



A hierarchical analysis of habitat area, connectivity, and quality on amphibian diversity across spatial scales

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Abstract

Context Habitat fragmentation can alter species distributions and lead to reduced diversity at multiple scales. Yet, the literature describing fragmentation effects on biodiversity patterns is contradictory, possibly because most studies fail to integrate spatial scale into experimental designs and statistical analyses. Thus, it is difficult to extrapolate the effects of fragmentation to large-scaled systems in which conservation management is of immediate importance.

Objectives To examine the influence of fragmentation on biodiversity across scales, we (1) estimated the effects of habitat area, connectivity, and quality at both local (i.e. community) and regional (i.e.

metacommunity) scales; and (2) evaluated the direction, magnitude, and precision of these estimates at both spatial scales.

Methods We developed a multi-region community occupancy model to analyze 13 years (2005–2017) of amphibian monitoring data within the National Capital Region, a network of U.S. National Parks.

Results Overall, we found a positive effect of park size and a negative effect of isolation on species richness at the park-level (i.e. metacommunity), and generally positive effects of wetland area, connectivity, and quality on species richness at the wetland-level (i.e. community), although parameter estimates varied among species. Covariate effects were less precise, but effect sizes were larger, at the local wetland-level as compared to the park-level scale.

Conclusions Our analysis reveals how scale can mediate interpretation of results from scientific studies, which might help explain conflicting narratives concerning the impacts of fragmentation in the literature. Our hierarchical framework can help managers and policymakers elucidate the relevant spatial scale(s) to target conservation efforts.

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Introduction

Habitat fragmentation can dramatically decrease species richness through reductions in available habitat, a loss of connectivity among habitats, and degradation of remaining habitat (Haddad et al. 2015). The effects of habitat area, connectivity, and quality on biodiversity have been examined extensively through experiments and in small-scale observational studies across taxa (e.g. Haddad et al. 2015; Humphrey et al. 2015; Fletcher et al. 2016). Yet, results from empirical studies are often contradictory as to the exact cause(s) of species loss (Debinski and Holt 2000; Fahrig 2003; Prugh et al. 2008; Ibáñez et al. 2014; Reynolds et al. 2018), and thus there is no consensus on the specific drivers of species declines in fragmented landscapes (Hodgson et al. 2009; Doerr et al. 2011; Hodgson et al. 2011; Fahrig 2013; Haddad et al. 2017a). For example, a recent review of long-term fragmentation experiments found that both decreased area and increased isolation (i.e. lack of connectivity) have significant negative effects on species richness (Haddad et al. 2015), whereas a meta-analysis of approximately 800 species (over 1000 population networks) indicated habitat area and isolation are not good predictor variables of species occupancy (Prugh et al. 2008). Moreover, the spatial scale of habitat fragmentation studies often does not match the scale relevant to the target species' ecology (Betts et al. 2014; Resasco et al. 2017), which renders comparisons difficult and may contribute to conflicting results. A recent review of multiscale species-landscape studies found that ~ 70% of studies did not report biological justification for the selection of scale (Jackson and Fahrig 2015). Determining the spatial scales at which fragmentation processes are related to species extirpations, and thus the spatial scale(s) at which to target management, is critical for conservation success.

Inferences on biological phenomena are influenced by the scale of observation (Levin 1992), which makes drivers of species distribution and biodiversity patterns challenging to assess. The occurrence of an individual at a particular location is nested hierarchically such that local species pools (alpha diversity) are constrained by the regional species pool (gamma diversity) and dispersal pathways (Leibold et al. 2004; Brown et al. 2011). The environmental drivers that affect geographic variation in species richness can

thus occur at, and interact across, multiple scales (Wiens 1989; Heffernan et al. 2014). Along with these cross-scale interactions, spatial heterogeneity can impede translation of ecological processes from local to broad scales (Wu 1999; Fei et al. 2016). Specifically, non-linear patterns of species richness across spatial extents make it difficult to scale up estimates of biodiversity from local-scale sampling grids for inferences at the level of the landscape, region, or continent ('domains of scale'; Wiens 1989; Chesson et al. 2005; Azaele et al. 2015). Studies that investigate the effects of fragmentation on biodiversity patterns hierarchically across multiple scales are scarce (McGarigal and Cushman 2002; Chandler and Hepinstall-Cymerman 2016; Haddad et al. 2017b; Reynolds et al. 2017; Fletcher et al. 2018; Fahrig et al. 2019; but see Cecala et al. 2018), but necessary to determine the mechanisms shaping species distribution patterns.

Species richness is a commonly used metric to summarize biodiversity patterns (MacArthur and Wilson 1967; Yoccoz et al. 2001). However, it is difficult to determine the exact number of species in a location or region, particularly for communities that contain rare and/or cryptic species. Failure to account for imperfect and variable detection can lead to biased inferences of local and regional species pools (Boulinier et al. 1998; Guillera-Aroita et al. 2014). Multi-species site occupancy models can account for these limitations mechanistically, linking multiple single-species occupancy models (MacKenzie 2006) in a unified hierarchical framework (Dorazio and Royle 2005; Dorazio et al. 2006). Recent developments have extended community models into a multi-region context, allowing parameters to vary spatially among independent units (e.g. reserves, parks, biomes, etc.; Sutherland et al. 2016). This approach facilitates estimation of species richness hierarchically across environmental gradients at multiple scales within a single, analytical framework. Such models allow for analysis of large-scale datasets to estimate the effects of fragmentation on the size and structure of local communities and metacommunities, while incorporating relevant habitat covariates, spatial variation, and species detectability (Yoccoz et al. 2001; Sutherland et al. 2016).

In the last 20 years, the National Park Service (NPS) initiated a spatially extensive monitoring program to track the status of park ecosystems across the country, with the goal of improving management

(Parsons 2004; Fancy et al. 2009). The National Capital Region Network (NCRN) is an ecoregional network of 11 National Parks in and surrounding the greater Washington, DC metropolitan area (NPS 2005). The NCRN is ideal for assessing the impacts of fragmentation (i.e. area, connectivity, and quality) across scales, as parks within the network (1) are limited in size such that factors external to park boundaries have significant influence (Stottlemeyer 1987), (2) exist along an urban–rural gradient (Lookingbill et al. 2014), and (3) vary by purpose and thus landscape use and history (e.g. parks are principally designated as ecological vs. cultural via legislation; NPS 2006). Amphibians have been monitored within the NCRN since 2005 as an indicator of biological integrity (‘Vital Sign’) for each park, and for the region as a whole (NPS 2005). The lentic amphibian community is an ideal case-study within this network because (1) species exist in well-defined patches (i.e. wetlands), (2) individuals have limited mobility (relative to other vertebrates), and (3) populations are expected to be sensitive to both local (i.e. patch) and broad-scale (i.e. landscape or regional) perturbations (Cushman 2006; Grant et al. 2016). The minimal disturbance within the protected parks, urban sprawl in the region, and dispersal constraints of amphibians limit the interactions of communities within parks to other natural areas, forming distinct metacommunities at the park-level (Leibold et al. 2004; Goodwin and Shriver 2014; Lookingbill et al. 2014). Management decisions are also made at the park-level, such that understanding amphibian processes within individual parks is critical for effective conservation. These characteristics of the network provide a unique opportunity to evaluate the effect of patch- and landscape-scale factors in the context of habitat fragmentation on a metacommunity of sensitive species (McGarigal and Cushman 2002; Fahrig 2003).

The objective of our study is to estimate amphibian species occurrence and richness within and among parks, and determine the key drivers (related to area, connectivity, and quality) of species’ occupancy trends over time and across scales within the NCRN. To do this, we fit a multi-region, community occupancy model (Sutherland et al. 2016) to estimate species- and park-specific occupancy and detection rates. We estimated species richness at both the local wetland (i.e. patch) and park (i.e. landscape) scales, and evaluated the effects of wetland-scale drivers on

species occupancy rates and community size, and landscape-scale drivers on the metacommunity size. Our results help to evaluate how conservation actions can mitigate threats to amphibians at both local and regional scales, as well as elucidate the relevant spatial scale(s) at which practitioners may target resource management efforts.

Methods

Study area

Our study area encompasses the NCRN of the NPS which includes National Parks in the District of Columbia, Maryland, West Virginia, and Virginia in the Mid-Atlantic region of the United States (NPS 2005). The network includes 11 parks (abbreviated with four letter acronyms): Antietam National Battlefield (ANTI), Catoctin Mountain Park (CATO), Chesapeake & Ohio Canal National Historical Park (CHOH), George Washington Memorial Parkway (GWMP), Harpers Ferry National Historical Park (HAFE), Manassas National Battlefield Park (MANA), Monocacy National Battlefield (MONO), National Capital Parks – East (NACE), Prince William Forest Park (PRWI), Rock Creek Park (ROCR), and Wolf Trap National Park for the Performing Arts (WOTR). These parks lie mostly within the Potomac River Basin and include both the coastal plain and piedmont ecoregions with forest cover that is mainly mixed/deciduous forest. Each park has a principle purpose to preserve either cultural or natural resources, and/or provide recreational opportunities (e.g. civil war battlefields, urban parks, and natural forests; NPS 2005; Lookingbill et al. 2014). Parks vary in size, habitat composition and configuration, and isolation with respect to other amphibian habitats outside the park boundaries, as well as the years sampled (Table 1).

