

RESEARCH ARTICLE

Estimating spatially varying occupancy trends for multi-scale conservation: An amphibian case study in the midwestern United States

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Abstract

1. Species population and distribution trends are essential inputs in the development of conservation plans. While trend estimates at broad spatial scales provide fundamental information, such estimates may mask spatial heterogeneity occurring at local levels. Local variations in occupancy trends can be particularly meaningful for taxonomic groups such as amphibians that are experiencing precipitous large-scale declines as a result of localized and variable patterns of habitat loss/degradation, climate change and disease.
2. Here we develop a spatial occupancy model that provides nuanced inferences on multi-scale occupancy trends. Using volunteer-collected, participatory science data, we apply our framework to estimate multi-scale trends for 11 anuran species across Minnesota, USA from 1996 to 2015.
3. We found substantial fine-scale spatial variation in occupancy trends across all 11 species, suggesting localized drivers of anuran occupancy dynamics across the state. Spatial variation in trends was highly species-specific, with some species having positive trends that varied in magnitude across the state (e.g. boreal chorus frog [*Pseudacris maculata*]), and others that showed both positive and negative trends across the state (e.g. northern leopard frog [*Lithobates pipiens*]).
4. Statewide projections of occupancy trends provided fine-scale insights on anuran distribution changes that were not possible when fitting simpler models. Our Bayesian approach allows trends to be summarized across areal units (e.g. ecological strata, management units) that are directly relevant for management and conservation planning. For example, the statewide trend for American toad (*Anaxyrus americanus*) was effectively zero, but finer scale analyses across ecological strata (used for statewide wildlife conservation planning) revealed multiple areas of both localized increases and declines.
5. *Synthesis and applications.* Our spatial modelling approach allows practitioners to estimate trends across multiple spatial scales to inform local and regional management priorities, particularly when summarizing trends within key areal units

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used for conservation planning. Our framework can be used to identify hotspots of decline across multiple sympatric species for targeted monitoring or management actions. Further, estimation of spatially varying trends provides an improved ability to assess effects of protected areas or management actions, inform spatial prioritization and hypothesize drivers of occupancy trends.

KEYWORDS

anuran, citizen science, hierarchical modelling, range shifts, species distribution model

1 | INTRODUCTION

A wide variety of wildlife species including insects (Wagner et al., 2021), amphibians (Grant et al., 2016) and bats (Rodhouse et al., 2019) have experienced severe population declines across large spatial extents as a result of habitat loss/degradation, climate change, invasive species and other abiotic and biotic stressors. These factors directly and indirectly affect the demographic parameters that determine population size, ultimately resulting in abundance changes and distribution shifts (Miller et al., 2018). However, the specific factors that are most important in determining the decline or growth of a population often vary across a species' range (Amburgey et al., 2018). Such spatial variation in species' sensitivities to abiotic and biotic factors occurs as a result of variations in the stressor itself (e.g. spatial variation in disease pressure), as well as spatial variability in the effect of the stressor across different parts of a species range (e.g. a species may be more sensitive to climate change at the edge of its range compared to the centre; Rollinson et al., 2021).

Together, these processes result in spatial variability in population and occupancy trends across multiple spatial scales, making extrapolation of trends from one part of a species range to another unreliable and potentially misleading (Rousseau & Betts, 2022). Similarly, while trends summarized across large spatial scales are necessary for determining regional or national conservation policies (e.g. IUCN Red List of Endangered Species), such trends may mask spatial heterogeneity in population dynamics and distribution shifts occurring at local scales (e.g. Simpson's paradox; Miller & Grant, 2015; Doser et al., 2021). Thus, quantifying spatial variation in population or occupancy trends across both local and broad spatial extents is necessary for accurate assessments of population status, targeted management and flexible conservation strategies to meet local and regional objectives (Barnett et al., 2021; Smith et al., 2024).

Understanding local variation in occupancy trends is particularly relevant for taxonomic groups such as amphibians that face myriad stressors across their ranges (Barnett et al., 2021). Amphibian declines have been well documented over the last few decades at regional and continental scales (Adams et al., 2013; Green et al., 2020; Weir et al., 2014). Climate change has been shown to influence amphibian demographic processes through a variety of mechanisms such as extreme summer temperatures, water availability, and winter severity (Amburgey et al., 2018; Miller et al., 2018; Weiskopf

et al., 2022). Disease risk, specifically from the amphibian chytrid fungus *Batrachochytrium dendrobatidis* (Bd; Olson et al., 2013), is a prominent threat to amphibians globally (Pounds et al., 2006; Zipkin & DiRenzo, 2022), while other stressors such as land-use change (Cushman, 2006), pesticide use (Grant et al., 2016), light/sound pollution (Lengagne, 2008; Touzot et al., 2020) and shifts in species interactions (Davis et al., 2017) also play prominent roles in determining amphibian metapopulation dynamics.

Despite widespread declines in amphibian populations across geographic regions and taxonomic groups, there is limited evidence that a single overall threat is responsible for the loss of amphibians, especially across large spatial scales (Grant et al., 2016, 2020). Further, the effects of climate change, disease and species interactions are nonstationary (i.e. context dependent) across space and species (Amburgey et al., 2018; Grant et al., 2016; Miller et al., 2018), presenting a challenge for the implementation of regional or continental scale management strategies (Muths et al., 2017). Accordingly, effective amphibian conservation requires a multi-species, multi-scale approach in which local at-risk populations and species can be identified for subsequent monitoring and management, in addition to identifying how such local processes scale up to broader regional patterns (Cushman, 2006).

Given the logistical complexities with implementing long-term, multi-species monitoring approaches, participatory science programs leverage volunteers who provide much needed field-based data collection effort to inform multi-scale amphibian conservation. Targeted monitoring programs are often narrow in spatiotemporal extent due to limited resources, which is particularly true for amphibians (Estes-Zumpf et al., 2022). This presents substantial difficulties in identifying occupancy trends and associated drivers for species that show high inter-annual variation in abundance and nonstationary drivers of decline (Grant et al., 2016). Volunteer-based monitoring programs can provide large amounts of data to inform multi-scale conservation due to an increased ability to monitor across large spatial regions over long time periods (Stillman et al., 2023). Participatory science data are increasingly collected under structured and semi-structured designs that provide information to account for important observational and sampling biases that occur during data collection (Dickinson et al., 2010; Kelling et al., 2019). Together with state-of-the-art spatial modelling approaches that enable multi-scale inference on occupancy trends while accounting for observational biases in the data collection process, participatory science data have great potential for informing local-scale amphibian conservation management.

Multi-season occupancy models are often used to quantify temporal changes in amphibian populations across large spatial scales (e.g. Adams et al., 2013; Miller & Grant, 2015; Weir et al., 2014). Occupancy models can estimate changes in the probability a species occupies a site over multiple time periods while explicitly accounting for variation in detection probability across surveys (MacKenzie et al., 2017). Importantly, estimating occupancy change over time does not require identifying and counting individuals and rather only requires accurately identifying the species present at a site during a survey. Using occupancy as a state variable for studies of amphibian population change over time is thus particularly attractive when using data from participatory monitoring programs, as approaches to accurately count individuals may be too time-consuming and require substantial training relative to aural-based surveys that can reliably indicate species presence.

Here we present a flexible spatial occupancy model to quantify spatially varying occupancy trends as a key first step in establishing multi-scale conservation management strategies. Using data from a structured volunteer-based monitoring program, we apply our framework to estimate spatially varying occupancy trends and distribution changes for 11 anuran species from 1996 to 2015 across Minnesota, USA. Our framework allows for summarizing spatial trends across multiple species and spatial scales to identify hotspots of anuran decline across the state, which can help focus future monitoring and management actions. We highlight how visualization of

local trend estimates can yield insights into the potential factors driving distribution changes across sympatric species, while also providing methodological insights on where additional monitoring could help reduce uncertainty. We conclude with a discussion of how our modelling framework, together with structured participatory science data, can provide an effective approach for developing, and subsequently adapting, multi-scale monitoring and conservation priorities across states or regions.

