Received: 14 May 2024 | Revised: 3 September 2025 | Accepted: 30 September 2025

DOI: 10.1002/ecy.70258

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

ARTICLE

Landscape structure and species life history affect abundance-occupancy relationships

Tad A. Dallas[1] | **Lauren A. Holian**[1] | **Cleber Ten Caten**[1,2]

[1]Department of Biological Sciences, University of South Carolina, Columbia, South Carolina, USA

[2]Department of Botany, University of Wisconsin, Madison, Wisconsin, USA

Correspondence
Tad A. Dallas
Email: tad.a.dallas@gmail.com

Funding information
National Science Foundation, Grant/Award Numbers: NSF-DEB-2017826, NSF-DEB-2420769

Handling Editor: Marta Rodriguez-Rey

Abstract

More widespread species tend to be more locally abundant. This hypothesis has received support when considering single species abundance (mean density of individuals across sites) and occupancy (fraction of occupied sites) through time (intraspecific relationship) and comparing different species sampled at a single point in time (interspecific relationships). But while abundance-occupancy relationships are fairly well supported in observational studies, the underlying factors driving them are less clear. For instance, variation in demographic rates, dispersal, and spatial network structure could all influence resulting abundance-occupancy relationships. We used a simulation model to explore these relationships in spatial networks of variable size and dispersal connectivity. We simulated population dynamics on spatial networks by starting from entirely neutral communities and then systematically incorporated complexity in the form of (co)variation in species demographic rates and dispersal processes. The effect of spatial network structure on abundance-occupancy relationships was dependent on the community dynamics and the covariation imposed on demographic and dispersal parameters. Together, we demonstrate the interplay between the spatial network and variation in demographic and dispersal rates, generating testable hypotheses for when abundance-occupancy relationships would be more likely to be observed, as well as how these relationships may change with habitat fragmentation and shifts in community composition.

KEYWORDS
distribution-abundance, macroecology, population dynamics, simulation model, spatial network, species distribution

INTRODUCTION

Species that occupy numerous sites are predicted to be more locally abundant on average (Brown et al., 1995; Gaston et al., 2000; Hanski, 1982; He & Gaston, 2003). This prediction is based largely on observational studies and is at the center of abundance-occupancy relationships, which posits that the fraction of sites occupied by a given species is positively related to average abundance (Blackburn et al., 2006; Gaston et al., 1998, 2000; Hanski, 1982; He & Gaston, 2003; Steenweg et al., 2018). Here, average abundance is most commonly estimated considering all occupied patches. Abundance-occupancy relationships are within a more general group of relationships called distribution-abundance relationships, which could include the scaling between geographic range size and mean abundance (Venier & Fahrig, 1996). Positive abundance-occupancy relationships are well documented in natural systems (Blackburn et al., 2006; Gaston et al., 1998, 2000; Webb et al., 2012), though there are also numerous studies that have failed to detect these relationships (Gaston & Curnutt, 1998; Symonds & Johnson, 2006; Webb et al., 2007), with some finding negative relationships (Donald & Fuller, 1998; Komonen et al., 2009). Studies in natural systems have highlighted the roles of dispersal limitation (Gaston et al., 2000) and temporal variation in demographic rates caused by variation in resources (Webb et al., 2019) or climatic tolerances (Verberk et al., 2010) on resulting abundance-occupancy relationships. Despite numerous observational explorations of abundance-occupancy relationships, there have been few theoretical examinations (Freckleton, Gill, et al., 2005; Freckleton, Noble, & Webb, 2005; Picard & Favier, 2011).

Abundance-occupancy relationships can be examined both for a given species (intraspecific) or between species (interspecific), where intraspecific relationships explore how the fraction of occupied patches is associated with mean local abundance over time (see Borregaard & Rahbek, 2010 for an extension of this). The underlying idea of intraspecific abundance-occupancy relationships is that time periods with higher than average abundance across the sampled locations will also promote expansion and colonization of previously unoccupied sites. Interspecific abundance-occupancy relationships—which tend to be stronger than their intraspecific counterparts (Borregaard & Rahbek, 2010; Gaston et al., 2000)—are sampled at a single point in time or aggregated across time points, and consider the relationship between the fraction of occupied patches and mean local abundance for each species. The underlying idea of interspecific abundance-occupancy relationships is that species occupying more sites will be more locally abundant, potentially as a result of life history differences which promote the growth and spread of certain species over others. There are a number of putative mechanisms to explain abundance-occupancy relationships as a function of measurement effects (e.g., sampling bias), structural effects (e.g., resource availability), dynamic effects (e.g., density-dependent habitat selection), and spatial nonindependence effects (e.g., individual aggregation) (reviewed in Borregaard & Rahbek, 2010).