Sampling methods

The Northeast region of U.S. Geological Survey’s Amphibian Research and Monitoring Initiative has monitored the lentic amphibian community in 9 of the 11 parks within the National Capital Region Network since 2005 (CATO, CHOH, GWMP, HAFE, MANA, MONO, NACE, PRWI and ROCR). However, not all

Table 1 The NCRN National Parks and their relevant descriptors, including the years in which they have been sampled, park size (in hectares), the percent forest cover within the park, and the percent of area within 1 km outside of the park that can be characterized by landcover classes that categorize developed and open water areas

Park	Years sampled	Size (ha)	% Forest	% Isolated
ANTI	–	1318	13.88	13.46
CATO	2015–2017	2331	95.18	15.18
CHOH	2005–2017	8435	67.22	26.42
GWMP	2017	2152	42.55	76.05
HAFE	2015–2016	1498	68.13	24.19
MANA	2013–2017	2055	34.76	36.26
MONO	2015–2017	656.0	19.17	35.69
NACE	2016	4600	42.83	74.70
PRWI	2017	5075	92.29	34.20
ROCR	2005–2017	1179	62.92	93.45
WOTR	–	53.00	48.79	59.96

parks were monitored every year nor did monitoring begin in 2005 for all parks (Table 1). All mapped wetlands which were isolated, palustrine, and < 0.4 ha in area were included for possible sampling (Mattfeldt et al. 2009). A subset of wetlands at each park was randomly selected for sampling.

Wetlands were sampled on 1–5 occasions (secondary sampling period) during the breeding season (March–July) each year (primary sampling period) a park was visited. Wetlands were only surveyed when water was present. On each sampling occasion, two observers independently walked the perimeter of the wetland (starting at opposite ends and walking in the same direction) and separately recorded the detection of any species encountered. A detection of an amphibian species occurred through an encounter of eggs, juveniles, or breeding adults (via visual/auditory encounters) or larvae (via dip-net surveys; full sampling protocols in Grant and Brand 2012). Each observer was treated as an individual replicate, yielding a potential maximum of 10 repeat sampling events for a given wetland within a year. We assumed amphibian occurrence status to be closed (i.e. no change in species-specific wetland occupancy) within a year (i.e. between secondary sampling periods), but allowed for occupancy status to change annually (i.e. between primary sampling periods).

We sampled 243 unique wetlands and observed 15 amphibian species across all parks and years of our study (2005–2017). Two species complexes (*Anaxyrus americanus/fowleri* and *Hyla versicolor/chrysocelis*) were analyzed together due to the inability to distinguish their tadpoles with certainty. The 15 amphibian species/complexes detected included *Acris crepitans* (northern cricket frog), *Ambystoma maculatum* (spotted salamander), *Ambystoma opacum* (marbled salamander), *Anaxyrus americanus/fowleri* (American/Fowler’s toad), *Hemidactylium scutatum* (four-toed salamander), *Hyla versicolor/chrysocelis* (gray treefrog complex), *Lithobates catesbeianus* (American bullfrog), *Lithobates clamitans* (northern green frog), *Lithobates palustris* (pickerel frog), *Lithobates sphenoccephalus* (southern leopard frog), *Lithobates sylvaticus* (wood frog), *Notophthalmus viridescens* (eastern newt), *Pseudacris crucifer* (spring peeper), *Pseudacris feriarum* (upland chorus frog), and *Scaphiopus holbrookii* (eastern spadefoot toad). We excluded data in cases where an individual could not be identified to the species/species complex level. Observers at ROCR during 2005–2015 only recorded the presence of three species (*Ambystoma maculatum*, *Ambystoma opacum*, and *Lithobates sylvaticus*), and sampling was not always conducted with two, independent observers due to logistical constraints.

Park covariates

We used three park-level covariates to estimate the effects of fragmentation on park-level species richness: park area, percent forest cover, and degree of isolation. Park area, the size of each park in hectares, ranged from 656 to 8435 ha (Table 1); we expected to find a positive effect of park area on species richness. We used percent forest cover to represent the landscape composition of each park. We also considered using a park-level index of forest fragmentation, which accounts for the spatial distribution of forest habitat within each park given the total amount of forest (i.e. an aggregation index of forested habitat calculated using the ‘landscapemetrics’ package in R; Hesselbarth et al. 2019), to characterize landscape configuration (McGarigal et al. 2012). However, this metric was highly correlated (> 0.90) with percent forest cover, suggesting that parks with large amount of forest generally had highly aggregated forest patches. Thus, we used only percent forest cover as a

proxy for habitat quality at the park-level. We hypothesized that landscapes with higher forest cover and more aggregated forest patches (i.e. natural resource parks) would have higher species richness than parks with a lower percentage forest cover and more dispersed forested patches (i.e. cultural resource parks), as the mid-Atlantic region was naturally forested pre-European colonization and thus the regional metacommunity evolved within forested ecosystems. Degree of isolation (% developed and open water land use classes surrounding park within 1 km buffer) is a proxy for the urban-natural gradient within the larger geographical region and correlated with forest fragmentation surrounding parks (Bailey et al. 2007; Lookingbill et al. 2014). We selected a 1 km buffer to conservatively represent the maximum dispersal limits of amphibians within our metacommunity (Smith and Green 2005). We expected that park isolation would be negatively correlated with park richness, as the loss in connectivity of a park to other natural areas (i.e. supporting metacommunities) should inhibit successful immigration and the ability to maintain biodiversity (Brown et al. 2011). The absolute values of all pair-wise Pearson's correlation coefficients between the park covariates were less than 0.35.

Wetland covariates

We considered five wetland-level variables that can influence local species' occupancy: wetland area, connectivity, conductivity, hydroperiod, and local precipitation. Wetland area (m²) is measured as the minimum product of the length and width taken across all sampling occasions in each year. We expected a positive effect of wetland area on species occupancy and richness because larger habitats should harbor and produce more juveniles, and are expected to have greater heterogeneity of microhabitats within wetlands. On each occasion, we measured water conductivity (μS) as a proxy for water quality, which we averaged across sampling events in a given year (Mattfeldt et al. 2009). We expected poor water quality resulting from exurban development (i.e. high conductivity) to negatively affect species occupancy rates (Turtle 2000). As an additional proxy for local habitat quality, we categorized each wetland by its hydroperiod—the length of time a wetland retains water—into one of three classes: temporary (dries

annually), semi-permanent (dries every two or more years), and permanent (never dries). Wetland connectivity was measured as a function of the distance (d) of a focal wetland i to all possible source wetlands j in the same park. To calculate connectivity, we used a negative exponential dispersal kernel equation:

$$conn_i = \sum_{j \neq i} e^{-\theta d_{ij}} area_j$$

which weights source wetlands by area, as larger wetlands generally have larger potential pools of dispersers (Moilanen and Nieminen 2002). We conservatively set the mean migration distance, $1/\theta$, to 750 m for all species (Werner et al. 2007; Zipkin et al. 2012). We hypothesized a positive effect of connectivity on species' occupancy, as high connectivity to other breeding habitat should increase colonization rates, yet other studies in the region have shown no effect of connectivity (in CHOH; Zipkin et al. 2012). To account for regional variation in climate conditions, we defined seasonal precipitation covariates as the cumulative daily precipitation (01 Feb–31 May, obtained from the regional PRISM model; Daly et al. 2008) for the park centroid location of all surveyed wetlands. Thus, precipitation was calculated as an annual value that varied by parks but not by wetlands within parks. We hypothesized that occupancy would be higher in years and parks with greater precipitation.

Statistical analyses

We analyzed species detection–nondetection data using a hierarchical multi-region, community modeling framework (Sutherland et al. 2016), which extends the multi-species 'community' occupancy model (Dorazio and Royle 2005; Dorazio et al. 2006) to jointly estimate species richness at wetland- and park-levels. This hierarchical approach allows for inference on species richness, at both the community and metacommunity levels, through estimation of species occupancy and detection probabilities using local and regional environmental covariates. We defined the amphibian metacommunity as the set of species within a given, spatially independent park (i.e. park richness), which is distinct from a local community, or the number of species present at a wetland (i.e. wetland richness).