2 | MATERIALS AND METHODS

2.1 | Study area

Minnesota (225,180 km²) consists of four distinct biomes and a diversity of land cover types (Figure 1). The four biomes are referred to as ecological provinces in line with the Ecological Classification System (ECS) created for the state by the Minnesota Department of Natural Resources and the U.S. Forest Service. The northeastern portion of the state is dominated by Laurentian Mixed Forest, with large contiguous areas of conifer forest, mixed hardwood and conifer forests and a diversity of bogs, swamps, and lakes. The Eastern Broadleaf Forest province dominates the central and southeastern portion of the state and serves as a transition zone between historically semi-arid prairies in the western portion of the state from

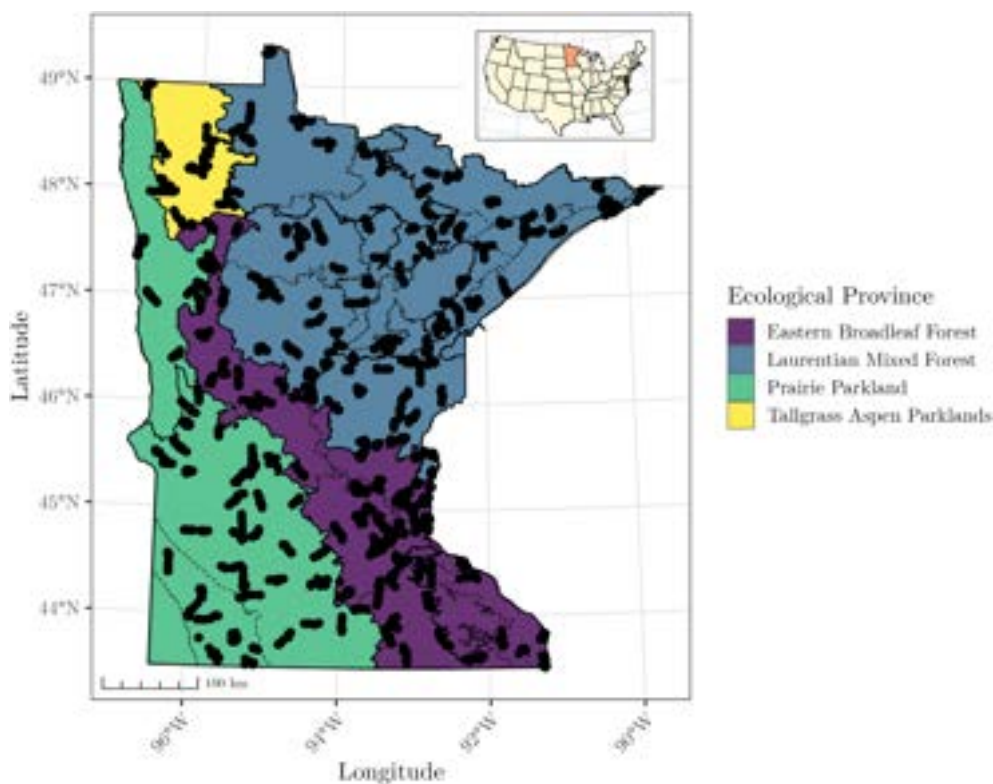


FIGURE 1 Locations of the $J = 2102$ stops (i.e. sites) sampled as part of the Minnesota Frog and Toad Calling Survey from 1996 to 2015 used in this analysis. Points are overlaid on the ecological provinces of Minnesota. The solid black lines within provinces represent boundaries of ecological sections, while the dashed black lines represent boundaries of ecological subsections within sections.

the semi-humid mixed forests in the northeast. Today the province is comprised of a diversity of agriculture, major urban centres and eastern deciduous forests and woodlands. The Prairie Parkland Province in the western part of the state was historically dominated by tallgrass prairies and today is heavily dominated by agriculture. The Tallgrass Aspen Parklands in northwestern Minnesota are characterized by open aspen savanna and tallgrass prairie vegetation.

The ECS subdivides the 4 ecological provinces into 10 ecological sections that represent areas defined by origin of glacial deposits, regional elevation, plant distributions and regional climate. These sections are further divided into 26 ecological subsections based on glacial deposition processes, surface bedrock formations, local climate, topographic relief, and tree species distributions. These units allow resource managers to consider ecological patterns, management opportunities, and constraints at varying spatial scales. In Minnesota's State Wildlife Action Plan (Minnesota Department of Natural Resources, 2026), the ECS provides a useful framework to describe the geographic areas where habitats for rare species occur.

2.2 | Sampling methods

We used data from the Minnesota Frog and Toad Calling Survey (MFTCS). The MFTCS is a volunteer-based monitoring program initiated in 1993 that uses the United States Geological Survey's North American Amphibian Monitoring Program (NAAMP) protocol to monitor frog and toad populations throughout the state (Weir & Mossman, 2005). Route locations were selected primarily according to a stratified sampling design, although a small subset were preferentially selected by volunteers. Preliminary analyses revealed little variation in results when including only routes selected as part of the stratified sampling design, and so we used all routes to leverage the entirety of the available data from 1996 to 2015. Volunteers documented audio calls of all anuran species at 10 stops along a pre-determined route, with stops along a route typically separated by at least 800m. Each stop was located at potential wetland habitat (e.g. pond, vernal pool). Routes were typically surveyed once during each of three designated periods of the breeding season to sample the entire variation in calling periods among Minnesota's anuran species: early spring (April to mid-May), late spring (mid-May to mid-June), and summer (late June to mid-July). The specific dates for each period were based on minimum water temperature and thus varied slightly across routes and by year. The minimum water temperature was 10°C for period 1, 16°C for period 2 and 21°C for period 3. Most routes were surveyed three times per breeding season, although we also used data from a subset of routes sampled during only one or two periods.

Observers performed surveys at night when minimum air temperatures were adequately high (minimum temperatures of 5.6°C, 10°C, and 12.8°C for the three survey periods, respectively) and wind was low. Observers listened for calls for 5 min at each stop and recorded a calling index from 1 to 3 as an index of abundance. We

converted this index to detected (1) or non-detected (0) for each species to model occupancy. Observers also recorded additional variables related to the sampling conditions that may influence detection probability and/or availability of the species, such as the amount of wind (scale from 0 to 5) and air temperature during the survey (see Foreman et al. (2017) for additional details). While observers were instructed to record calls for 5 min at each stop, the actual time spent recording could vary across surveys, leading to potential heterogeneity in effort across samples. The amount of sampling time per stop was not recorded, and thus, we could not include a stop-specific effort covariate in our analysis. However, we filtered out all surveys that we could reasonably assume did not sample for 5 min at each stop (i.e. had low effort) based on the total time it took to sample a route (i.e. we removed all surveys where sampling and travel time between stops was less than 60 min).

We used data from all stops that were sampled at least once between 1996 and 2015 and met the minimum effort criteria, which amounted to amphibian observations from 2102 stops sampled across 211 routes. We focused our analysis on species that were detected at least 200 times across the 20 year period, resulting in the inclusion of the following 11 species: American toad (*Anaxyrus americanus*), Great Plains toad (*Anaxyrus cognatus*), Canadian toad (*Anaxyrus hemiophrys*), Cope's grey treefrog (*Hyla chrysoscelis*), grey treefrog (*Hyla versicolor*), green frog (*Lithobates clamitans*), northern leopard frog (*Lithobates pipiens*), mink frog (*Lithobates septentrionalis*), wood frog (*Lithobates sylvaticus*), spring peeper (*Pseudacris crucifer*) and boreal chorus frog (*Pseudacris maculata*). Pickerel frog (*Lithobates palustris*) and American bullfrog (*Lithobates catesbeianus*) were detected 37 and 91 times, respectively, but were not included in the analysis as there were too few detections to estimate the multi-season occupancy models. This study did not require ethical approval.

2.3 | Statistical analysis

We developed a Bayesian spatial occupancy model to quantify spatially varying occupancy trends and species distribution shifts of the 11 anuran species while accounting for imperfect detection. We built individual single-species models rather than a multi-species occupancy model as initial model development revealed inferior performance (i.e. based on the Widely Applicable Information Criterion or WAIC; Watanabe, 2010) of a multi-species model due to large differences in where the 11 species occurred across the state. Our model uses a spatially varying coefficient (SVC) framework (Doser et al., 2025; Gelfand et al., 2003) that allows occupancy trends (i.e. a single value denoting overall change in occupancy over a specified interval) to vary smoothly across space. The use of SVCs allows us to flexibly estimate spatial variation in occupancy trends without restricting the spatial variation to occur within pre-specified boundaries (e.g. ecoregions; Doser et al., 2024). Our model accounts for nonlinearity in occupancy trajectories (i.e. the collection of annual occupancy

estimates across the entire time series) using cubic basis splines and random year effects, which together with the SVCs allows us to quantify nonlinear changes over time that can vary in form across the region to capture both spatial and temporal variation in occupancy probabilities (Smith et al., 2024). We implement our Bayesian model using Nearest Neighbor Gaussian Processes (NNGPs; Datta et al., 2016) and Pólya-Gamma data augmentation (Polson et al., 2013), which together allow for estimation of residual spatial autocorrelation and spatially varying trajectories in a computationally efficient manner.