Despite the wealth of studies on abundance-occupancy relationships in natural systems (reviewed in Borregaard & Rahbek, 2010), the development of the theory underlying abundance-occupancy relationships has lagged behind slightly (but see Hartley, 1998; Picard & Favier, 2011; Steenweg et al., 2018). Some of the theory that has been developed has raised the possibility that abundance-occupancy relationships could result from simple, and realistic, statistical assumptions (Hartley, 1998); an argument also raised in a similar form earlier (Wright, 1991). The argument stems from the assumed relationship between the binomial probability of species detection (p) and the Poisson abundance at a particular patch (μ). By posing the problem in this way, species detection probability is inherently linked to species abundance, and intraspecific abundance-occupancy relationships are a natural result of this. When applied to empirical systems, there are many things that can influence both abundance and detection probability which may decouple abundance and occupancy, weakening potential abundance-occupancy relationships. That is, despite claims that these relationships could be used to estimate species abundance (Tovo et al., 2019), the actual predictive power of abundance-occupancy relationships is quite small (Cowley et al., 2001; Gaston, 1996; Verberk et al., 2010).

So theoretical explorations of abundance-occupancy relationships would seem to suggest a clear relationship (Hartley, 1998), even in neutral models which consider all individuals in a community to be functionally equivalent (Hubbell, 1997), despite commonly observing weak or nonexistent relationships in natural systems (Cowley et al., 2001; Gaston, 1996; Ten Caten et al., 2021). But what factors influence the relative strength of abundance-occupancy relationships is largely unknown, leading to the observed mixed support for a quite general biogeographical relationship (Ten Caten et al., 2021). We aimed to explore how the spatial distribution of habitat patches and interspecific variation in demographic and dispersal parameters could result in differing levels of support for both intraspecific and interspecific abundance-occupancy relationships.

We propose a spatially explicit simulation model to explore intraspecific and interspecific relationships, simulating species population dynamics across a number of habitat patches connected by dispersal (hereafter referred to as a spatial network). Starting in a spatial network of suitable habitat patches, we vary the number and spatial distribution of suitable patches, along with species demographic rates and covariance between dispersal and demographic parameters. Essentially, we start from a completely neutral model of species occupying a spatial network, which treats species as equivalent and all simulations are initiated with species of the same occupancy, competition coefficient, and dispersal rates. We then systematically incorporate demographic and dispersal process variation in order to explore when we would expect to observe abundance-occupancy relationships and how strong they may be under a set of given assumptions. Further, we test how the spatial distribution of habitat patches and how variation in dispersal connections between habitat patches influence resulting abundance-occupancy relationships under different assumptions around species demographic rates and dispersal. Together, our findings provide evidence that suggests an interplay between the structure of the spatial network and species demographic and dispersal relationships on abundance-occupancy relationships.

METHODS

Spatial population dynamics

Population dynamics were modeled using the discrete time Ricker model, in which populations grow proportional to rate R and intraspecific competition α sets an upper bound to population size (N).

$$N_{t+1} = N_t\, R\, e^{-\alpha N_t} \tag{1}$$

We incorporate demographic stochasticity into this model by allowing the distribution of the number of offspring produced per generation to be drawn per individual from a Poisson distribution with mean R, and by incorporating survivorship as a binomial random variable with probability $e^{-\alpha N_t}$. Combining these processes results in the number of surviving individuals that go to the next generation (N_{t+1}) to be distributed as a compound binomial-Poisson distribution, where

$$N_{t+1} = \mathrm{Poisson}\left(N_t\, R\, e^{-\alpha N_t}\right) \tag{2}$$

This creates a situation where extinction is much more likely relative to a deterministic model, which we explore in Appendix S1. Further information on the stochastic Poisson Ricker model can be found in the supplemental methods of (Melbourne & Hastings, 2008) or in (Dallas et al., 2019).

