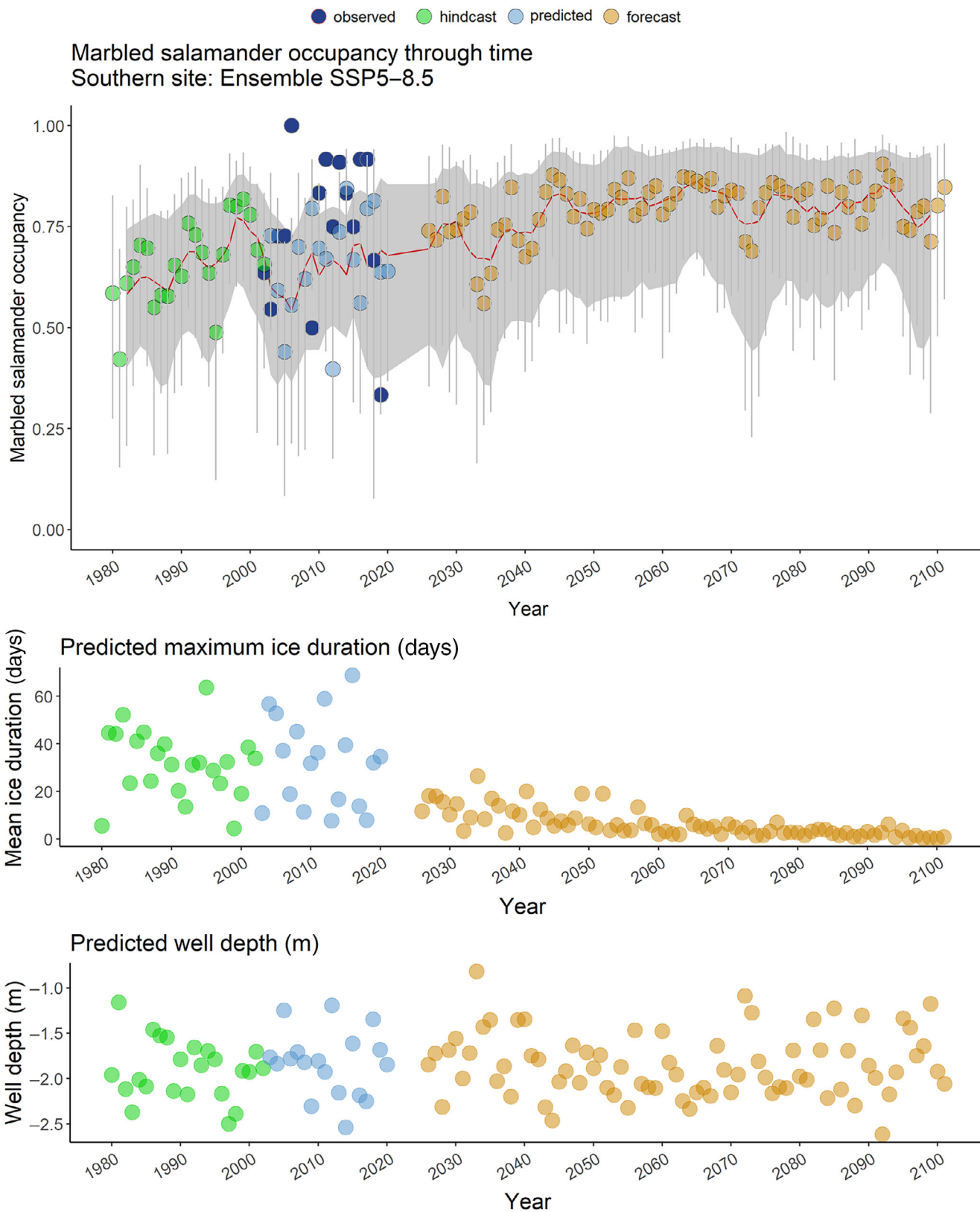
FIGURE 12 Ensemble projections for occupancy at the southern site. On top, marbled salamander's observed (dark blue) and ensemble predicted occupancy through time for hindcasts (green), current model predictions (light blue), and forecasts (orange) with 95% credible intervals for equally weighted results from the Community Earth System (CES), Beijing Climate Center (BCC), and Geophysical Fluid Dynamics Laboratory (GFDL) SSP5-8.5 models. Red line and gray shading indicate 5-year running average with 95% credible intervals. Middle and bottom panels indicate mean predicted average maximum ice duration and estimated well depths.