Occupancy models consist of two sub-models: (1) an ecological process model that assesses changes in species occupancy probabilities (i.e. presence/absence) over space and/or time; and (2) an observation model that quantifies the probability of detecting the species conditional on its presence at the site during a given time period (MacKenzie et al., 2002; Tyre et al., 2003). We define $z_{j,t}$ as the true presence (1) or absence (0) of a given species at site (i.e. stop) j during year t , where $t = 1, \dots, 20$ and $j = 1, \dots, 2102$. We modelled occupancy as

$$z_{j,t} \sim \text{Bernoulli}(\psi_{j,t}), \quad (1)$$

where $\psi_{j,t}$ is the probability the species occupies the wetland habitat at stop j during year t . We estimated $\psi_{j,t}$ as a function of spatially varying covariates to account for differences in species-specific habitat requirements, spatial random effects to account for residual spatial variability not explained by the spatial covariates, and a spatially varying trajectory. More specifically, we modelled $\psi_{j,t}$ according to

$$\text{logit}(\psi_{j,t}) = \beta_0 + w_{0j} + \beta_1 \cdot \text{FOREST}_j + \beta_2 \cdot \text{WETLAND}_j + \beta_3 \cdot \text{PPT}_j + \beta_4 \cdot \text{TMAX}_j + f(\text{YEAR}_t, \beta_{\text{YEAR}}, j), \quad (2)$$

where β_0 is an overall intercept, w_{0j} is a spatially varying intercept at each stop j to account for residual spatial autocorrelation across stops within a route and among stops in different routes, $f(\text{YEAR}_t, \beta_{\text{YEAR}}, j)$ is the occupancy trajectory that varies in shape and magnitude across each stop j , and β_1 , β_2 , β_3 , and β_4 are effects of percent forest area (FOREST), percent wetland area (WETLAND), annual precipitation (PPT) and maximum temperature (TMAX), respectively. Percent forest area and percent wetland area were calculated using the Annual National Land Cover Database (USGS, 2024), which provides high-resolution (30m) annual land cover maps across the continental U.S. from 1985 to 2023. We calculated percent forest area and percent wetland area within a 1 km radius of each survey stop each year of the study. We calculated yearly maximum temperature and total yearly precipitation from 1996 to 2015 at each stop using data from the Parameter-elevation Regression on Independent Slopes Model (Daly et al., 2008) project. We then averaged the yearly land cover and climate variables over time at each survey stop such that the variables represented average land cover or climate conditions across the entire 20 year time period. While more mechanistic climate variables could be included that directly relate to population

dynamics of individual species, our focus here was on trend estimation and the covariates we used were chosen to account for broad-scale spatial variation in climate and land use across the state.

We used cubic basis splines and SVCs to account for nonlinearity and/or spatial variability in occupancy trajectories over the 20 year period. More specifically, we modelled the temporal trajectory as follows:

$$f(\text{YEAR}_t, \beta_{\text{YEAR}}, j) = \left[\sum_{r=1}^5 (\beta_{\text{YEAR},r} + w_{rj}) \cdot x_{r,t} \right] + \eta_t, \quad (3)$$

where $x_{r,t}$ is the value of the r th column of the basis spline design matrix corresponding to year t , $\beta_{\text{YEAR}} = \{\beta_{\text{YEAR},1}, \beta_{\text{YEAR},2}, \beta_{\text{YEAR},3}, \beta_{\text{YEAR},4}, \beta_{\text{YEAR},5}\}$ controls the shape of the overall trajectory on average across all stops, and $w_j = \{w_{1j}, w_{2j}, w_{3j}, w_{4j}, w_{5j}\}$ is a vector of stop-specific effects that allows the trajectory at stop j to vary in shape and magnitude from the overall trajectory β_{YEAR} . Thus, by estimating an overall set of spline parameters β_{YEAR} and stop-specific differences, w_j , from the overall set, we were able to quantify spatial variation in both the magnitude and shape of the occupancy trajectory across all stops in the study region. We included a random, normally distributed year effect η_t with mean 0 and variance σ_η^2 to account for any residual temporal variation in occupancy probability across sites that is not explained by the basis splines.

We modelled the stop-level spatially varying intercept (w_{0j}) and the five spatially varying trajectory parameters (w_j) as arising from a NNGP within a SVC framework (Doser et al., 2025; Gelfand et al., 2003). NNGPs are a computationally efficient solution for modelling spatial variation in ecological processes when using large data sets (Datta et al., 2016; Doser et al., 2023). The amount and form of spatial variation in spatially varying parameters are determined by spatial variance parameters that control the magnitude of the spatial autocorrelation and spatial decay parameters that control the range of spatial autocorrelation. See [Supporting Information S1](#) for more details on the NNGP specification in our analysis and Doser et al. (2025) for complete statistical details on the use of NNGPs in SVC occupancy models.

To estimate occupancy probability while accounting for imperfect detection, we modelled the observed detection-nondetection data $y_{j,t,k}$ at each stop j during visit k within year t conditional on the true occupancy status of the species of interest (i.e. $z_{j,t}$). More specifically, we modelled $y_{j,t,k}$ according to

$$y_{j,t,k} | z_{j,t} \sim \text{Bernoulli}(p_{j,t,k} \cdot z_{j,t}), \quad (4)$$

where $p_{j,t,k}$ is the probability of detecting the target species at stop j during visit k of year t given that the species is present. Because species phenology and thus availability for detection varies across the sampling season, $p_{j,t,k}$ more accurately represents the product of availability and detection probability (Gray et al., 2013; Kéry & Royle, 2016). We modelled $p_{j,t,k}$ as a function of covariates that influenced the probability the species is available for detection (i.e. is vocalizing) and/or

influenced the probability the species is detected given it is available for detection. More specifically, we have

$$\text{logit}(p_{j,t,k}) = \alpha_0 + \alpha_1 \cdot \text{DAY}_{j,t,k} + \alpha_2 \cdot \text{DAY}_{j,t,k}^2 + \alpha_3 \cdot \text{TOD}_{j,t,k} + \alpha_4 \cdot \text{TOD}_{j,t,k}^2 + \alpha_5 \cdot \text{WIND}_{j,t,k} + \alpha_6 \cdot \text{TEMP}_{j,t,k} + \alpha_7 \cdot \text{TEMP}_{j,t,k}^2, \quad (5)$$

where α_0 is an intercept, α_1 and α_2 are linear and quadratic effects of ordinal date (DAY) to account for variation in availability across the breeding season, α_3 and α_4 are linear and quadratic effects of the survey start time of day (TOD), α_5 is the effect of wind (WIND), and α_6 and α_7 are the linear and quadratic effects of air temperature (TEMP) during the survey, which is known to influence the vocal activity of anurans, and thus the availability of species for detection.

To complete the Bayesian specification of the model, we assigned vague priors for all non-spatial parameters and moderately informative priors for the spatial variance and decay parameters (Supporting Information S1).

2.4 | Trend estimation and range shift indices

The spatially varying trajectory component $f(\text{YEAR}_t, \beta_{\text{YEAR}}, j)$ provides insights on nonlinear patterns in occupancy probability, which can be visualized to assess how the shape of occupancy trajectories changes over the 20-year period and across the state. However, we may also be interested in quantifying an occupancy trend over a specific time period. Following Smith et al. (2024), we estimated a spatially varying occupancy trend as a derived quantity. The Bayesian framework readily enables calculation of different trend metrics with fully propagated uncertainty. Occupancy trends can be defined in a variety of ways depending on the analysis objectives (Banner et al., 2019; MacKenzie et al., 2017). Here we calculated an occupancy trend at each stop j as

$$\text{trend}_j = \frac{1}{19} \sum_{t=2}^{20} (\psi_{j,t} - \psi_{j,t-1}), \quad (6)$$

such that trend_j represents the average annual change in occupancy probability at stop j over the 20-year period.