Spatial network formation

Habitat patches consist of individual populations, assembled into a spatial network of multiple habitat patches to allow dispersal. This allows both for local population dynamics within a habitat patch, as well as for immigration and emigration to influence population dynamics across the landscape through the exchange of individuals between patches. Spatial networks were constructed using a stochastic block model (Faust & Wasserman, 1992), originally designed to construct networks with a given modular structure. The degree of modularity is determined by the preference matrix $\mathbf{P}$, where entries in this matrix determine propensity of links to form within ($\mathbf{P}_{ii}$) and outside of ($\mathbf{P}_{ij}$) blocks. This allows us to control the number of blocks (b), where blocks are defined as clusters of habitat patches more closely connected to one another than to other groups of habitat patches, as well as the degree of modularity (determined by the preference matrix $\mathbf{P}$) and the number of dispersal connections in the network (Figure 1). By sampling ranges for the size of the spatial network (between 10 and 300 patches), number of blocks (between 2 and 5), and differences in the structure of the preference matrix ($\mathbf{P}$), we effectively sample a wide range of potential spatial network types (Table 1). We note that this does not capture the full range of spatial network configurations, including some which may be relevant to agricultural systems (e.g., lattice). The stochastic block model creates the identities of links within the network but can create networks that do not necessarily adhere to a spatial layout. We addressed this by using the Fruchterman-Reingold algorithm (Fruchterman & Reingold, 1991) to create a layout for the planar graph that approximates a spatial network, and then we assigned edgeweights between connected nodes in a manner that further enforced the spatial network layout (see next section). More information on the range of spatial networks generated is provided in Appendix S1.

Dispersal between patches was modeled by first considering dispersal to occur with some probability ω. The number of individuals dispersing at each timestep was modeled as a binomial random variable, which incorporates some degree of randomness by letting each individual disperse with probability ω. This effect will be most pronounced when population sizes are small. Dispersing individuals were then divided among connected patches based on distance to nearby patches, where closer patches received proportionally more individuals. Distance between patches, and subsequent dispersal potential, was modeled using a negative exponential dispersal kernel (Chesson & Lee, 2005) such that the functional interpatch distance between patches i and j (w_{ij}) is equal to $\exp\left(-2d_{ij}\right)$, where $d_{i,j}$ is the euclidean distance between patches i and j. These values serve as edgeweights of the spatial network constructed in the previous paragraph. We note that every dispersing individual does reach some connected patch (i.e., there is no mortality during dispersal), though others have explored how incorporating this could influence metapopulation persistence (Karnatak & Wollrab, 2020).

Parameter ranges were chosen to be intentionally broad in order to best capture the potential parameter space where abundance-occupancy relationships could