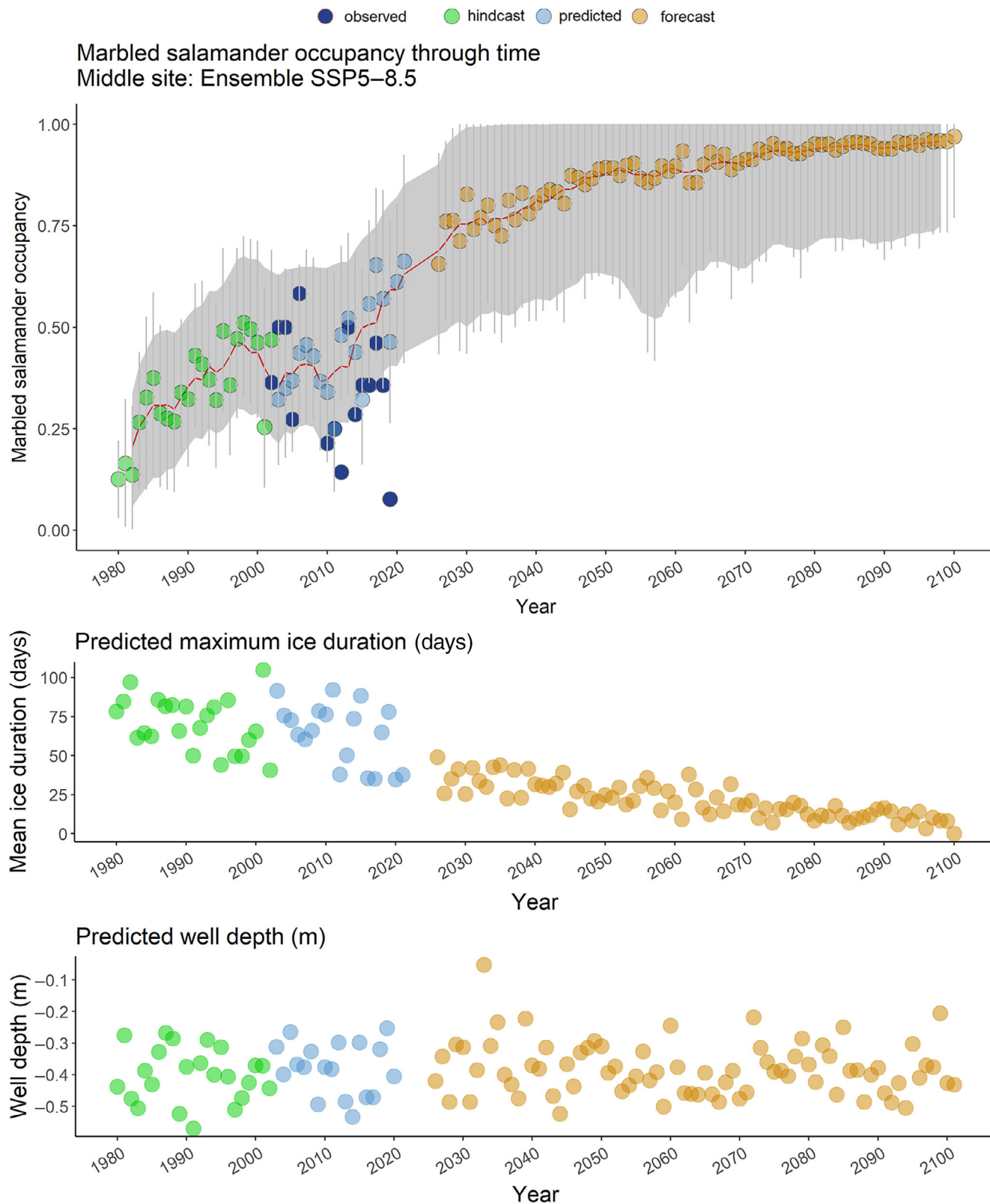
FIGURE 13 Ensemble projections for occupancy at the middle site. (Top) Marbled salamander's observed (dark blue) and ensemble predicted occupancy through time for hindcasts (green), current model predictions (light blue), and forecasts (orange) with 95% credible intervals for equally weighted results from CESM, BCC, and GFDL SSP5-8.5 models. Red line and gray shading indicate 5-year running average with 95% credible intervals. Middle and bottom panels indicate mean predicted average maximum ice duration and estimated well depths. Well depths are displayed to indicate no predicted change in them over time