The detection-nondetection data, $X_{i,r,j,t,k}$, consist of a binary variable (detection = 1, nondetection = 0) for species i (1, 2, ..., n_r) within park r (1, 2, ..., 9) at wetland j (1, 2, ..., j_r) during year t (1, 2, ..., t_r) on occasion k (1, 2, ..., $k_{r,t}$). A species present at a wetland may not be detected during every sampling event, leading to false negatives within the sampling data. Thus, we used a latent state variable, $Z_{i,r,j,t}$, to characterize the true occupancy of species i in park r , wetland j , and year t (where $Z_{i,r,j,t} = 1$ if the wetland is occupied by species i and 0 otherwise). By repeatedly sampling sites on multiple occasions during a time period when occupancy status is closed (i.e. within primary sampling period t), we can distinguish false negatives from true absences and explicitly estimate species' detection probabilities (MacKenzie et al. 2002). We do this by assuming that the data are distributed according to a Bernoulli random process where $X_{i,r,j,t,k} \sim \text{Bern}(p_{i,r,j,t,k} * Z_{i,r,j,t})$ and $p_{i,r,j,t,k}$ is the probability of detecting species i within park r at wetland j during year t on occasion k (conditional on presence of species i). Detection probability (p) is modeled using a logit-link function with covariates:

$$\text{logit}(p_{i,r,j,t,k}) = \beta 0_{i,r} + \beta 1_{i,r} \text{date}_{j,t,k} + \beta 2_{i,r} \text{date}_{j,t,k}^2 + \varepsilon_t$$

where $\beta 0$ is a species- and region-specific intercept term, $\beta 1$ and $\beta 2$ are the species- and region-specific linear and squared effects of day of year ($\text{date}_{j,t,k}$), and ε is a random effect of year t . We modeled detection by day of year to account for the differences of seasonal availability and breeding periods among species. The random year effect accounts for other seasonal variation (such as shifts in phenology) and is assumed to come from a normal distribution centered around zero with a variance that is also estimated in our model.

We then modeled the latent occupancy status, $Z_{i,r,j,t}$, according to a Bernoulli random process, $Z_{i,r,j,t} \sim \text{Bern}(\Psi_{i,r,j,t} * w_{i,r})$, in which $\Psi_{i,r,j,t}$ is the occupancy probability of species i within park r at wetland j during year t . The parameter $w_{i,r}$ indicates whether species i exists within the metacommunity at park r . If species i exists at park r , $w_{i,r} = 1$, otherwise, $w_{i,r} = 0$, in which case, species i cannot be present at any wetland within park r . We modeled $\Psi_{i,r,j,t}$ using a logit link function including an intercept term that is dependent on hydroperiod (hydro_j) as well as covariates for annual wetland area ($\text{area}_{t,j}$), wetland

connectivity (conn_j), seasonal precipitation ($\text{precip}_{r,t}$), and annual wetland conductivity ($\text{cond}_{j,t}$):

$$\text{logit}(\Psi_{i,r,j,t}) = \alpha 0_{i,r,\text{hydro}_j} + \alpha 1_{i,r} * \text{area}_{j,t} + \alpha 2_{i,r} * \text{conn}_j + \alpha 3_{i,r} * \text{precip}_{r,t} + \alpha 4_{i,r} * \text{cond}_{j,t} + \varepsilon_{i,r,t}$$

We included a random year effect for each species i in each park r for each year t to account for otherwise unexplained variation, drawn from a global-level distribution in which $\varepsilon_{i,r,t} \sim \text{Norm}(0, \sigma_{\Psi,t}^2)$.

We used data augmentation (Royle et al. 2007) to estimate park-level species richness and $w_{i,r}$, the variable indicating whether species i exists within the metacommunity at park r . To do this, we augmented the data with m all-zero encounter histories. We chose to augment the data with $m = 15$ species as the size of the potential species pool (30, including the 15 observed, see 'Sampling Methods' section) is well above the known number of lentic-breeding amphibian species within the geographic region (Grant and Brand 2012). We then assumed that $w_{i,r}$ is characterized by a Bernoulli random process, $w_{i,r} \sim \text{Bern}(\Omega_r)$, where Ω_r is the probability that species i exists in the metacommunity in park r . We modeled Ω_r using a logit link function with covariates on park size (size_r), percent forest cover (forest_r), and park isolation (isolation_r):

$$\text{logit}(\Omega_r) = \gamma 0 + \gamma 1 * \text{size}_r + \gamma 2 * \text{forest}_r + \gamma 3 * \text{isolation}_r$$

The metacommunity size S_r (i.e. park-level species richness) is the total number of species estimated within park r :

$$S_r = \sum_1^{n+m} w_{i,r}$$

where n is the number of species observed across all parks (15). Our estimates of metacommunity size are conceptually similar to the asymptote of a species accumulation curve or the total number of species as the number of sites sampled approaches infinity (Zipkin et al. 2009). Annual wetland-specific species richness $N_{r,j,t}$ (i.e. community size) is a derived parameter calculated by the summation of the latent state variable $Z_{i,r,j,t}$ in region r at site j in time t across all species.

We assumed that each of the species-specific occupancy and detection parameters are drawn from common park-level normal distributions (e.g. $\alpha_{1i,r} \sim Norm(\mu_{z1,r}, \sigma_{z1}^2)$) with a mean hyper parameter (e.g. $\mu_{z1,r}$) that is in turn drawn from a global-level (i.e. across all parks) normal distribution (e.g. $\mu_{z1,r} \sim Norm(\bar{\mu}_{z1}, \bar{\sigma}_{z1}^2)$). The variance parameters of the park-level distributions ($\bar{\sigma}_{z1}^2$) do not vary by park, which allowed us to fit the model for parks with sparse data.

We estimated the parameters in our model using a Bayesian framework within the program JAGS (Plummer 2003) implemented in R (R Core Team 2016) using the ‘jagsUI’ package (Kellner 2016). We set vague priors for the global-level hyper parameters. The global-level mean hyper parameters for intercept terms (e.g. $\bar{\mu}_{z0}$) each have normal prior distributions with a mean of 0 and a variance of 2.70 (Lunn et al. 2012). The global-level mean hyper parameters for slope terms (e.g. $\bar{\mu}_{z1}$) each have normal prior distributions with a mean of 0 and a variance of 10. The variance parameters have gamma priors with shape and scale parameters of 0.1. We summarized posterior distributions for each parameter by their mean and 95% credible interval. We standardized all continuous covariates to have a mean of zero and a standard deviation of one, and then estimated missing covariate data (starting the first year a park was monitored) through an imputation approach (using the mean and variance of the covariate values) embedded in the hierarchical model (Kéry and Royle 2015). Convergence was determined for all structural parameters by visually monitoring the corresponding trace plots and assuring that the Gelman and Rubin convergence diagnostic (\hat{R} statistic) was less than 1.1 (Gelman and Rubin 1992; Gelman and Shirley 2011). See Online Resource 1 for the JAGS and R code describing the multi-region, community occupancy model.

In post hoc analyses, we used Pearson’s correlation coefficients to evaluate the relationship between the estimated species richness for each posterior sample (at both spatial scales) with the area, connectivity, and quality covariates. The correlation coefficients for each covariate are organized by the median and 95% credible intervals across all posterior samples. We conducted these analyses to assess the cumulative effects of fragmentation on species richness patterns, a derived parameter, at both wetland and park scales. We categorized relationships as strong ($0.71 < r < 1.0$), moderate

($0.51 < r < 0.71$), weak ($0.31 < r < 0.51$), or negligible ($0.11 < r < 0.31$; Hinkle et al. 2003).

Results

Metacommunity (Park-level) occupancy and richness

Park-level characteristics describing habitat area, quality and isolation had important effects on metacommunity amphibian richness (Fig. 1a, b). Percent isolation had a moderate negative correlation with metacommunity richness ($r = -0.582$, 95% Credible Interval [CI] -0.862 to -0.112 CI; Fig. 1c), and the largest mean effect on species occupancy within a park (Ω_r ; -0.234 , -0.582 – 0.119 CI). Park area had a positive, but slightly weaker, effect on mean species occupancy within a metacommunity (0.158 , -0.152 – 0.463 CI), and was weakly correlated with metacommunity richness ($r = 0.436$, 0.103 – 0.657 CI; Fig. 1d). Percent forest cover had a small, slightly negative effect on mean metacommunity occupancy (-0.158 , -0.503 – 0.183 CI). However, there was a negligible correlation between percent forest cover and metacommunity richness ($r = -0.067$, -0.447 – 0.325 CI; Fig. 1e). The 95% CIs for all of the park-level covariates overlapped zero, although this is not necessarily surprising given the life history diversity of amphibian species within this region. The number of species observed in each park (i.e. metacommunity richness) varied from a low of six in ROCR to a high of 14 in CHOH. Estimated metacommunity richness was higher than observed richness in all parks, except CHOH where sampling was most intensive (Fig. 1b).