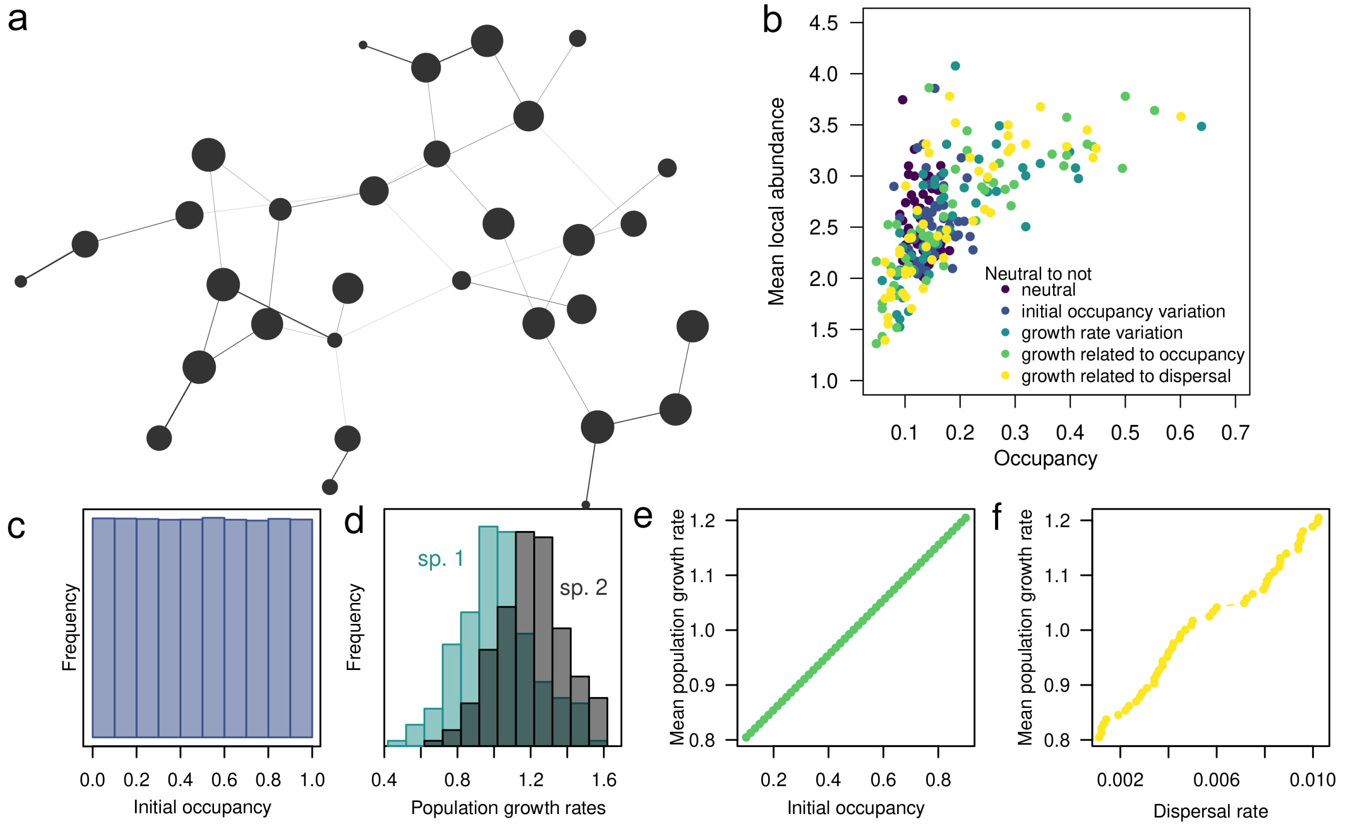

FIGURE 1 Species dynamics were simulated across simulated spatial networks (example spatial network in panel a), where node size is proportional to population size. In our simulations, we start with variation in patches in population growth rates across the spatial network, but no variation among species growth rates, dispersal abilities, or initial occupancy (simulation "neutral" in panel b). That is, patches differ in their growth rates, but species do not. We build on this neutral case by allowing species-level variation in initial occupancy (panel c), shifting population growth rate distributions (panel d), enforcing a positive relationship between mean population growth rate and initial occupancy (panel e) and dispersal (panel f). Example interspecific abundance-occupancy relationships for each of these five simulation scenarios are shown in panel (b), where each point is a species. Slopes from the relationships in panel (b) would correspond to a single interspecific abundance-occupancy relationship for one of the five scenarios, where repeated simulation across a wide parameter range leads to the distribution of slopes seen in Figure 2.

TABLE 1 Parameters used in the construction of spatial networks and subsequent simulation of dynamics across them.

Parameter	Definition	Range
n	No. habitat patches	10–300
b	No. blocks	2–5
$\mathbf{P}_{i,i}$	Diagonal of preference matrix (intragroup links)	0.01–0.2
$\mathbf{P}_{i,j}$	Non-diagonal of preference matrix (intergroup links)	0.1–0.9
ω	Dispersal probability	0.001–0.25
o	Initial occupancy	0.1–0.9
R_i	Population growth rate	0.8–2
σ_R	Variation in population growth rate	0.01–0.5

Note: Here, subscripts i and j correspond to pairs of geographic sites. These ranges were chosen to encompass the largest ranges of reasonable values related to the construction of spatial networks and the dynamics of biological populations.

be detected. Some parameter ranges are fairly realistic, such as the number of habitat patches in the spatial network (10–300) as this encompasses the range of sites typically sampled in observational data collection efforts. Other parameter ranges were more theoretical, such as the range of dispersal probabilities—a notoriously difficult parameter to estimate in natural systems—which we vary between 0.001 and 0.25, corresponding to either 0.1% of individuals dispersing on average to 25% of the population dispersing. Values in the preference matrix were sampled to fully explore the range of potential spatial network structures. That is, despite using the stochastic block model as a spatial network generator, exploring such a wide range of entries in the preference matrix (P) allows us to construct spatial networks which vary markedly in their modularity (see Appendix S1: Figure S1). See Table 1 for parameter descriptions and ranges considered.

From neutral to not

We constructed a set of 500 spatial networks which population dynamics can occur on. To test how abundance-occupancy relationships may manifest from assumptions about species attributes, we start with the simplest neutral case, building further complexity in incrementally. By neutral, we assume that all species in a community do not compete with one another, have the same initial occupancy (o) and intraspecific competition coefficient ($\alpha = 0.05$) across the entire spatial network, and disperse with equal probability (dependent on the connections of the spatial network). This value of intraspecific competition was kept constant for all simulations, though this did not influence our overall findings. Across patches, variation was incorporated in population growth rate (R_i) for each patch in the spatial network—drawn from a uniform distribution bound between 0.8 and 2—but species did not differ in these patch-specific population growth rates. That is, all species had the same measure of population growth rate, dependent on the occupied patch i (see Appendix S1 for an incorporation of species-specific differences in patch population growth rates). Further, see Appendix S1 for an exploration of how altering population growth rates and intraspecific competition coefficients does not influence our results. Habitat patches that were occupied at the start of the simulation had initial population size drawn from a uniform distribution bounded between 0 and 30 individuals. Each simulation was for a particular species, and no interspecific competition was incorporated into the model.