even though they are not a feature of the middle site's model and thus do not affect projections.
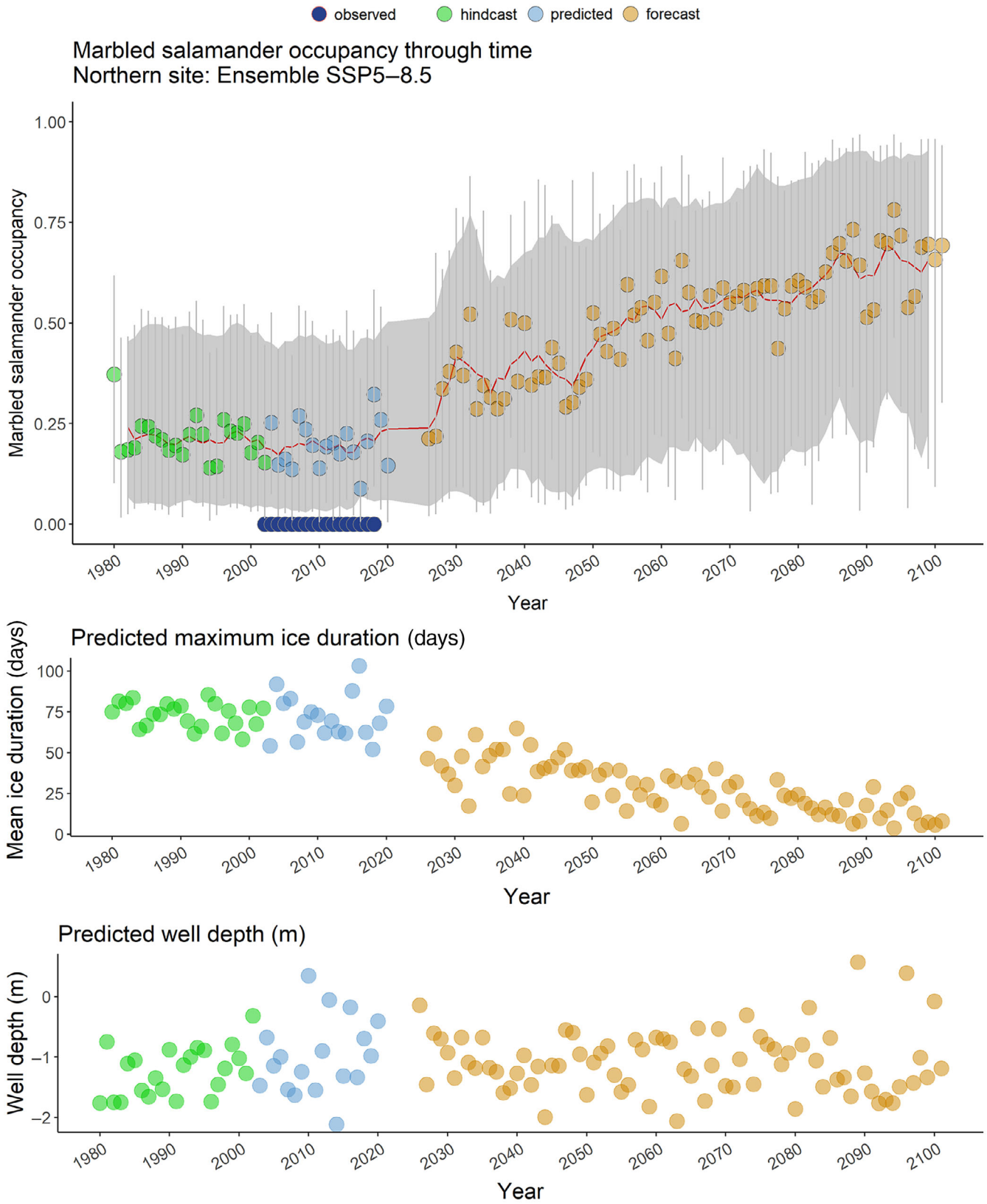
FIGURE 14 Ensemble projections for northern site. (Top) Marbled salamander's observed (dark blue) and ensemble predicted occupancy through time for hindcasts (green), current model predictions (light blue), and forecasts (orange) with 95% credible intervals for equally weighted results from CESM, BCC, and GFDL SSP5-8.5 models. Red line and gray shading indicate 5-year running average with 95% credible intervals. Middle and bottom panels indicate mean predicted average maximum ice duration and estimated well depths.