Community (Wetland-level) occupancy and richness

Wetland area (0.448 , -0.042 – 0.942 CI) and connectivity (0.284 , -0.321 – 0.954 CI) had mean positive effects on community-level occupancy (Ψ) at the global-level (i.e. across all parks) and for the majority of parks (though 95% CIs overlapped zero; Fig. 2a, Online Resource 2). Both wetland area ($r = 0.344$, 0.311 – 0.390 CI; Fig. 3a) and connectivity ($r = 0.372$, 0.331 – 0.411 CI; Fig. 3b) had weak positive correlations with annual wetland-specific (community) richness ($N_{r,j,t}$). Wetland conductivity had a negative

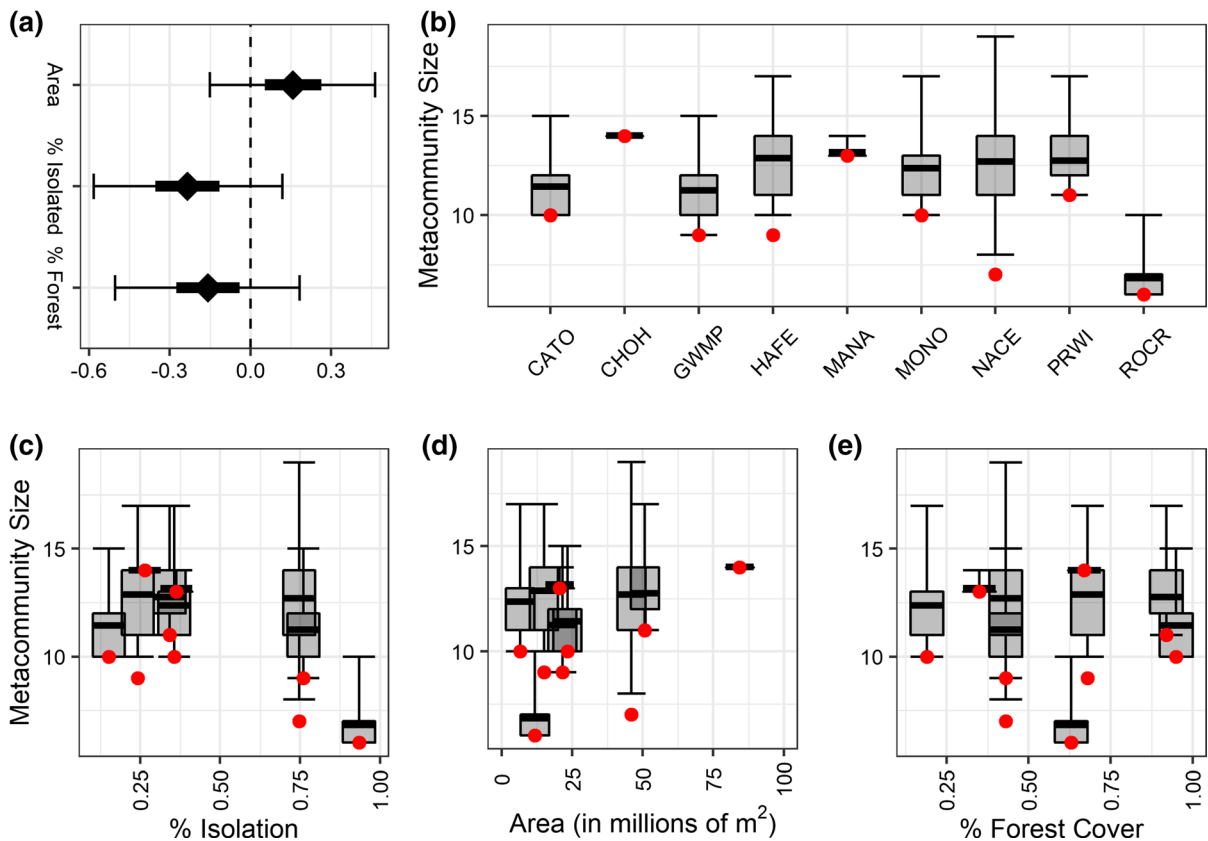


Fig. 1 **a** Effects of park-level variables (percent isolation, area, and percent forest cover) on the probability that individual species exist in the metacommunity of a given park. Black diamonds show mean effects. The thick black lines show 50% credible intervals (CI) and thin black lines show the 95% CIs. The dashed vertical line shows no effect. **b** Estimated (mean values indicated with horizontal lines, 50% CIs indicated with boxes, and 95% CIs indicated with error bars) and observed (red

dots) metacommunity richness (number of species) at each of the nine parks within the NCRN that are included in our study. **c–e** Metacommunity richness in each park (mean values indicated with horizontal lines, 50% CIs indicated with boxes, and 95% CIs indicated with error bars; observed values indicated with red dots) plotted against each park-level variable: percent isolation (**c**), area (**d**), and percent forest cover (**e**)

impact on occupancy at the global-level (-0.436 ; -0.870 to -0.026 CI), and for each park (Fig. 2a), but a negligible correlation ($r = -0.152$, -0.185 to -0.119 CI; Fig. 3c) with wetland richness. Correlations among community richness and the continuous covariates varied by wetland hydroperiod, with generally positive effects of area and connectivity and negative effects of conductivity (Fig. 3).

Annual wetland richness was considerably higher for permanent wetlands (4.88, 4.59–5.29 CI) than semi-permanent (4.09, 3.83–4.42 CI) and temporary wetlands (2.46, 2.23–2.72 CI), with non-overlapping 95% CIs among the hydroperiod categories. This is unsurprising as mean community-level occupancy was generally highest for permanent wetlands (0.450,

0.148–0.788 CI) followed by semi-permanent wetlands (0.295, 0.095–0.584 CI) and lowest in temporary wetlands (0.134, 0.052–0.282 CI), with no considerable variation among parks (Fig. 2b, Online Resource 2). Precipitation had a small positive mean effect on species occupancy at the global-level (0.102, -0.345 – 0.613 CI), but was close to zero for a number of parks indicating little annual or spatial variation in occupancy related to precipitation (Fig. 2a).

Detection

As expected, detection probabilities varied by parks (Fig. 4a) and species (Fig. 4b) along a seasonal gradient (i.e. day of year). Across parks, detection

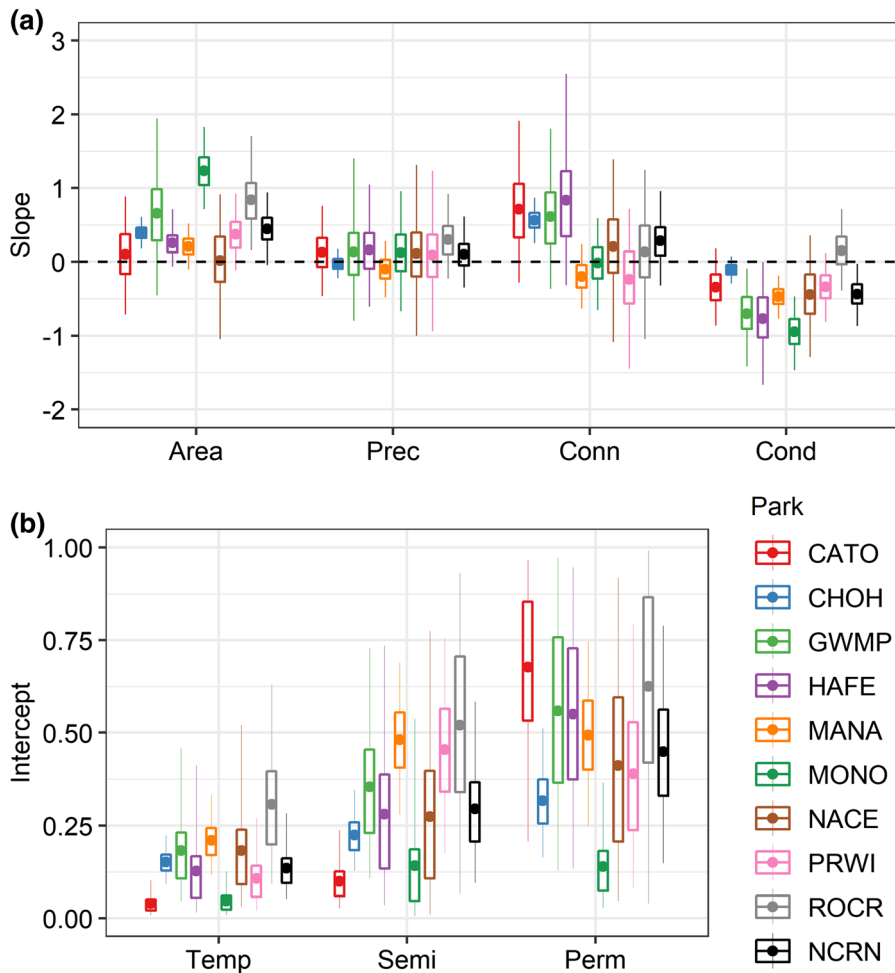


Fig. 2 **a** Effects of wetland-level variables (the area of each wetland in m^2 —‘Area’; the cumulative precipitation at each park in mm—‘Prec’; the connectivity of each wetland to other wetlands within the park—‘Conn’; and the measured water conductivity of each wetland in μS —‘Cond’) on the probability

probabilities for metacommunities generally peaked in May. However, at the species-level, detection varied widely throughout the sampling period related to the breeding phenology of individual species (Fig. 4b).