To this neutral model, we considered four layers of additional complexity. First, we sampled initial occupancy (defined above as the fraction of occupied patches) from a uniform distribution bounded between 0 and 1, creating a situation where initial occupancy, dispersal limitation, and stochastic population dynamics could alter abundance-occupancy relationships. That is, abundance-occupancy relationships are a result of variation in stochastic population dynamics, where low initial occupancy and randomized abundance could result in populations that stochastically go extinct, potentially altering abundance-occupancy relationships.

Second, we incorporated variation among species in their population growth rates R by adding a constant value—drawn from a uniform distribution between −0.2 and 0.2—to the population growth rates for each species. This serves to create variation among species in simplified landscapes, while preserving dispersal connections, spatial network structure, and the rank order of demographic rates. This begins to test how spatial variation in demographic rates—caused by variation in resources or climate—can influence species dynamics.

Third, we considered this variation in population growth rates R to positively covary with initial occupancy. That is, species that had higher population growth rates were also species who initially occupied more patches. This serves to reduce the likelihood of dispersal limitation for species with large R values, while still serving to keep spatial network structure and dispersal connections the same across species. This assumption starts to create a situation where faster growing species also have higher initial occupancy. However, the role of spatial network structure and dispersal still may limit the detectability of abundance-occupancy relationships in this scenario.

Finally, we allowed positive covariance between initial occupancy, dispersal probability, and population growth rates, creating a situation where species with high initial occupancy were also more likely to disperse, and had the greatest ability to grow quickly due to higher population growth rates. Intraspecific competition coefficients were kept at 0.05 for all species through all these scenarios. Biologically, this situation creates the most variation among species, as species with the highest population growth rates also are not dispersal limited (highest initial occupancy and dispersal probabilities).

Intraspecific and interspecific abundance-occupancy relationships

We simulated population dynamics for 40 species for each spatial network ($n = 500$ networks total), with the dynamics of each species simulated for 500 generations. Intraspecific abundance-occupancy relationships were assessed by considering the temporal dynamics of the species across the spatial network after accounting for some initial abundance fluctuations. To account for this, we did not consider the first 10 generations in the calculation of mean local abundance and occupancy (see Appendix S1: Figures S8 and S9). Some species went extinct during simulations, with average extinction time between 40 and 60 timesteps. We only considered their dynamics up until the point of extinction. Mean local abundance was the mean abundance across all occupied patches, and occupancy was estimated as the fraction of occupied patches in a given generation. The relationship between these two quantities was measured using Spearman's correlation coefficients, providing a relative measure of the sign and strength of the relationship between abundance and occupancy.

Interspecific relationships were also estimated using Spearman's correlations. In order to explore interspecific abundance-occupancy relationships across a range of species richness and across all the simulated spatial networks, we constructed communities by sampling noninteracting species randomly and assembling communities of between 2 and 40 species. Here, abundance-occupancy relationships were estimated by considering abundance to be mean local abundance for each species over time, and occupancy was quantified as the mean occupancy observed over time for that species. Importantly, we did not incorporate species interactions apart from intraspecific competition. This was intentional, as the estimation of the competition matrix is nontrivial (Fort, 2018; May, 1973; Yonatan et al., 2022), has implications for species coexistence (Adler et al., 2018; Barabás et al., 2016), and actively detracts from the main goal of exploring intraspecific and interspecific abundance-occupancy relationships from the same starting point (i.e., neutrality). It is also important to note the difference in how intraspecific and interspecific abundance-occupancy relationships are estimated, as each point for the abundance-occupancy relationship may relate either to a sampled time period (intraspecific relationship) or an entire species (interspecific relationship). This also allows for the estimation of how interspecific abundance-occupancy relationships may change as a function of time (Martinez et al., 2017).

Statistical analyses

Above, we estimated the strength of abundance-occupancy relationships using Spearman's rank correlations. Across the full set of simulations, we further explored how the strength of abundance-occupancy relationships varied as a function of characteristics of the spatial network across our five different treatments (i.e., starting at neutrality and adding realistic complexity in demographic parameters). Specifically, we used linear regression to explore how abundance-occupancy relationships varied as a function of network size and structure. Network size was estimated as the total number of sites (or nodes) in the spatial network, and structure was estimated as the standardized variability of dispersal connections (the CV in dispersal weights). This serves to assess the role of overall spatial network size as well as the variation in connectivity. In Appendix S1, we also explore how network-level measures of network structure (e.g., modularity) are related to abundance-occupancy relationships. Models were fit to each of the simulation cases (e.g., neutral) and separate models were fit for network size and CV in dispersal connections for clarity and to avoid the potential collinearity between our two measures of network structure.