salamander occupancies through time. The best southern climate–habitat model performed well except that it predicted 50% occupancy at pond NR-10, even though this pond was never inhabited. This result might stem from an inability to model a rare habitat type that consistently had the most observed ice coverage. Although groundwater well height improved model performance when added singly, it was not selected in the best model for the southern site. The rarity of high-rainfall years in our observational record might explain this result, especially given the penalty imposed by outliers when using leave-one-out performance metrics. Lacking well height, the model also overpredicted years with high rainfall (e.g., 2019).

The best performing climate–habitat model for the middle site performed well at describing both temporal and spatial patterns of occupancy, but overpredicted years characterized by high autumn rainfall, despite including this predictor, and overpredicted recent years. This latter result might reflect that species do not immediately colonize ponds that have become suitable or, alternatively, that well height affects occupancy nonlinearly.

Overall, correlative climate–habitat models described marbled salamander distributions well, returning AUC values >0.87 for both sites (Table 2). Despite the correlative models' strong success at describing local occupancy patterns, they displayed more variable performance in predicting the other site's occupancy patterns. The middle site's model explained the southern occupancy patterns with moderate loss of AUC performance, but poorly predicted low-occupancy years and ponds without marbled salamander populations (Figure 6). The southern model did an even poorer job of predicting the middle occupancy patterns, doing no better than a random model (Figure 5).

Building a more mechanistic model

We next parameterized a metapopulation occupancy model, which allowed us to replicate observed colonization-extirpation dynamics in amphibians (Marsh & Trenham, 2001; Skelly, 2001; Skelly et al., 2003), while also incorporating uncertainties about occupancy. Both colonization and extirpation probabilities depended on autumn pond water depth and winterkill probability as a function of the maximum duration of continuous ice cover. We initially modeled colonization probability from nearby ponds by assuming an exponential decay function of interpond distance, but none of the best models included dispersal. We suspect that local dispersal dynamics might eventually become important at the middle site as marginally suitable ponds become more suitable in the future, but this dynamic might not yet be observable if the distances between the source and newly suitable habitats are still too great.

We tried multiple submodels for ice duration, ranging from simple temperature thresholds to a mechanistic physical model of lake ice formation (Kirillin et al., 2011; Seidou et al., 2006; Thompson et al., 2005). The physical FLake model with a pond-specific groundwater component best explains the observed ice cover. Despite FLake's performance, the model likely would be improved by accounting for the nonlinear relationship between ice depth and snow cover owing to the insulating effect of snow on ice (Vavrus et al., 1996). Snowfall might also increase winterkill hypoxia by decreasing light transmission in places where underwater oxygen production by photosynthesis could occur under thin ice cover (Greenbank, 1945). In correlative analyses, snowfall was associated with more marbled salamanders, as well as interacting with cold air temperatures to decrease their negative impact, suggesting an overriding positive effect of snow on occupancy. Hence, some of the errors in our metapopulation model were likely due to differences in annual snowfall and its nonlinear effect on ice depth.

Few models are fully mechanistic, but instead hybridize elements of correlative and mechanistic modeling (Buckley et al., 2010). We predicted the longest duration of ice cover using a mechanistic model of ice formation parameterized for each pond. Yet, we lacked a mechanistic submodel that relates ice cover to mortality for marbled salamanders. This submodel would ideally incorporate measurements of pond-specific water volume, organic sediment content, and temperature-dependent respiration, as well as the critical lethal oxygen limits for marbled salamander larvae. Similarly, we envision creating hydrological models for each pond basin that relate annual precipitation and evapotranspiration to water levels followed by a submodel that predicts salamander recruitment from these water levels. An unresolved question is how much model complexity is needed to improve accuracy in this and other systems (Urban et al., 2022).

Comparing modeling approaches

By comparing three modeling approaches, we revealed important insights about performance trade-offs between correlative and more mechanistic models (Figure 15). First, adding habitat data greatly improved models based on climate alone. Local habitat variation is ubiquitous, and therefore our results caution against climate-only models that ignore local habitat variation (Vanreusel et al., 2007) or climate change refugia (Morelli et al., 2016).