We predicted occupancy probability for each species across a 2×2 km grid. These predicted values represent the probability a given species occupies a potential wetland habitat in the centre of each grid cell. We subsequently generated an occupancy trend for each grid cell following Equation (6) to visualize spatial variation in occupancy trends across the state. Further, we calculated two range shift indices as simple quantitative measures of directional distribution change within the state as statewide summaries of the local trends. Following Clement et al. (2016) and Rushing et al. (2019), we calculated a mean latitude index and mean longitude index, which can be used to quantify shifts of a species distribution latitudinally and longitudinally, respectively (Clement et al., 2016). More specifically, the indices were calculated as the sum of the cell latitudes/longitudes weighted by the occupancy probability of each grid cell

and divided by the total occupancy probability across all cells. We calculated the metrics using all posterior samples, which allowed us to calculate 95% credible intervals for the resulting estimates. Because our study area was limited to only a portion of the species' ranges, these metrics do not correspond to overall range shifts. Rather, given that Minnesota falls along the range edge for 9 of the 11 anuran species (all species except northern leopard frog and boreal chorus frog), such indices instead provide insights into potential range contraction and/or expansion along a portion of the species range.

2.5 | Candidate models and model implementation

We compared our model to 11 simpler candidate models to assess the amount of support for spatiotemporal variation and nonlinearities in occupancy trajectories for each of the 11 species (Table 1) and the resulting implications on estimated statewide trends. The 12 models varied only in their ability to explain spatial and temporal variation in occupancy probability, with the model for detection being consistent across all candidate models. More specifically, the models varied in whether they included: (1) a spatially varying intercept to account for residual spatial autocorrelation in occupancy probability; (2) a simple linear trend parameter constant across all sites; (3) cubic basis splines for the trend parameter to account for nonlinear trends over time that are constant across space; (4) SVCs for the trend parameters to account for spatial variation in trends across the state; and (5) random year effects to account for additional variability in occupancy probability over time. We assessed the performance of the candidate models using WAIC (Watanabe, 2010) and compared the estimated trend metric to determine differences in trends under the different model structures.

We fit all models using the `spOccupancy` package (Doser et al., 2022) in R (R Core Team, 2024). For all models without spatially varying parameters, we ran three chains, each with 50,000 iterations with a burn-in period of 30,000 and a thinning rate of 10, resulting in a total of 6000 samples from the posterior distribution. For models with spatially varying parameters, we ran three chains, each with 200,000 iterations with a burn-in period of 120,000 iterations and a thinning rate of 40, resulting in a total of 6000 samples from the posterior distribution.

3 | RESULTS

We found strong support for spatial variation in occupancy trends across all 11 anuran species (Figure 2). Spatial variation in occupancy trends was highly species-specific, with some species having positive trends across the majority of the state but variation in the magnitude of the trend (e.g. boreal chorus frog), some with stable trends over the 20 year period (e.g. northern leopard frog), some with predominantly negative trends (e.g. mink frog), and others with both strong positive and strong negative trends across the state (e.g. wood frog,

TABLE 1 Characteristics of the 12 candidate models that varied in their ability to explain spatial and temporal variation in occupancy probability.

Model	SVI	Linear trend	Spline trend	SVC	Random year effect
Linear		✓			
Linear + RE		✓			✓
Spline			✓		
Spline + RE			✓		✓
SVI + Linear	✓	✓			
SVI + Linear + RE	✓	✓			✓
SVI + Spline	✓		✓		
SVI + Spline + RE	✓		✓		✓
SVC + Linear	✓	✓		✓	
SVC + Linear + RE	✓	✓		✓	✓
SVC + Spline	✓		✓	✓	
SVC + Spline + RE	✓		✓	✓	✓

Note: SVI indicates models with a spatially varying intercept, SVC indicates models that incorporate a spatially varying coefficient for the associated trend parameters, and RE indicates models with an unstructured random effect of year.

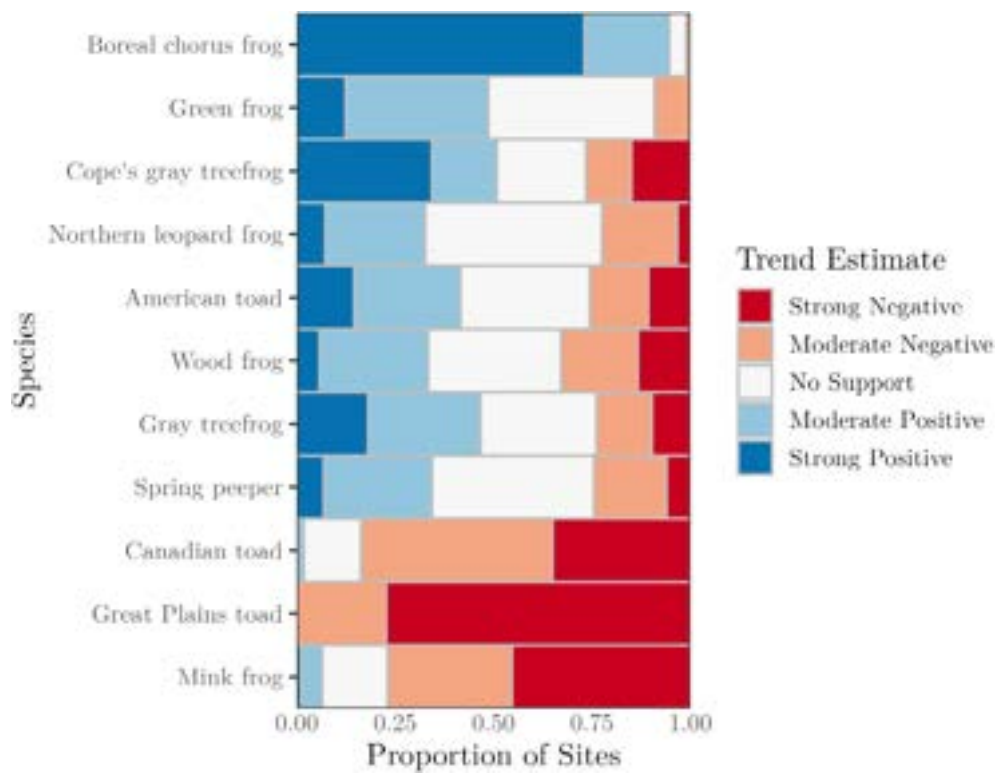


FIGURE 2 Summary of the spatially varying trends for the 11 anuran species. The width of each bar corresponds to the proportion of locations for the given species whose trend has the sign (i.e. positive, negative, no effect) and strength (i.e. strong, moderate) indicated by the colour. Blue indicates support for positive trends and red indicates support for negative trends, which are both determined based on the probability of the trend being greater than 0 (i.e. $p(\text{trend} > 0)$). More specifically: (1) Dark blue=Strong Positive: $p(\text{trend} > 0) > 0.8$; (2) Light blue=Moderate Positive: $0.6 < p(\text{trend} > 0) \leq 0.8$; (3) White=No effect: $0.4 < p(\text{trend} > 0) \leq 0.6$; (4) Light red=Moderate Negative: $0.2 < p(\text{trend} > 0) \leq 0.4$; (5) Dark red=Strong Negative: $p(\text{trend} > 0) < 0.2$. Estimates come from the top-performing model for each species. Only locations where a given species was ever detected over the 20-year period were included. Species are ordered by their overall median trend across locations.

Cope's grey treefrog; Figures 2 and 3). Spatial variation in occupancy trends was fine-scale relative to the extent of the study area, suggesting localized drivers of temporal occupancy trends (Table S1).