Discussion

Our analysis revealed that the spatial grain and extent of a study can mediate the interpretation of results and the perceived importance of environmental drivers on ecological processes (Field et al. 2009). We found that park isolation is the most important factor influencing

of occupancy (Ψ), and **b** park-level and global-level (NCRN) intercept parameter estimates (mean values indicated with horizontal lines, 50% CIs indicated with boxes, and 95% CIs indicated with error bars) for hydroperiod (temporary—‘Temp’; semi-permanent—‘Semi’; and permanent—‘Perm’)

metacommunity (park-level) amphibian richness (negative association with metacommunity occupancy and richness), followed closely by park area (positive association with metacommunity occupancy and richness). However, we did not find an effect of percent forest cover, which we used as a proxy for park habitat quality, on metacommunity richness (Fig. 1). In contrast, at the local-level, habitat quality as measured by wetland hydroperiod was the most important factor influencing community size, followed by wetland area, wetland connectivity, and then wetland conductivity (Figs. 2 and 3). While the relative effect of each variable varied by scale, parameter estimates for covariate effects were

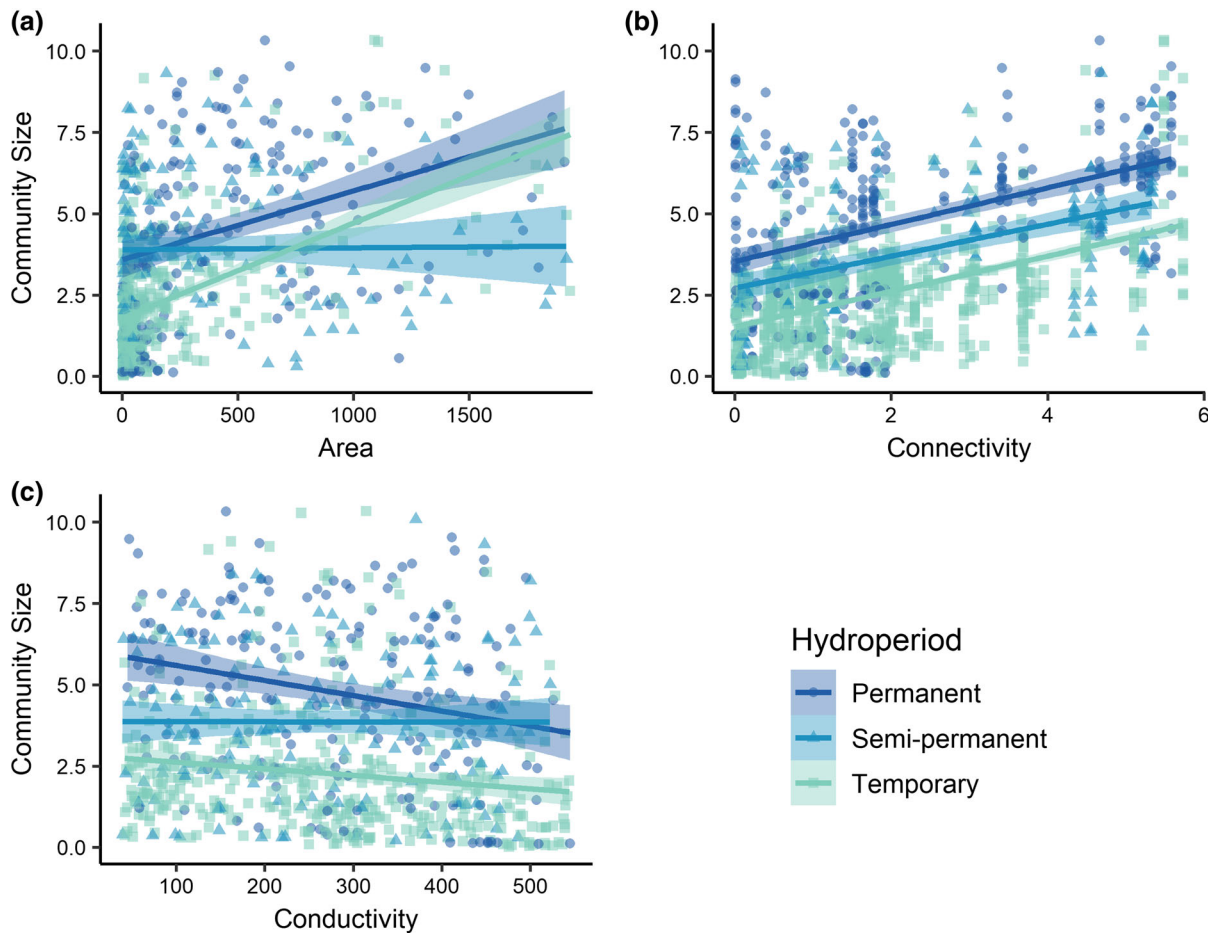


Fig. 3 Mean community richness for each wetland by hydroperiod (Permanent = dark blue circle, Semi-permanent = light blue triangle, Temporary = green square) plotted against

wetland **a** area, **b** connectivity, and **c** conductivity. Lines and shaded areas show post hoc regression estimates (means and 95% CIs) for each variable and hydroperiod category

consistently larger at the smaller spatial scale (i.e. wetland-level), but also less precise (Figs. 1a and 2a). Local and global patterns are intricately linked (Wiens 1989; Heffernan et al. 2014), but many studies consider species responses to habitat at only one scale, which tends to be small (Holland et al. 2004). From a practical standpoint, our sampling scale matched the scales of distinct habitat patches (wetlands) and of discrete natural areas and administrative units (parks), which are the scales that best reflect amphibian community and metacommunity dynamics. Importantly, these are the scales on which management is most likely to be implemented (Potter et al. 2016).

Effects of habitat area and connectivity on amphibian richness were positive at both the park- and

wetland-levels, suggesting an overall negative effect of habitat fragmentation. Ecological theory has consistently predicted negative consequences of habitat fragmentation on species richness patterns (MacArthur and Wilson 1967; Diamond 1975; Temple 1981), although there has been a lack of consistency in *how* fragmentation affects species communities among empirical studies (Connor et al. 2000; Prugh et al. 2008; Fletcher et al. 2016; Fahrig 2017; Wintle et al. 2019). Importantly, it is unclear whether inferences on the impacts of fragmentation in these studies are scale-related, or if the effects of fragmentation on species richness and occurrence patterns vary by landscape and species (Betts et al. 2014), which makes generalization difficult. The differing effects of habitat quality on species richness at the two spatial