Climate change refugia buffer against climate change and include habitats such as valleys that trap cold air, cold
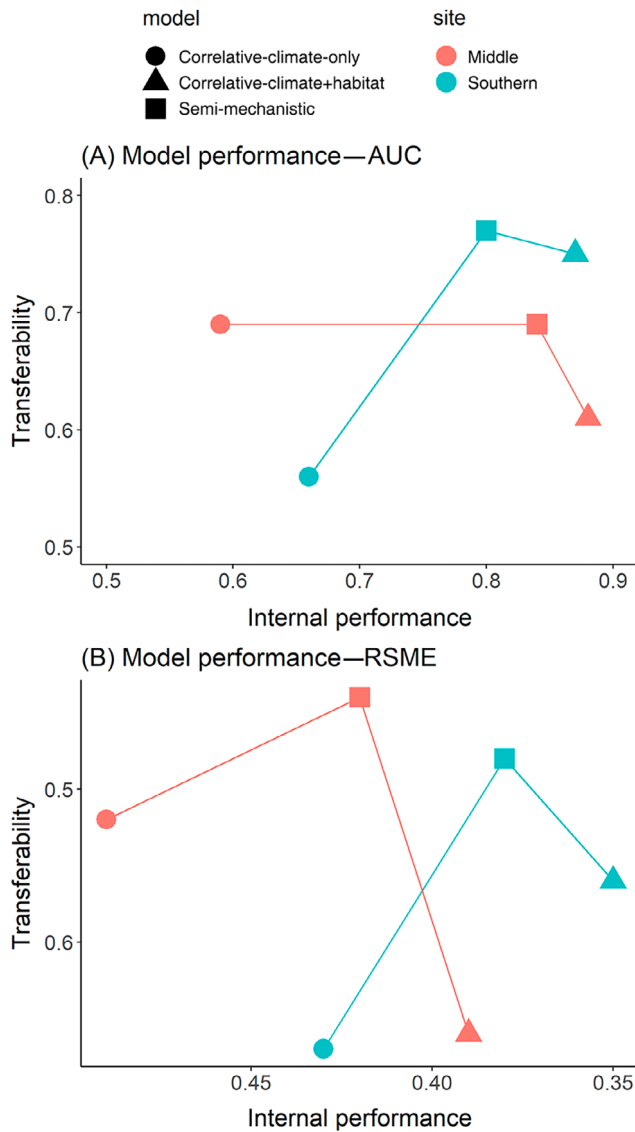
FIGURE 15 Comparison of internal and external (transferability) performance by model (symbols) and site (color) using (A) area under the curve (AUC) and (B) root mean squared error (RMSE). The RMSE axis has been reversed so that better performing models occur to the top or right to match the directionality of the AUC graph. The graph reveals a trade-off between describing training data and predicting out-of-sample data such that hybrid mechanistic models do better at prediction and correlative models do better at describing existing data.

mountain slopes, and groundwater-fed water bodies (McLaughlin et al., 2017; Morelli et al., 2016). Not accounting for climate change refugia might create an overly pessimistic view of regional colonization or persistence for a species. In our system, however, groundwater-fed ponds would typically have been viewed as climate change refugia because they buffer pond temperatures from regional climate change. Yet, the more variable, precipitation-fed ponds buffer pond communities and ecosystems from the increasing risk of an expanding predator,

suggesting the need to incorporate trophic climate change refugia into our thinking.

Our models reveal a proposed—but seldom demonstrated—trade-off between correlative and mechanistic model performance. The key part of any prediction is comparing its performance to data collected from elsewhere in time or space (Urban, 2019; Urban et al., 2022). Correlative climate–habitat models performed better at describing training data than hybrid mechanistic models at both sites, whereas hybrid mechanistic models performed better at predicting data at other sites (Figure 15). This loss of performance occurred even though we applied conservative cross-validation procedures to pick the best models. Overfitting, it seems, is still a powerful detriment to correlative modeling. In addition, our sites might differ in the types or importance of different biological processes, although the performance of our hybrid mechanistic models in extrapolation suggests substantial overlap in key mechanisms.

The biological information to parameterize fully mechanistic models seldom is available (Urban et al., 2016), and therefore hybrid correlative-mechanistic models offer a useful compromise (Buckley et al., 2010). If the mechanisms underlying species distributions are linked to climate variation and those relationships remain constant in the future, then both approaches should provide similar predictions (Kearney et al., 2010). However, correlative predictions could become increasingly inaccurate when climate is mediated by nonclimate factors such as species interactions, when climate factors become no-analog, or if populations adapt to changing conditions (Gilman et al., 2010; Williams & Jackson, 2007; Zurell et al., 2016).