These fine-scale changes in occupancy probability are clearly observed in maps of the study area (Figure 3), and in associated trend uncertainty maps, where uncertainty quickly increases as distance

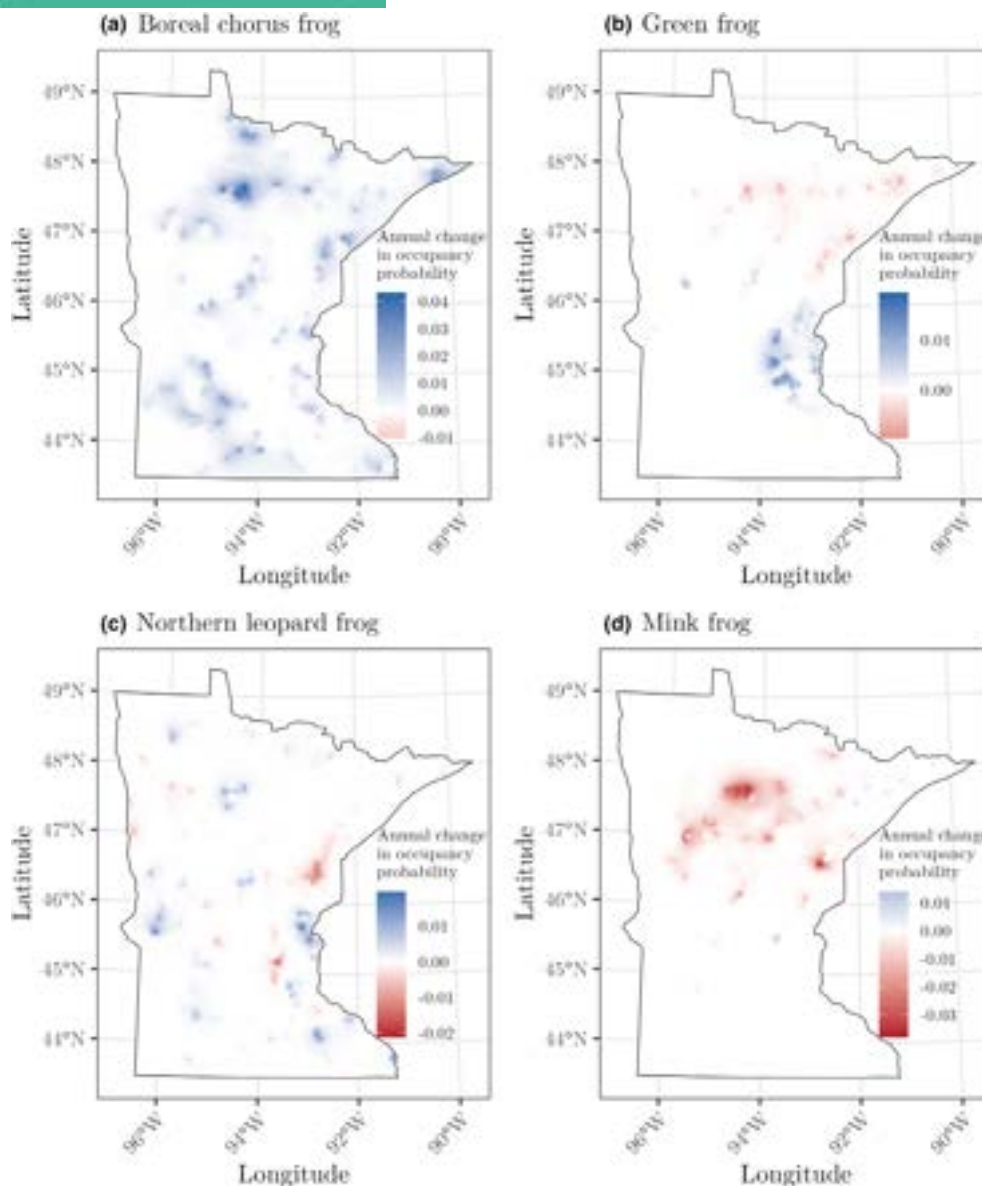


FIGURE 3 Median trend estimates for (a) boreal chorus frog (*Pseudacris maculata*), (b) green frog (*Lithobates clamitans*), (c) northern leopard frog (*Lithobates pipiens*), and (d) mink frog (*Lithobates septentrionalis*). Colour corresponds to the median average annual change in occupancy probability from 1996 to 2015. See [Supporting Information](#) for corresponding uncertainty maps.

from a sampled location increases (Figures S12–S22). Across the state, only one species, boreal chorus frog, had a significant statewide trend on annual occupancy (median = 0.008; 95% credible interval 0.003–0.013), which corresponded to an average increase in occupancy probability of 0.16 from 1996 to 2015. The statewide trends for all other species were not significantly different from zero (Figure 4).

Models estimating a spatially varying, nonlinear occupancy trajectory substantially outperformed simpler models according to WAIC for all species (Figure S2). Averaged statewide trends (across all stops) showed substantial variation across the 12 candidate models (Figures S3 and S5). For some species (e.g. spring peeper, boreal chorus frog), the sign and significance of the statewide trend were fairly consistent across models, while other species (e.g. wood

frog, grey treefrog) showed substantial differences in statewide trends when incorporating different components into the model. Importantly, differences in trend estimates between the candidate models were not consistent across species. Estimates of detection/availability probability were consistent across models. Day of year had the most prominent effects on detection/availability probability (Figure S10), although all covariates showed significant relationships across multiple species (Figure S11).

Summarizing species-specific trend maps across the state revealed a complex distribution of positive and negative trends across the 11 amphibian species (Figure 5). Fifty-seven percent of prediction locations across the state had support for more species with a negative trend compared to a positive trend, 36% had the same number of species with positive and negative trends,

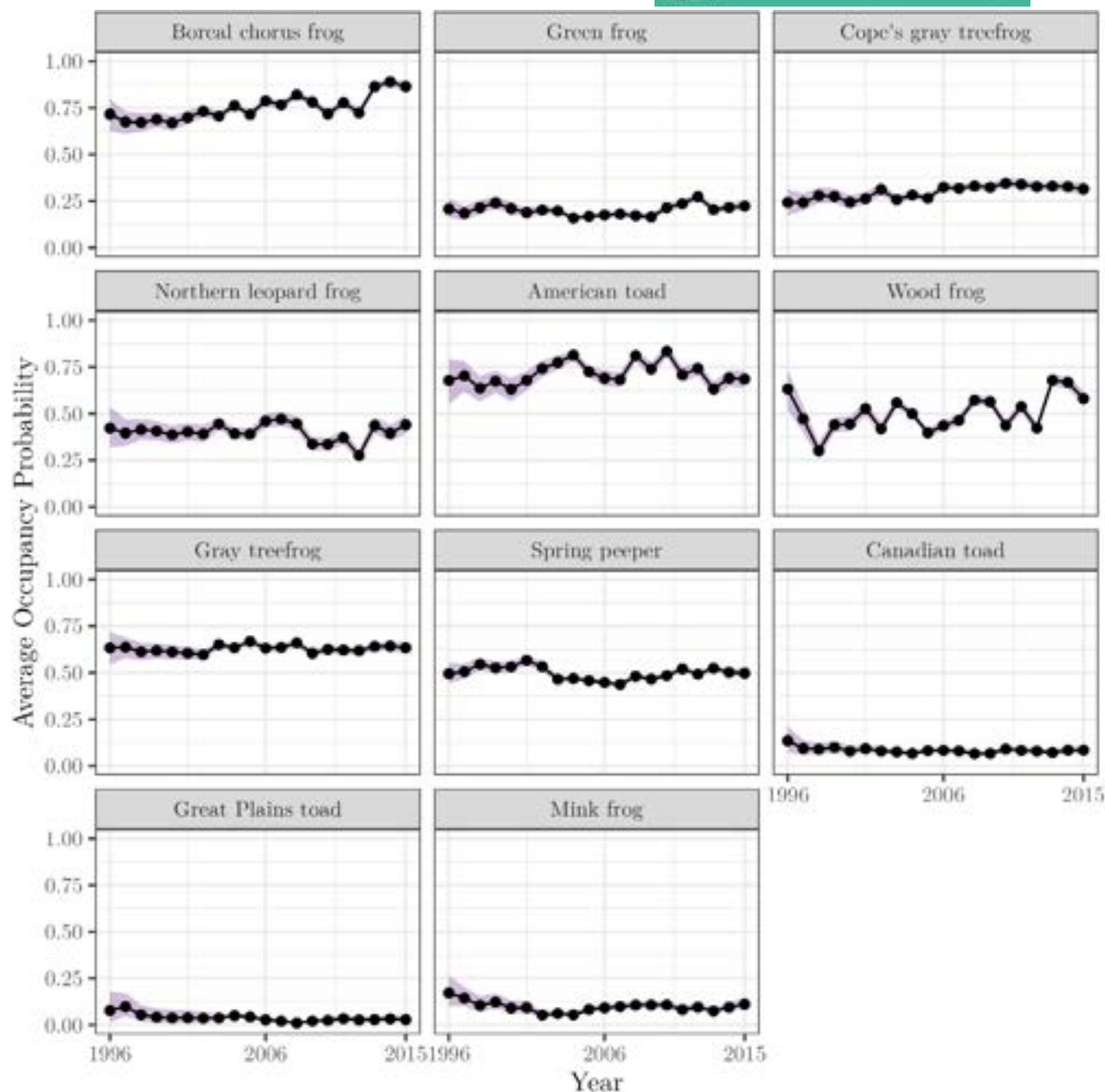


FIGURE 4 Average occupancy trajectories for the 11 anuran species across all sampled locations. Points correspond to the median average occupancy probability, with the shaded region indicating the 95% credible interval for the average occupancy probability across sampled locations. Estimates come from the top-performing model for each species. Species are ordered by their overall median trend across locations.

and only 7% had support for more species with positive trends compared to negative trends. Overlaying the hotspot maps with ecological subsections provides an opportunity to assess the status of anuran communities within distinct ecological units that are directly relevant for management and monitoring initiatives in the Minnesota State Wildlife Action Plan (Minnesota Department of Natural Resources, 2026).