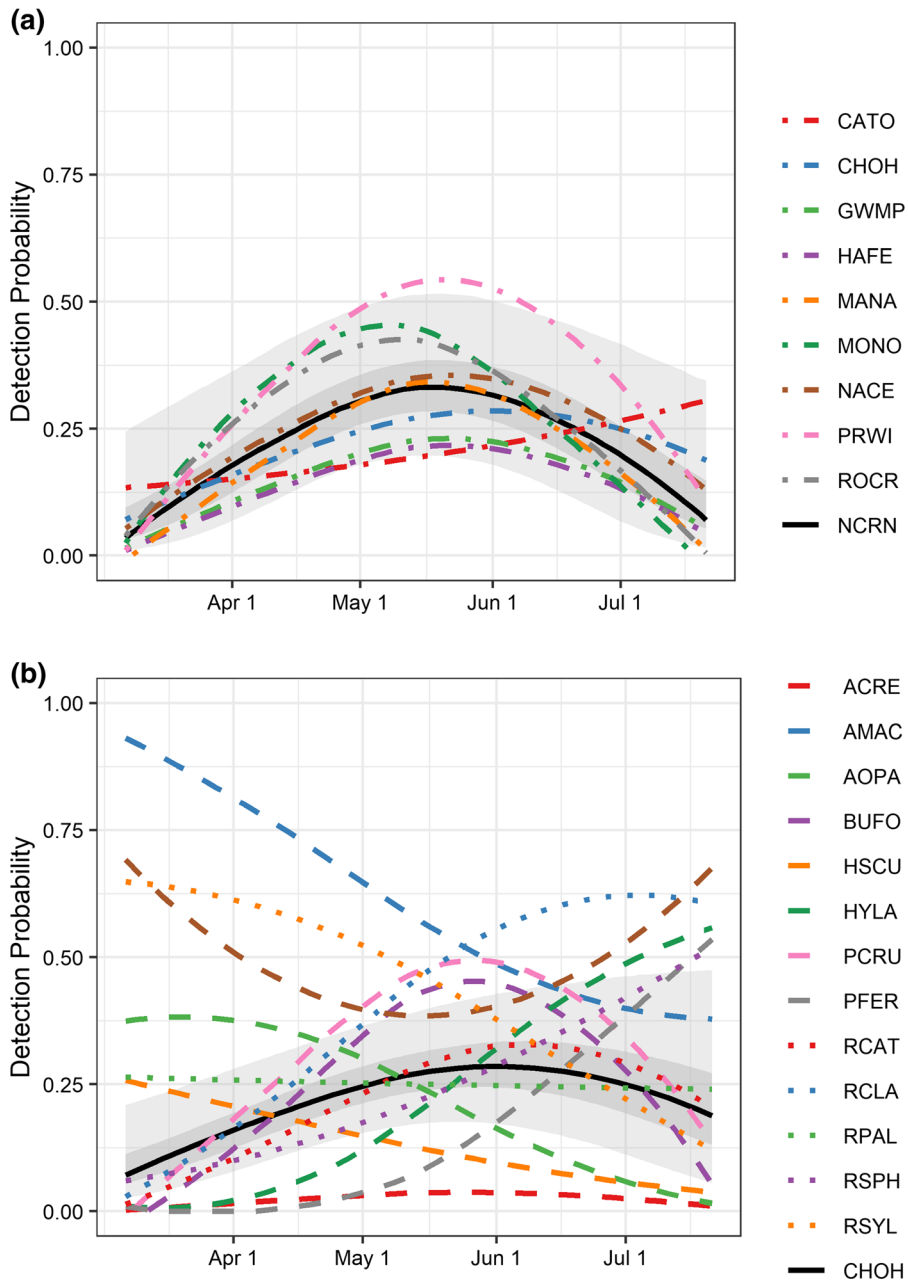


Fig. 4 **a** Mean park-level detection probabilities plotted by day of year. Dashed lines show each park while the solid black line shows the average across parks (with shaded dark grey 50% CI and light grey 95% CI). **b** Mean species-specific detection

probabilities plotted by day of year in CHOH, the park with the most data. Dashed lines show the relationship for each species while the solid black line shows the average across all species (with shaded dark grey 50% CI and light grey 95% CI)

scales (park and wetland) were contrary to our original hypotheses, where we expected that the amount of forest cover within parks (defining the permeability and suitability of the park matrix) would be positively associated with metacommunity richness (Prugh et al.

2008; Watling et al. 2011). It is difficult to assess whether the lack of an effect at the park-level is an artifact of our monitoring program’s sampling extent or the selection of an appropriate habitat metric. First, lack of forest cover reduces migratory success of both

juvenile and adult amphibians (Rothermel 2004; Todd et al. 2009). While forest cover varies widely among our sampled parks (Table 1), the habitat matrices of all parks are minimally disturbed compared to areas outside of national parks (Goodwin and Shriver 2014). Thus, even parks with low amounts of forest may still retain a sufficient amount of habitat for amphibian dispersal. Second, defining environmental variables at broad scales is challenging as covariates that are scaled up to a coarser grain are less likely to capture micro-variations in habitat conditions that are important to population processes (Guisan et al. 2007; Gottschalk et al. 2011). Simplifying biological mechanisms into a single covariate value for inference on broad-scale processes may mask the localized conditions that influence fine-scaled processes and thus, inaccurately characterize the habitat relevant to amphibians. The mechanisms that underlie biological processes may be similar across scales. For example, decreased wetland connectivity lowers community richness by inhibiting successful immigration from other amphibian communities, and increased isolation of parks lowers metacommunity richness by inhibiting successful immigration from other amphibian metacommunity complexes. However, comparisons focused on the relative strengths of mechanisms are difficult as the general characteristics of the dynamics governing processes vary significantly across scales (e.g. rate of system change, length of time lags, and importance of indirect effects; Wiens 1989).

Parameter effect sizes at the wetland-level were larger than at the park-level. Small spatial scales capture less biological and physical complexity overall than intermediate and large scales (Kotliar and Wiens 1990), and thus individual variables can explain a larger proportion of the true variation within the system. Regional-level analyses are complicated as observed patterns emerge from multiple, interacting local-scale processes but are also constrained by regional and even global-scaled dynamics (Heffernan et al. 2014). Larger-scale processes affect a greater spatial extent, leading to more heterogeneous relationships within ecological systems, and thus, weaker effects within sampling units (Elith et al. 2006; Hernandez et al. 2006). Although greater in effect size, the slope estimates of area, connectivity, and quality were less precise (wider CIs) at the wetland-level than at the park-level. Broadening the spatial grain of observation increases the number of

occurrence samples available per unit (i.e. increase in sample size), which decreases the variance around the estimated mean (Dungan et al. 2002; Guisan et al. 2007; Loe et al. 2012). There is a trade-off in experimental design of selecting the optimal sample size (to increase precision) and the most biologically-realistic spatial scale per sampling unit (to increase accuracy). There was also considerable variation of parameter estimates both among and within parks. This may result from structural constraints that have led to an unevenness in the sampling data across parks (NPS 2005; Bailey et al. 2007). Fiscal limitations and budget cycles have impacted the amount and spatial extent of sampling, which is typical of large-scale monitoring schemes (Keller et al. 2008; Lindenmayer et al. 2012).

Our results underscore the importance of studies that span multiple scales across broad geographical extents to offer a mechanistic understanding in variation of the size and composition of amphibian communities and metacommunities (Cushman 2006; Steenweg et al. 2017). The loss of biodiversity, and amphibians in particular, is occurring at an alarming rate (Houlahan et al. 2000; Stuart et al. 2004; Butchart et al. 2010; Adams et al. 2013), but the effect and exposure of global stressors (e.g. habitat fragmentation, climate change, etc.) on biodiversity varies regionally and by population (Grant et al. 2016). Fragmentation is thought to impact amphibians via multiple pathways (e.g. area, connectivity, and quality), and our results indicate that spatial scale may mediate these relationships. Ecological systems are organized at multiple hierarchical levels and the factors influencing the occurrence of species, and resulting biodiversity patterns, likely vary at each level. Basic units (in our case, wetlands) tend to respond to local-scale factors (e.g. wetland hydroperiod and conductivity significantly influence amphibian community dynamics), but aggregate units (parks) are limited by broad-scale factors (e.g. the connectivity of the park in a regional context was the strongest factor influencing metacommunity dynamics). Previous research has described specific ecological requirements for amphibian occupancy at the local, wetland, level (Snodgrass et al. 2000; Babbitt et al. 2003; Werner et al. 2007; Mattfeldt et al. 2009; Zipkin et al. 2012; Green et al. 2013; Semlitsch et al. 2015), but studies that hierarchically span multiple scales specifically allow scientists and managers to evaluate where,

and at what scale, the constraints in species assembly occur (Smith and Green 2005).

Well-designed large-scale and long-term monitoring programs have immense potential to address scientific questions concerning the spatial and temporal dynamics of various ecological properties (Yoccoz et al. 2001; Nichols and Williams 2006; Lindenmayer et al. 2012). Thoughtful consideration on the incorporation of space in a study's design and analysis can facilitate the strategic use of available resources when planning related biological management and monitoring programs at broad spatial scales (Fischer et al. 2004; Dorazio et al. 2010; Tobler et al. 2015). For resource managers, an understanding of the impacts of environmental changes (e.g. climate change, species invasions, disease, fragmentation) at multiple scales is necessary for planning biological reserves and for managing existing ones (Diamond 1975; Temple 1981; Resasco et al. 2017). Large-scale conservation requires collaboration across traditional jurisdictional and political boundaries through informal governance networks (Bixler et al. 2016; Scarlett and McKinney 2016). Combining results from multi-scaled research with an understanding of the jurisdictional boundaries in a decision context can help identify optimal management strategies and which stakeholders should be responsible for implementing decisions at each scale (e.g. wetland, park, region). Moving forward in the face of complex and pressing global change, the explicit linkage of processes across space and time in management plans is necessary to solve environmental problems and protect biodiversity (Heffernan et al. 2014; Levy et al. 2014).

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for descriptive purposes only and does not imply endorsement by the U.S. Government.

Data availability Code and data are available on Zenodo (<https://doi.org/10.5281/zenodo.3600532>) and on the Zipkin Quantitative Ecology Lab Github site (https://github.com/zipkinlab/Wright_et_al_2020_LandEcol).