R code and data to reproduce the analyses are provided in Dallas et al. (2022) in Figshare at https://doi.org/10.6084/m9.figshare.17072759.

RESULTS

Intraspecific abundance-occupancy relationships

We found quite weak intraspecific abundance-occupancy relationships, as estimated by the correlation between mean abundance across the landscape for a given sampling period and the fraction of occupied patches during that same sampling event (Figure 1). Intraspecific abundance-occupancy relationships were fairly unaffected by incorporating different processes (Figure 2), suggesting that differences in simulated species in demographic rates, dispersal, and initial patch occupancy did not strongly influence the resulting intraspecific abundance-occupancy relationships. Larger networks tended to have slightly more positive intraspecific abundance-occupancy relationships (top row of Figure 3), but this only occurred after we enforced positive covariance between demographic parameters and initial occupancy. Similarly, we found weak positive relationships between the CV in dispersal connections and intraspecific abundance-occupancy relationship strength, but only when covariance in demographic parameters and occupancy was enforced (top row of Figure 4).

Interspecific abundance-occupancy relationships

Intraspecific abundance-occupancy relationships were generally weakly positive and not strongly influenced by variation in demographic rates and covariance in demography, dispersal, and initial occupancy. However, interspecific abundance-occupancy relationships were sensitive to the differing assumptions of the simulation models (Figure 2). When species dynamics were neutral (i.e., communities were formed with noninteracting species who only differed in growth rates and initial occupancy values), we observed fairly weak positive interspecific abundance-occupancy relationships (Figure 2 and Appendix S1: Figure S3). By incorporating variation in initial occupancy among species, we found over 50% simulated spatial networks led to significantly positive relationships. By incorporating interspecific differences in population growth rates by shifting the growth rates by a constant, we introduced enough interspecific differences to produce significant interspecific abundance-occupancy relationships for 99% of simulated spatial networks (Appendix S1: Figure S3). By enforcing covariance between mean population growth rate and initial occupancy and dispersal rate, we observed positive interspecific abundance-occupancy relationships for all simulated

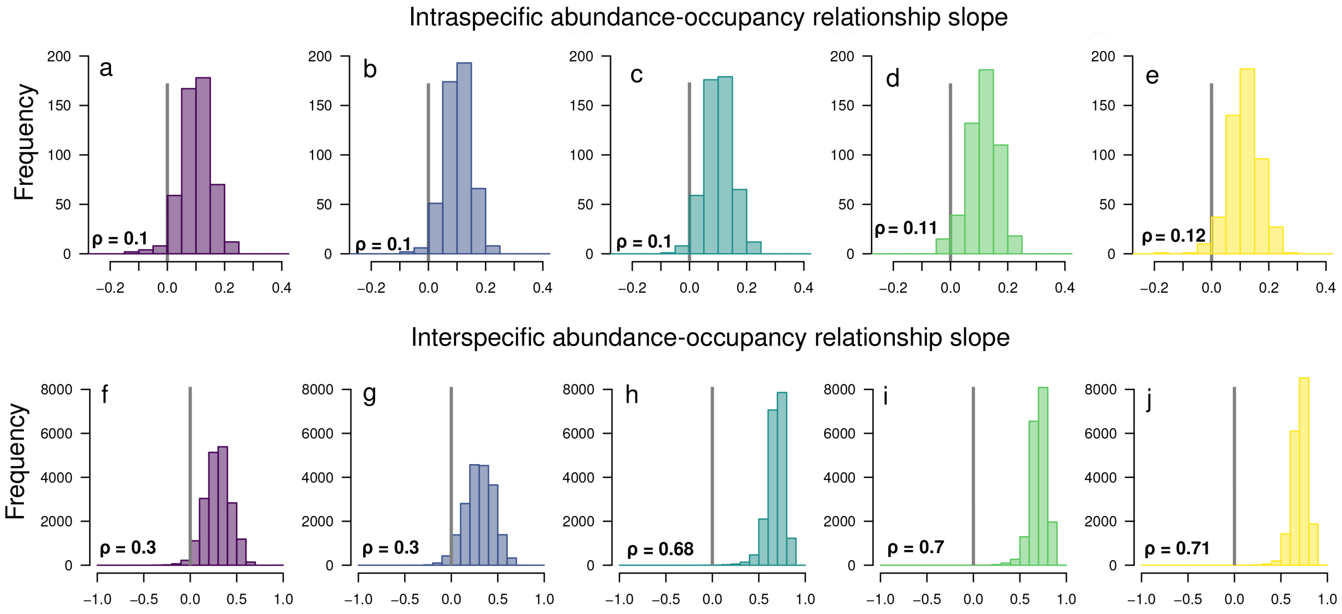

FIGURE 2 Intraspecific (a–e) and interspecific (f–j) abundance-occupancy relationships under different null model scenarios. Intraspecific relationships are based on simulations of individual species (500 simulations), while interspecific relationships are based on assembled communities. See Figure 1 for an explanation of the five treatments, which start with neutral communities (a and f), and become progressively non-neutral.