Predictions of spatially varying occupancy trends across the state provided fine-scale insights on anuran distribution change that

were not possible when solely estimating an overall statewide trend (Figures S12–S22). Figure 3 highlights four species that exemplify the range of patterns across the 11 species. Boreal chorus frog, a wide-ranging frog with its core distribution in Minnesota, increased or remained stable in occupancy probability across nearly the entire state (Figure 3a). Green frog, whose western range boundary falls within Minnesota, showed negative trends in the northeastern Laurentian forest province, with primarily positive trends in the central portion of the state (Figure 3b), highlighting the potential for variation

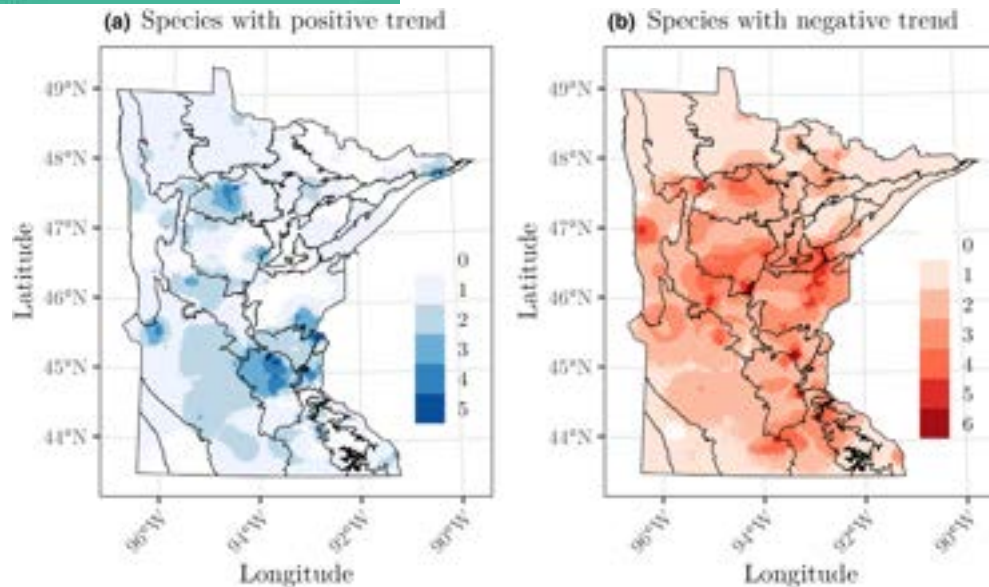


FIGURE 5 Spatially explicit maps showing the number of species across Minnesota with (a) strong support (probability of the trend being positive >0.8) for a positive trend and (b) strong support (probability of the trend being negative >0.8) for a negative trend.

in trend estimates across latitude. Northern leopard frog showed highly variable and localized trends across the state (Figure 3c). Mink frog declined across much of its existing range in the northern half of the state, which is particularly relevant in the context of range contraction given that Minnesota falls on the southern border of this species' range (Figure 3d). Within the state, we did not find support for latitudinal or longitudinal range shifts across any of the 11 species (Figures S7 and S8).

Scaling the spatially varying annual trend estimates across the 20-year time period revealed substantial local changes in occupancy probability over the time period (Table 2). Occupancy probability decreased by at least 25% for the Great Plains toad, mink frog, and Canadian toad at 79%, 47% and 36%, respectively, of the survey locations where the species was ever detected from 1996 to 2015. Further, we found declines of at least 75% of initial occupancy probability at 13%, 8% and 14% of sites for the aforementioned three species. Occupancy probability increased by over 75% of initial occupancy probability at 30% and 13% of sites for Cope's grey treefrog and boreal chorus frog, respectively, from 1996 to 2015.

The flexibility of our Bayesian approach allowed us to generate trend estimates (and associated uncertainty) within areal units directly relevant for management and conservation planning. For example, while the statewide trend for American toad indicates essentially no change in occupancy each year (Figure 6a), trends summarized within ecological provinces, sections and subsections reveal clear locations of both positive and negative annual trends (Figure 6). In addition to summarizing the annual trends, we can summarize the full occupancy trajectories within distinct areal units to assess spatial variation in the trend and shape of the trend over time across management-relevant areas (Figure 7). Summaries at the

TABLE 2 Summary statistics on the magnitude and ecological relevance of occupancy change from 1996 to 2015.

Species	$\Delta < -75\%$	$\Delta < -25\%$	$\Delta > 25\%$	$\Delta > 75\%$
American toad	0.03	0.13	0.10	0.06
Boreal chorus frog	0.00	0.01	0.25	0.13
Canadian toad	0.14	0.36	0.02	0.01
Cope's grey treefrog	0.11	0.19	0.36	0.30
Grey treefrog	0.04	0.15	0.11	0.07
Great Plains toad	0.13	0.79	0.00	0.00
Green frog	0.00	0.00	0.18	0.04
Mink frog	0.08	0.47	0.04	0.02
Northern leopard frog	0.00	0.09	0.12	0.04
Spring peeper	0.03	0.10	0.12	0.04
Wood frog	0.03	0.16	0.03	0.00

Note: Values indicate the proportion of sites where the occupancy probability from 1996 to 2015 declined by 75% ($\Delta < -75\%$), declined by 25% ($\Delta < -25\%$), increased by 25% ($\Delta > 25\%$) or increased by 75% ($\Delta > 75\%$). Percent change is defined as the estimated site-specific annual trend (Equation 6) by the estimated occupancy probability for the site in 1996. Note that only those sites where a species was observed at least once were used in calculation of the percent change metrics.

ecological section level reveal varying amounts of spatial variation in the shape of trajectories over the 20-year time period (Figure 7). Some species show clear spatial variation in the shape of occupancy trajectories across ecological sections (e.g. grey treefrog, Cope's grey treefrog, Canadian toad), while others show fairly consistent shapes across the distinct sections (e.g. boreal chorus frog, northern leopard frog).