References

- Adams MJ, Miller DA, Muths E, Corn PS, Grant EH, Bailey LL, Fellers GM, Fisher RN, Sadinski WJ, Waddle H, Walls SC (2013) Trends in amphibian occupancy in the United States. *PLoS ONE* 8:e64347
- Azaele S, Maritan A, Cornell SJ, Suweis S, Banavar JR, Gabriel D, Kunin WE (2015) Towards a unified descriptive theory for spatial ecology: predicting biodiversity patterns across spatial scales. *Methods Ecol Evol* 6:324–332
- Babbitt KJ, Baber MJ, Tarr TL (2003) Patterns of larval amphibian distribution along a wetland hydroperiod gradient. *Can J Zool* 81:1539–1552
- Bailey LL, Grant EHC, Mattfeldt SD (2007) Amphibian monitoring protocol revision 1.3. Natural resource technical report. National Park Service, Fort Collins, Colorado, USA
- Betts MG, Fahrig L, Hadley AS, Halstead KE, Bowman J, Robinson WD, Wiens JA, Lindenmayer DB (2014) A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. *Ecography* 37:517–527
- Bixler RP, McKinney M, Scarlett L (2016) Forging new models of natural resource governance. *Front Ecol Environ* 14:115
- Boulinier T, Nichols JD, Sauer JR, Hines JE, Pollock KH (1998) Estimating species richness: the importance of heterogeneity in species detectability. *Ecology* 79:1018–1028
- Brown BL, Swan CM, Auerbach DA, Campbell Grant EH, Hitt NP, Maloney KO, Patrick C (2011) Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems. *J N Am Benthol Soc* 30:310–327
- Butchart SH, Walpole M, Collen B, Van Strien A, Scharlemann JP, Almond RE, Baillie JE, Bomhard B, Brown C, Bruno J, Carpenter KE (2010) Global biodiversity: indicators of recent declines. *Science* 328:1164–1168
- Cecala KK, Maerz JC, Halstead BJ, Frisch JR, Gragson TL, Hepinstall-Cymerman J, Leigh DS, Jackson CR, Peterson JT, Pringle CM (2018) Multiple drivers, scales, and interactions influence southern Appalachian stream salamander occupancy. *Ecosphere* 9:e02150
- Chandler R, Hepinstall-Cymerman J (2016) Estimating the spatial scales of landscape effects on abundance. *Landscape Ecol* 31:1383–1394
- Chesson P, Donahue MJ, Melbourne BA, Sears AL (2005) Scale transition theory for understanding mechanisms in metacommunities. In: Holyoak M, Leibold MA, Holt RD (eds) *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago, pp 279–306

- Connor EF, Courtney AC, Yoder JM (2000) Individuals-area relationships: the relationship between animal population density and area. *Ecology* 81:734–748
- Cushman SA (2006) Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biol Conserv* 128:231–240
- Daly C, Halbleib M, Smith JI, Gibson WP, Doggett MK, Taylor GH, Curtis J, Pasteris PP (2008) Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *Int J Climatol* 28:2031–2064
- Debinski DM, Holt RD (2000) A survey and overview of habitat fragmentation experiments. *Conserv Biol* 14:342–355
- Diamond JM (1975) The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biol Conserv* 7:129–146
- Doerr VA, Barrett T, Doerr ED (2011) Connectivity, dispersal behaviour and conservation under climate change: a response to Hodgson et al. *J Appl Ecol* 48:143–147
- Dorazio RM, Kery M, Royle JA, Plattner M (2010) Models for inference in dynamic metacommunity systems. *Ecology* 91:2466–2475
- Dorazio RM, Royle JA (2005) Estimating size and composition of biological communities by modeling the occurrence of species. *J Am Stat Assoc* 100:389–398
- Dorazio RM, Royle JA, Söderström B, Glimskär A (2006) Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology* 87:842–854
- Dungan JL, Perry JN, Dale MR, Legendre P, Citron-Pousty S, Fortin MJ, Jakomulska A, Miriti M, Rosenberg M (2002) A balanced view of scale in spatial statistical analysis. *Ecography* 25:626–640
- Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol S* 34:487–515
- Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *J Biogeogr* 40:1649–1663
- Fahrig L (2017) Ecological responses to habitat fragmentation per se. *Annu Rev Ecol Evol S* 48:1–23
- Fahrig L, Arroyo-Rodríguez V, Bennetta JR, Boucher-Lalonde V, Cazetta E, Currie DJ, Eigenbrod F, Fordg AT, Harrison SP, Jaegeri JAG, Koper N, Martin AE, Martin JL, Metzgerm JP, Morrisona P, Rhodessn JR, Saunders DA, Simberloff D, Smith AC, Tischendorf L, Vellend M, Watling JI (2019) Is habitat fragmentation bad for biodiversity? *Biol Conserv* 230:179–186
- Fancy SG, Gross JE, Carter SL (2009) Monitoring the condition of natural resources in US national parks. *Environ Monit Assess* 151:161–174
- Fei S, Guo Q, Potter K (2016) Macrosystems ecology: novel methods and new understanding of multi-scale patterns and processes. *Landscape Ecol* 31:1–6
- Field R, Hawkins BA, Cornell HV, Currie DJ, Diniz-Filho JA, Guégan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM (2009) Spatial species-richness gradients across scales: a meta-analysis. *J Biogeogr* 36:132–147
- Fischer J, Lindenmayer DB, Cowling A (2004) The challenge of managing multiple species at multiple scales: reptiles in an Australian grazing landscape. *J Appl Ecol* 41:32–44
- Fletcher RJ, Burrell NS, Reichert BE, Vasudev D, Austin JD (2016) Divergent perspectives on landscape connectivity reveal consistent effects from genes to communities. *Curr Landsc Ecol Rep* 1:67–79
- Fletcher RJ, Didham RK, Banks-Leite C, Barlow J, Ewers RM, Rosindell J, Holt RD, Gonzalez A, Pardini R, Damschen EI, Melo FPL, Ries L, Prevedello JA, Tscharntke T, Laurance WF, Lovejoy T, Haddad NM (2018) Is habitat fragmentation good for biodiversity? *Biol Conserv* 229:9–15
- Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple sequences. *Stat Sci* 7:457–472
- Gelman A, Shirley K (2011) Inference from simulations and monitoring convergence. In: Brooks S, Gelman A, Jones GL, Meng XL (eds) *Handbook of markov chain monte carlo*. CRC Press, Boca Raton, pp 163–174
- Goodwin SE, Shriver WG (2014) Using a bird community index to evaluate national parks in the urbanized national capital region. *Urban Ecosyst* 17:979–990
- Gottschalk TK, Aue B, Hotes S, Ekschmitt K (2011) Influence of grain size on species-habitat models. *Ecol Model* 222:3403–3412
- Grant EHC, Brand AB (2012) National capital region network amphibian monitoring protocol: revision 1.4 10 January 2012. Natural resource technical report. National Park Service, Fort Collins, Colorado, USA
- Grant EHC, Miller DA, Schmidt BR, Adams MJ, Amburgey SM, Chambert T, Cruickshank SS, Fisher RN, Green DM, Hossack BR, Johnson PT (2016) Quantitative evidence for the effects of multiple drivers on continental-scale amphibian declines. *Sci Rep* 6:25625
- Green AW, Hooten MB, Grant EH, Bailey LL (2013) Evaluating breeding and metamorph occupancy and vernal pool management effects for wood frogs using a hierarchical model. *J Appl Ecol* 50:1116–1123
- Guillera-Aroita G, Lahoz-Monfort JJ, MacKenzie DI, Wintle BA, McCarthy MA (2014) Ignoring imperfect detection in biological surveys is dangerous: a response to 'fitting and interpreting occupancy models'. *PLoS ONE* 9:e99571
- Guisan A, Graham CH, Elith J, Huettmann F, NCEAS Species Distribution Modelling Group (2007) Sensitivity of predictive species distribution models to change in grain size. *Divers Distrib* 13:332–340
- Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci Adv* 1:e1500052
- Haddad NM, Gonzalez A, Brudvig LA, Burt MA, Levey DJ, Damschen EI (2017a) Experimental evidence does not support the habitat amount hypothesis. *Ecography* 40:48–55
- Haddad NM, Holt RD Jr, Fletcher RJ, Loreau M, Clobert J (2017b) Connecting models, data, and concepts to understand fragmentation's ecosystem-wide effects. *Ecography* 40:1–8
- Heffernan JB, Soranno PA, Angilletta MJ, Buckley LB, Gruner DS, Keitt TH, Kellner JR, Kominoski JS, Rocha AV, Xiao J, Harms TK (2014) Macrosystems ecology: understanding