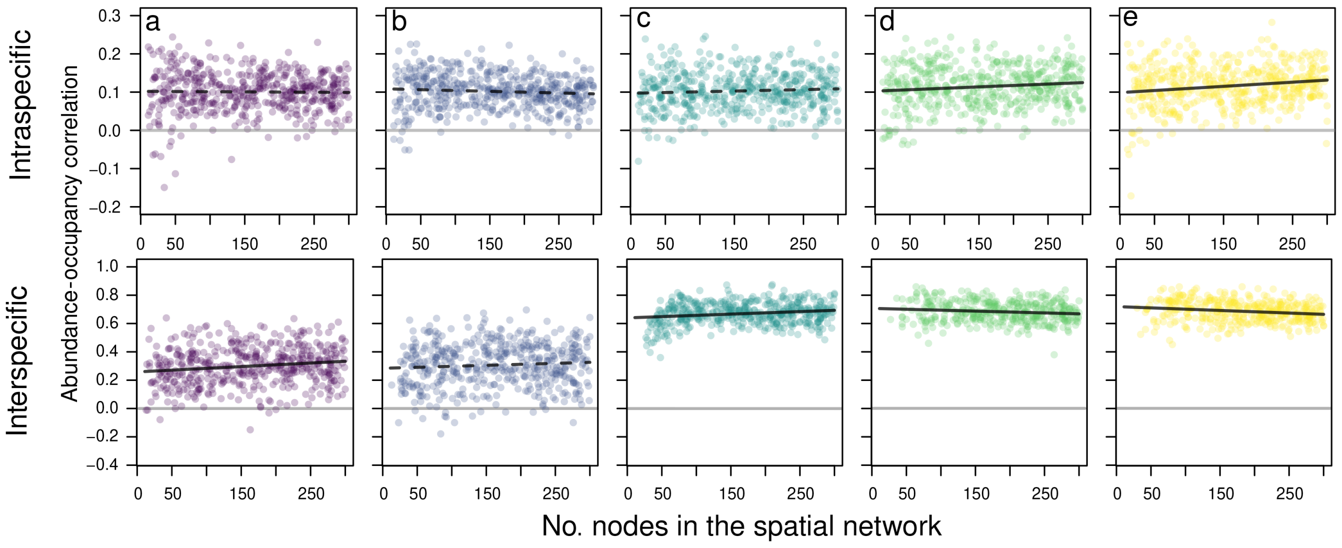

FIGURE 3 The strength of intraspecific (top row) and interspecific (bottom row) abundance-occupancy relationships across the 500 spatial networks and the number of habitat patches in the simulated networks. See Figure 1 for an explanation of the five treatments, which start with neutral communities (a and e), and become progressively non-neutral. Plotted lines are based on linear models, where solid lines are significant relationships ($\alpha < 0.05$).

spatial networks. Both the number of habitat patches in the spatial network and the variation in dispersal connectivity were positively related to interspecific abundance-occupancy relationships (Figure 4), though the positive covariance between spatial network size and variation in dispersal connectivity ($r = 0.72$, $p < 0.0001$) makes it difficult to parse out the relative influence of each.

Effects of community richness on interspecific abundance-occupancy relationships

We assembled null communities by sampling between 2 and 40 simulated species randomly, creating communities of essentially noninteracting species, but that did