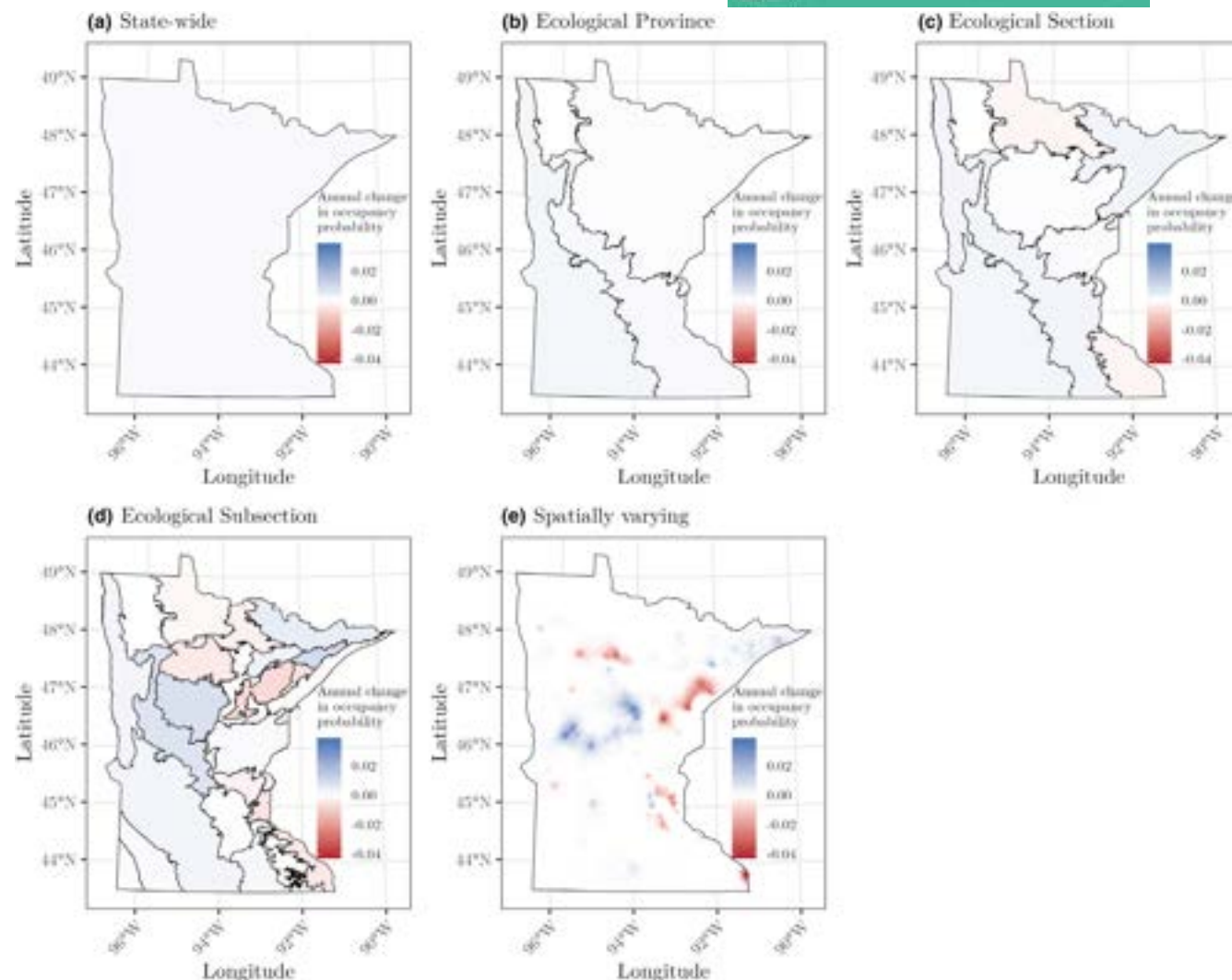


FIGURE 6 Median occupancy trend estimates for American toad (*Anaxyrus americanus*) summarized across different areal units of management interest in Minnesota. The full spatially varying trend (e) is averaged within areal units to generate area-wide trend estimates for (a) the entire state, (b) ecological provinces, (c) ecological sections and (d) ecological subsections. Colour corresponds to the median average annual change in occupancy within the given stratum.

4 | DISCUSSION

Accurate estimates of occupancy trends at both local and broad spatial scales are critical for informed conservation and management, especially as threats such as habitat loss/degradation, climate change, and disease are increasing. Identifying local trends and how such trends scale up regionally is particularly important for taxonomic groups such as amphibians that are in widespread decline (Adams et al., 2013) and face myriad, nonstationary stressors across their ranges (Grant et al., 2016, 2020). Using a 20-year participatory science data set, we quantified spatially varying occupancy trends in 11 anuran species across Minnesota, USA, which represents an important transition zone between boreal forest, eastern deciduous forest, and prairie grasslands in North America. Across all species, we found strong support for both spatially varying trends and nonlinear occupancy trajectories. Our modelling approach revealed

species-specific, fine-scale occupancy trends across Minnesota that were obscured when using simpler models aggregating key factors driving ecological heterogeneity. We refer to this phenomenon—commonly encountered in ecological analyses—as aggregate trend dilution. More broadly, we showcased how our framework can be used to identify hotspots of decline across multiple species for targeted monitoring or management actions, as well as generate trend estimates within specific areal units of management interest.

The magnitude of occupancy change estimated in our analysis is broadly consistent with patterns reported in other large-scale amphibian monitoring studies in North America. Analyses of NAAMP calling survey data from the northeastern United States documented widespread declines in anuran occupancy over a similar decadal time frame, with substantial heterogeneity among species and states (Weir et al., 2014). Likewise, national-scale assessments of amphibian occupancy trends across the United States have reported

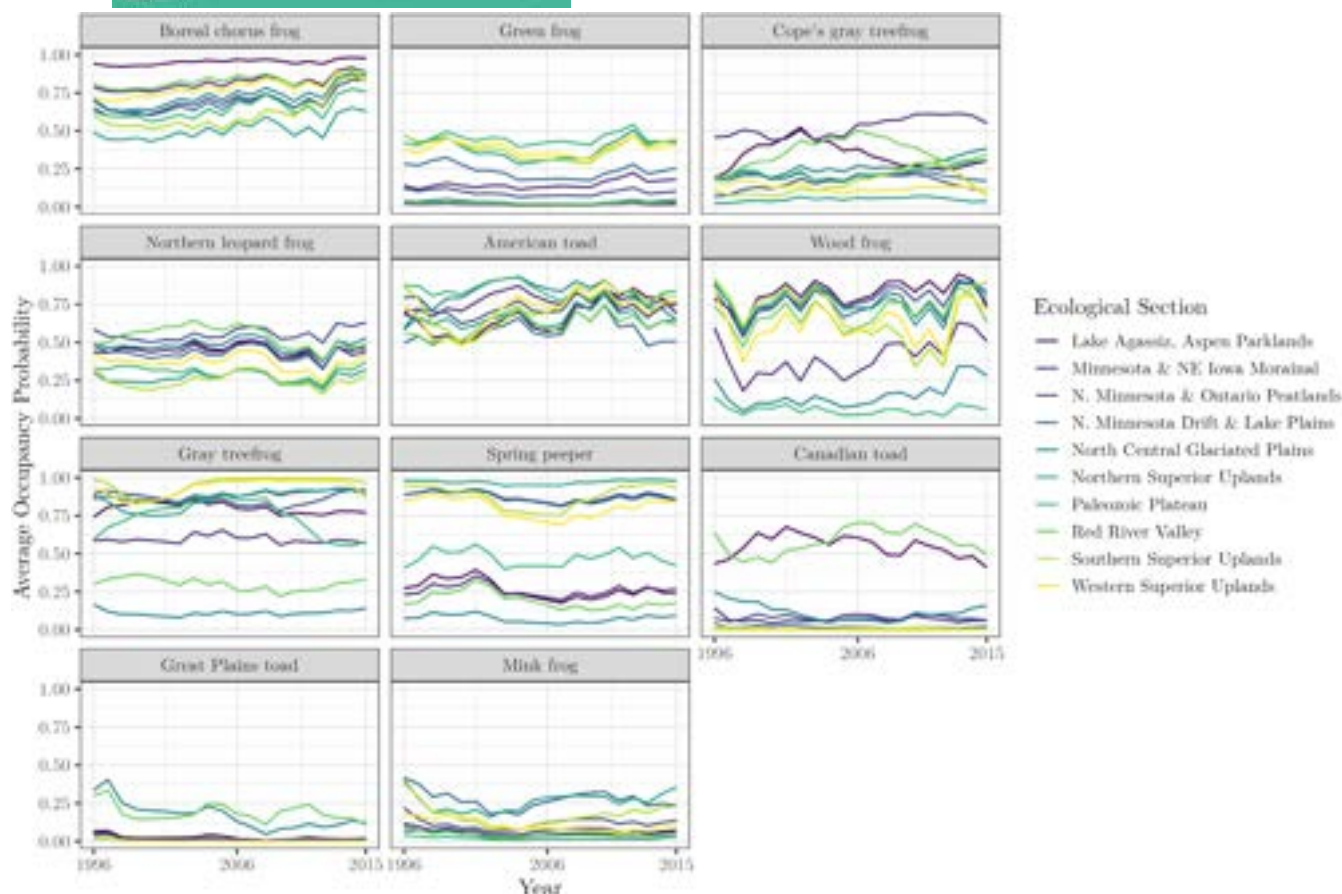


FIGURE 7 Occupancy trajectories for the 11 anuran species summarized across the 10 ecological sections of Minnesota. Lines represent the median average occupancy probability over time for a location within the specific ecological section. Estimates come from the top-performing model for each species. Species are ordered by their overall median trend across locations.

modest annual declines for many species that, when accumulated over multiple decades, result in substantial reductions in occupancy (Adams et al., 2013). Although direct quantitative comparisons are complicated by differences in spatial extent, survey protocols and modelling approaches, the magnitude and variability of trends observed in Minnesota align with the broader conclusion that anuran populations across North America are experiencing persistent, spatially heterogeneous declines.