- ecological patterns and processes at continental scales. *Front Ecol Environ* 12:5–14
- Hernandez PA, Graham CH, Master LL, Albert DL (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29:773–785
- Hesselbarth MH, Sciaini M, With KA, Wiegand K, Nowosad J (2019) Landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography* 42:1648–1657
- Hinkle DE, Wiersma W, Jurs SG (2003) Applied statistics for the behavioral sciences, 5th edn. Houghton Mifflin, Boston
- Hodgson JA, Moilanen A, Wintle BA, Thomas CD (2011) Habitat area, quality and connectivity: striking the balance for efficient conservation. *J Appl Ecol* 48:148–152
- Hodgson JA, Thomas CD, Wintle BA, Moilanen A (2009) Climate change, connectivity and conservation decision making: back to basics. *J Appl Ecol* 46:964–969
- Holland JD, Bert DG, Fahrig L (2004) Determining the spatial scale of species' response to habitat. *AIBS Bull* 54:227–233
- Houlahan JE, Findlay CS, Schmidt BR, Meyer AH, Kuzmin SL (2000) Quantitative evidence for global amphibian population declines. *Nature* 404:752
- Humphrey JW, Watts K, Fuentes-Montemayor E, Macgregor NA, Peace AJ, Park KJ (2015) What can studies of woodland fragmentation and creation tell us about ecological networks? A literature review and synthesis. *Landsc Ecol* 30:21–50
- Ibáñez I, Katz DS, Peltier D, Wolf SM, Barrie C, Benjamin T (2014) Assessing the integrated effects of landscape fragmentation on plants and plant communities: the challenge of multiprocess–multiresponse dynamics. *J Ecol* 102:882–895
- Jackson HB, Fahrig L (2015) Are ecologists conducting research at the optimal scale? *Global Ecol Biogeogr* 24:52–63
- Keller M, Schimel DS, Hargrove WW, Hoffman FM (2008) A continental strategy for the National ecological observatory network. *Front Ecol Environ* 6:282–284
- Kellner KF (2016) jagsUI: a wrapper around 'rjags' to streamline JAGS analyses. R package version 1(4):4
- Kéry M, Royle JA (2015) Applied hierarchical modeling in ecology: Analysis of distribution, abundance and species richness in R and BUGS. Academic Press, Cambridge
- Kotliar NB, Wiens JA (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253–260
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 7:601–613
- Levin SA (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* 73:1943–1967
- Levy O, Ball BA, Bond-Lamberty B, Cheruvilil KS, Finley AO, Lottig NR, Punyasena SW, Xiao J, Zhou J, Buckley LB, Filstrup CT, Keitt TH, Kellner JR, Knapp AK, Richardson AD, Tcheng D, Toomey M, Vargas R, Voordeckers JW, Wagner T, Williams JW (2014) Approaches to advance scientific understanding of macrosystems ecology. *Front Ecol Environ* 12:15–23
- Lindenmayer DB, Likens GE, Andersen A, Bowman D, Bull CM, Burns E, Dickman CR, Hoffmann AA, Keith DA, Liddell MJ, Lowe AJ (2012) Value of long-term ecological studies. *Austral Ecol* 37:745–757
- Loe LE, Bonenfant C, Meisingset EL, Mysterud A (2012) Effects of spatial scale and sample size in GPS-based species distribution models: are the best models trivial for red deer management? *Eur J Wildl Res* 58:195–203
- Lookingbill TR, Schmit JP, Tessel SM, Suarez-Rubio M, Hilderbrand RH (2014) Assessing national park resource condition along an urban–rural gradient in and around Washington, DC, USA. *Ecol Indic* 42:147–159
- Lunn D, Jackson C, Best N, Spiegelhalter D, Thomas A (2012) The BUGS book: a practical introduction to Bayesian analysis. CRC Press, Boca Raton
- MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton Univ Press, Princeton
- MacKenzie DI (2006) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, Cambridge
- MacKenzie DI, Nichols JD, Lachman GB, Droege S, Andrew Royle J, Langtimm CA (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255
- Mattfeldt SD, Bailey LL, Grant EH (2009) Monitoring multiple species: estimating state variables and exploring the efficacy of a monitoring program. *Biol Conserv* 142:720–737
- McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecol Appl* 12:335–345
- McGarigal K, Cushman SA, Ene E (2012) FRAGSTATS v4: Spatial Pattern Analysis Program for categorical and continuous maps. Computer Software Program produced by the authors at the University of Massachusetts, Amherst. <http://www.umass.edu/landeco/research/fragstats/fragstats.html>
- Moilanen A, Nieminen M (2002) Simple connectivity measures in spatial ecology. *Ecology* 83:1131–1145
- National Park Service (2005) Long-term monitoring plan for natural resources in the National Capital Region Network. Inventory and Monitoring Program, Center for Urban Ecology, Washington, DC
- National Park Service (2006) A conceptual basis for natural resource monitoring. Center for Urban Ecology, Washington, DC
- Nichols JD, Williams BK (2006) Monitoring for conservation. *Trends Ecol Evol* 21:668–673
- Parsons DJ (2004) Supporting basic ecological research in US national parks: challenges and opportunities. *Ecol Appl* 14:5–13
- Plummer M (2003) JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Proceedings of the 3rd international workshop on distributed statistical computing, pp 20–22
- Potter KM, Koch FH, Oswalt CM, Iannone BV (2016) Data, data everywhere: detecting spatial patterns in fine-scale ecological information collected across a continent. *Landsc Ecol* 31:67–84

- Prugh LR, Hodges KE, Sinclair AR, Brashares JS (2008) Effect of habitat area and isolation on fragmented animal populations. *Proc Natl Acad Sci USA* 105:20770–20775
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Resasco J, Bruna EM, Haddad NM, Banks-Leite C, Margules CR (2017) The contribution of theory and experiments to conservation in fragmented landscapes. *Ecography* 40:109–118
- Reynolds C, Fletcher RJ, Carneiro CM, Jennings N, Ke A, LaScaleia MC, Lukhele MB, Mamba ML, Sibiyi MD, Austin JD, Magagula CN (2018) Inconsistent effects of landscape heterogeneity and land-use on animal diversity in an agricultural mosaic: a multi-scale and multi-taxon investigation. *Landsc Ecol* 33:1–15
- Reynolds TW, Collins CD, Wassie A, Liang J, Briggs W, Lowman M, Sisay TS, Adamu E (2017) Sacred natural sites as mensurative fragmentation experiments in long-inhabited multifunctional landscapes. *Ecography* 40:144–157
- Rothermel BB (2004) Migratory success of juveniles: a potential constraint on connectivity for pond-breeding amphibians. *Ecol Appl* 14:1535–1546
- Royle JA, Dorazio RM, Link WA (2007) Analysis of multinomial models with unknown index using data augmentation. *J Comput Graph Stat* 16:67–85
- Scarlett L, McKinney M (2016) Connecting people and places: the emerging role of network governance in large landscape conservation. *Front Ecol Environ* 14:116–125
- Semlitsch RD, Peterman WE, Anderson TL, Drake DL, Ousterhout BH (2015) Intermediate pond sizes contain the highest density, richness, and diversity of pond-breeding amphibians. *PLoS ONE* 10:e0123055
- Smith MA, Green DM (2005) Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography* 28:110–128
- Snodgrass JW, Komoroski MJ, Bryan AL, Burger J (2000) Relationships among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulations. *Conserv Biol* 14:414–419
- Steenweg R, Hebblewhite M, Kays R, Ahumada J, Fisher JT, Burton C, Townsend SE, Carbone C, Rowcliffe JM, Whittington J, Brodie J (2017) Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. *Fron Ecol Environ* 15:26–34
- Stottlemeyer R (1987) External threats to ecosystems of National Parks. *Environ Manage* 11:87–89
- Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues AS, Fischman DL, Waller RW (2004) Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783–1786
- Sutherland C, Brambilla M, Pedrini P, Tenan S (2016) A multi-region community model for inference about geographic variation in species richness. *Meth Ecol Evol* 7:783–791
- Temple SA (1981) Applied island biogeography and the conservation of endangered island birds in the Indian Ocean. *Biol Conserv* 20:147–161
- Tobler MW, Zúñiga Hartley A, Carrillo-Percegué SE, Powell GV (2015) Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. *J Appl Ecol* 52:413–421
- Todd BD, Lühring TM, Rothermel BB, Gibbons JW (2009) Effects of forest removal on amphibian migrations: implications for habitat and landscape connectivity. *J Appl Ecol* 46:554–561
- Turtle SL (2000) Embryonic survivorship of the spotted salamander (*Ambystoma maculatum*) in roadside and woodland vernal pools in southeastern New Hampshire. *J Herpetol* 34:60–67
- Watling JI, Nowakowski AJ, Donnelly MA, Orrock JL (2011) Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat. *Global Ecol Biogeogr* 20:209–217
- Werner EE, Yurewicz KL, Skelly DK, Relyea RA (2007) Turnover in an amphibian metacommunity: the role of local and regional factors. *Oikos* 116:1713–1725
- Wiens JA (1989) Spatial scaling in ecology. *Funct Ecol* 3:385–397
- Wintle BA, Kujala H, Whitehead A, Cameron A, Veloz S, Kukkala A, Moilanen A, Gordon A, Lentini PE, Cadenhead NCR, Bekessy SA (2019) Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proc Natl Acad Sci USA* 116:909–914
- Wu J (1999) Hierarchy and scaling: extrapolating information along a scaling ladder. *Can J Remote Sens* 25:367–380
- Yoccoz NG, Nichols JD, Boulinier T (2001) Monitoring of biological diversity in space and time. *Trends Ecol Evol* 16:446–453
- Zipkin EF, DeWan A, Royle JA (2009) Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. *J Appl Ecol* 46:815–822
- Zipkin EF, Grant EH, Fagan WF (2012) Evaluating the predictive abilities of community occupancy models using AUC while accounting for imperfect detection. *Ecol Appl* 22:1962–1972

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