Ecological forecast horizons measure the time until model accuracy drops below a predetermined threshold (Petchey et al., 2015). Most models decline in accuracy over time, but correlative models are likely to decline faster, eventually dropping below the accuracy of more mechanistic models. For example, simulations suggest that correlative models are accurate for near-term projections, but become increasingly inaccurate over time (Zurell et al., 2016). This switch point between correlative and mechanistic forecast horizons is critical, but seldom known. Future work should seek to estimate the forecast horizon switch point and predict when it occurs based on the model type and organism traits. Then weighted ensemble projections could be created that switch from correlative projections early on to more mechanistic projections later.

The future is *opacum*

Projected ice cover duration declines substantially under future climate scenarios at all sites. Although marbled

salamanders likely have approached their maximum distribution at the southern site, marbled salamanders at the middle site are predicted to grow to full occupancy by 2060, and salamanders are expected to colonize and expand at the northern site in the next 20 years. The northern model predicted that marbled salamanders should already occupy a small proportion of ponds. One might be skeptical of the model given this mismatch with reality. However, some ponds appear to be already suitable based on observations of open water in winter and oxygen profiles. Therefore, dispersal limitation might play an important role here. According to available data, the nearest population is >10 km from the northern site, compared with a maximum dispersal distance of <1 km for the species (Petranka, 1998). So, the climate conditions might already be suitable, but dispersal limits prevent them from taking immediate advantage of newly suitable habitats. We expect this dynamic to be true for many species that cannot disperse far enough to track climate change (Dullinger et al., 2012; Urban et al., 2013). In addition, observations suggest that marbled salamanders undergo a distinct colonization-extinction metapopulation dynamic. Consequently, we expect that range expansion depends on overcoming a threshold at which enough habitats become suitable to support a viable metapopulation (Holt & Keitt, 2000). Once enough suitable habitat becomes available and colonization occurs, the increase in occupancy can occur quickly, creating a stepped distribution pattern across climate gradients.

We created biologically meaningful models of occupancy and attempted to reduce overfitting by validating models on spatially divergent sites, which revealed the performance of hybrid mechanistic models. However, we also excluded additional mechanisms which could be important, such as adaptation. In addition, we did not evaluate other potential effects of climate change on adults besides adult movement, such as changes in temperature or terrestrial food resources. Future work will benefit by collecting data on and modeling the additional effects of climate change on adult life stages. Ultimately, future observations will be necessary to test and compare the performance of the different models. We expect to learn through a continuous process of model development, validation, and revision to develop more accurate projections in the future (Dietze et al., 2018; Urban et al., 2016).

CONCLUSIONS

We found strong evidence that winterkill restricts the marbled salamander's local and geographic distributions, and that periodic high-water years contribute to interannual variation. Given their sensitivity to climate and strong ecological impacts, we propose that marbled salamanders are biotic multipliers of climate change in temporary ponds in the northeastern USA. Warming winters are predicted to facilitate the spread of marbled salamanders, along with their disproportionate impacts on temporary pond ecosystems. We demonstrate the importance of incorporating habitat variation into models and the performance trade-off between correlative and hybrid mechanistic models in describing local patterns versus predicting external data. Ecologists are often interested in predicting dynamics under altered conditions, particularly considering nonlinear climate change, and thus hybrid mechanistic models that incorporate biological processes offer a practical advance. Because such models are data-intensive, we suggest prioritizing their development for biotic multiplier species with high climate sensitivity and disproportionate ecological impacts, like the marbled salamander. Combining observations, experiments, and hybrid correlative-mechanistic modeling provided convergent evidence that enabled better and more accurate predictions.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Pond characteristics, marbled salamander distribution data, and novel code used in this study are archived in Urban et al. (2023) in Zenodo at https://doi.org/10.5281/zenodo.7757778. Publicly available datasets used for this research are as follows (with full query details for each of these data sets described in Appendix S1: Section S1): daily weather station data were downloaded from the National Centers for Environmental Information https://www.ncei.noaa.gov/; long-term climate variables for FLake modeling were downloaded from the 1970–2020 NCEP North American Regional Re-analysis (https://psl.noaa.gov/data/gridded/data.narr.html); well height data were downloaded from the United States Geological Survey Groundwater Data for the Nation (https://waterdata.usgs.gov/nwis/gw); and future climate data were downloaded from the Coupled Model Inter-Comparison 6 (CMIP6) database (https://esgf-node.llnl.gov/projects/cmip6/).

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SUPPORTING INFORMATION

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