Ignoring spatial variation and/or nonlinearity in occupancy trajectories limits the ability to explore variation in trends across local scales. Notably, models including spatially varying nonlinear occupancy trajectories consistently outperformed simpler alternatives according to WAIC for all 11 species, highlighting the utility of this framework for taxa characterized by high inter-annual variability in abundance and/or reproduction (Green, 1997; White, 2019). A key inferential benefit of our SVC approach is its ability to simultaneously depict localized occupancy trends (Figure 3) and summarize broader-scale patterns relevant to conservation actions and policy (Figure 6). Maps of local trends can provide insights into potential drivers of occupancy dynamics (Barnett et al., 2021; Doser et al., 2024), while highlighting hotspots of decline and areas where conservation actions or targeted intervention may be most warranted (Smith et al., 2024).

Aggregating local estimates within Minnesota's ecological subsections further enables identification of priority habitats for conservation action (Figure 6d). By highlighting the ecological strata showing the steepest occupancy declines for each species, our results identify both broad regions of concern and specific locations within subsections where management interventions or focused follow-up studies could be most effectively applied. In particular, areas experiencing pronounced declines can serve as focal locations for targeted field investigations or integrative assessments aimed at identifying underlying drivers of anuran population change, such as habitat alteration, hydrologic modification, or land-use practices. Our findings can be used to guide decisions on where management actions designed to provide, protect, or enhance anuran habitat may have the greatest benefit for one or multiple anuran species.

By overlaying species-specific occupancy trends, our spatial modelling framework enables the identification of community-level hotspots that can inform the prioritization of monitoring and conservation efforts across broad spatial extents (Figure 5). Interestingly, several species exhibited positive trends in the highly developed Twin Cities metropolitan area (Figure 5a), and extensive hotspots of decline were evident elsewhere across the state (Figure 5b). Such hotspot maps provide a practical tool for

allocating limited conservation resources and designing targeted monitoring programs with the potential to benefit multiple species simultaneously.

Our work highlights the importance of participatory science monitoring programs in providing data on multi-species communities across large spatiotemporal regions. We found large variation in species-specific trends across the state, which suggests conservation actions based on a single species, or in a smaller portion of the state, would provide only limited conservation benefits for the anuran community in Minnesota. Given the logistical difficulties with long-term monitoring of multiple species across large spatial extents, participatory science monitoring programs offer the possibility to understand fine-scale trends in wildlife communities that are infeasible with limited agency resources. The accuracy of semi-structured amphibian participatory science data that followed a similar protocol used in our study was on par with surveys performed by professional biologists (Estes-Zumpf et al., 2022). Moreover, participatory science data have been used to inform targeted conservation actions for amphibians (Cosentino et al., 2014). We strongly encourage state agencies, universities, and non-profit organizations to assist in the coordination of participatory science programs to ensure sustainability of long-term monitoring programs. Public engagement with wildlife is often a key objective of state or federal government wildlife action plans, and thus coordination of participatory science programs can provide increased engagement with wildlife while also helping agencies achieve monitoring objectives.

Our spatially explicit trend maps offer opportunities to identify new locations where targeted monitoring in participatory science programs could help minimize uncertainty in trends for species or areas of conservation priority. In particular, researchers and agency personnel could assist in determining new survey locations in participatory science programs to mitigate potential problems with preferential sampling that often hinder the use of participatory science data for conservation management (Tang et al., 2021). By prioritizing new sampling locations based on a spatially adaptive cluster sampling design (e.g. Pacifici et al., 2016) or generalized random tessellation stratified protocol (Stevens Jr & Olsen, 2004), the survey design of participatory science programs could be made more robust while simultaneously providing data across scales that are infeasible to collect via traditional monitoring approaches.

While the model we present provides a unique ability to predict complex occupancy trajectories across multiple spatial scales, our approach requires larger sample sizes across both space and time relative to simpler trend estimation approaches (e.g. a non-spatial occupancy model with a random trend across ecological strata). While specific sample size requirements are likely dependent on a variety of ecological and sampling characteristics of a given data set, simulation results on multi-season SVC occupancy models from Doser et al. (2024) suggest at least 100 spatial locations are required for accurate estimation of spatially varying occupancy trends. We expect the number of locations and time periods required for accurate and precise estimates to increase for

occupancy trajectories exhibiting large amounts of nonlinearity. We encourage the use of simulation studies based on empirical data set characteristics to understand the feasibility of estimating spatially varying, nonlinear occupancy trajectories (DiRenzo et al., 2023).

5 | CONCLUSIONS

Our case study on anurans in Minnesota showcases the conservation utility of estimating spatially varying occupancy trends to evaluate species distribution change across multiple scales. Localized species trends can be used to assess effects of management actions, inform spatial prioritization of protected areas (Taylor et al., 2022), and hypothesize drivers of occupancy and/or population trends (Crossley et al., 2021). As wildlife communities continue to face myriad stressors, a crucial first step in conservation and management initiatives is to identify how populations and communities are changing locally, and how such local trends scale up to broader spatial extents. Our flexible spatial occupancy model can be fit using user-friendly functions in the `spOccupancy` R package (Doser et al., 2022), and thus can be readily applied to a variety of taxa and geographic locations to yield detailed understanding of species distribution changes.

AUTHOR CONTRIBUTIONS

Jeffrey W. Doser, Christopher S. Jennelle, and Margaret Edwards designed the analysis methodology. Krista A. Larson coordinated the MN Frog and Toad survey from 2007 to 2017 and conceived numerous concepts related to anuran trend estimation in MN. Krista A. Larson, Margaret Edwards, and Christopher S. Jennelle managed and curated the data. Jeffrey W. Doser analysed the data with insights from Elise F. Zipkin and Christopher S. Jennelle. Jeffrey W. Doser led the writing of the manuscript. All authors contributed critically to the drafts.

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CONFLICT OF INTEREST STATEMENT

We declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All code associated with this manuscript is available at <https://doi.org/10.5281/zenodo.18868094> (Doser et al., 2026). The amphibian data contain location information for sensitive species considered non-public under Minnesota state statute, and thus the data cannot be made publicly accessible.

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SUPPORTING INFORMATION

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

Table S1. Median estimates of the effective spatial range (in km) for the spatially varying intercept and trend components for the top-performing model for each species.

Figure S1. Hypothetical example of a spatially varying trajectory using cubic basis splines.

Figure S2. Model comparison results using WAIC for the 11 anuran species across the 12 candidate models.

Figure S3. Comparison of overall trend estimates for the 11 anuran species across the 12 candidate models.

Figure S4. Average occupancy trajectories for the 11 anuran species across all sampled locations.

Figure S5. Differences in species-specific average occupancy trajectories for the four candidate models including a spatially varying coefficient (SVC).

Figure S6. Naive occupancy probability trajectories using the raw detection-nondetection data.

Figure S7. Mean latitude index for the 11 anuran species across Minnesota.

Figure S8. Mean longitude index for the 11 anuran species across Minnesota.

Figure S9. Estimates of the relationship between spatial covariates and occupancy probability for the 11 anuran species.

Figure S10. Estimated relationship between detection probability and day of the year for the 11 anuran species.

Figure S11. Estimates of the relationship between covariates and detection probability for the 11 anuran species.

Figure S12. Predicted occupancy trends and occupancy probability for American toad *Anaxyrus americanus*.

Figure S13. Predicted occupancy trends and occupancy probability for Great Plains toad *Anaxyrus cognatus*.

Figure S14. Predicted occupancy trends and occupancy probability for Canadian toad *Anaxyrus hemiophrys*.

Figure S15. Predicted occupancy trends and occupancy probability for Cope's gray treefrog *Hyla chrysoscelis*.

Figure S16. Predicted occupancy trends and occupancy probability for gray treefrog *Hyla versicolor*.

Figure S17. Predicted occupancy trends and occupancy probability for green frog *Lithobates clamitans*.

Figure S18. Predicted occupancy trends and occupancy probability for Northern leopard frog *Lithobates pipiens*.

Figure S19. Predicted occupancy trends and occupancy probability for mink frog *Lithobates septentrionalis*.

Figure S20. Predicted occupancy trends and occupancy probability for wood frog *Lithobates sylvaticus*.

Figure S21. Predicted occupancy trends and occupancy probability for spring peeper *Pseudacris crucifer*.

Figure S22. Predicted occupancy trends and occupancy probability for Boreal chorus frog *Pseudacris maculata*.

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