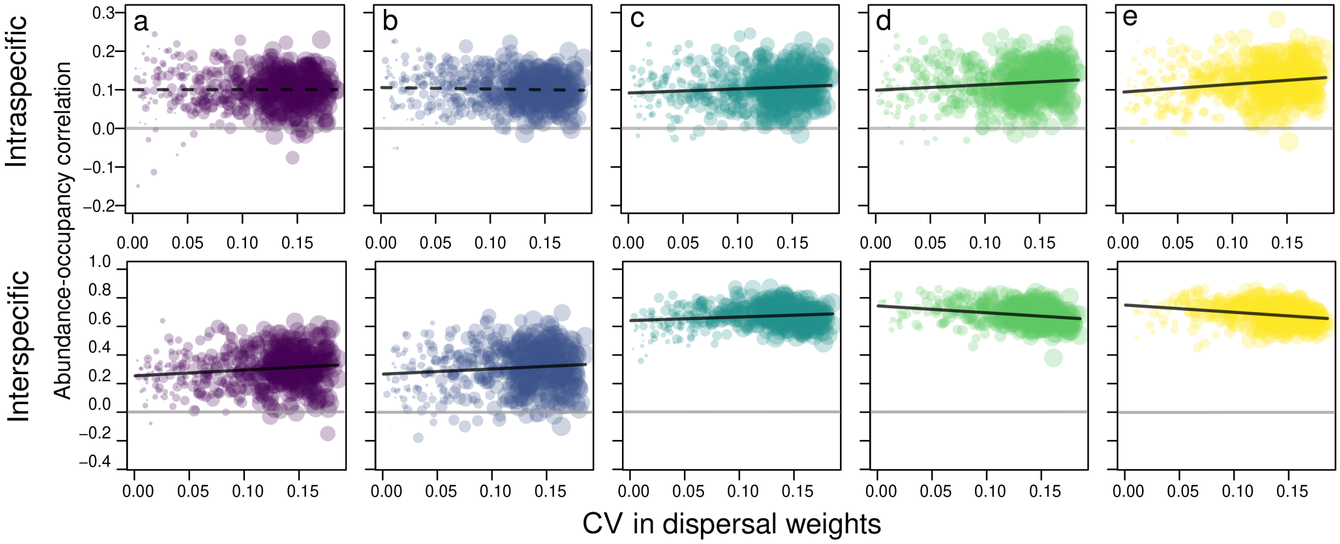

FIGURE 4 The strength of intraspecific (top row) and interspecific (bottom row) abundance-occupancy relationships across the 500 spatial networks and the CV (variance divided by the mean) for dispersal connections in the simulated networks. Point size is proportional to the log of the number of nodes in the network. See Figure 1 for an explanation of the five treatments, which start with neutral communities (a and e), and become progressively non-neutral. Plotted lines are based on linear models, where solid lines are significant relationships ($\alpha < 0.05$).

vary in demographic and dispersal parameters, dependent on the underlying set of assumptions in the simulation model (Figure 1), which is controlled by enforcing (co)variation in demographic and dispersal parameters (Appendix S1: Figure S12). Species richness did not have a strong effect on subsequent interspecific abundance-occupancy relationships (Appendix S1: Figure S12). This is likely due to the lack of interspecific competition in the simulation model, as competition for space or food resources may strongly influence species abundances and community composition.

Spatial network size and interspecific abundance-occupancy relationships

Spatial network size may influence abundance-occupancy relationships by imposing dispersal limitations or generating almost independent groups of populations whose dynamics are different from other sections of the spatial network. The effects of spatial network size may manifest at both intraspecific and interspecific scales. We investigate this across a range of spatial network sizes, providing evidence for conflicting relationships, with the number of nodes in the spatial network being positively related to interspecific abundance-occupancy relationships and negatively related to intraspecific abundance-occupancy relationships under the spatial neutral null model (Figure 3a). However, this relationship is completely removed when realistic demographic variation is added to the null model simulations (Figure 3b–e). The underlying cause of this change in the relationship is certainly motivation for further research.

DISCUSSION

Here, we use a simulation model to explore how variation in species demography, dispersal, and the spatial distribution of habitat patches influence subsequent intraspecific and interspecific abundance-occupancy relationships. We find that intraspecific abundance-occupancy relationships were fairly weak and not strongly influenced by spatial network structure or the incorporation of (co)variance in demographic parameters (e.g., enforcing a relationship between population growth rate and dispersal). On the other hand, we find clear evidence for strong interspecific abundance-occupancy relationships, even under neutral assumptions of species with equal demographic and dispersal rates. Incorporating covariance between occupancy, population growth rates, and dispersal (e.g., species with higher growth rates would also be more likely to disperse) further strengthens interspecific abundance-occupancy relationships. The structure of the spatial network, specifically the variation in dispersal connectivity between habitat patches, was positively related to interspecific abundance-occupancy strength when simulated communities were fairly neutral, but changed to a negative relationship once initial occupancy positively covaried with mean population growth rate. This highlights the importance of the spatial structure of the landscape, and that the effects of the spatial landscape can be overwhelmed by differences among species. Together, we provide evidence that suggests that abundance-occupancy relationships depend on both the structure of the spatial network and assumptions about species demographic and dispersal rates, and that the interplay between these two is important (e.g., network size positively influenced interspecific abundance-occupancy relationships in the neutral simulations, and negatively when we enforced positive covariation between dispersal probability and population growth rate).

The observation of fairly weak or undetectable intraspecific abundance-occupancy relationships matches many observational studies in natural systems, including both aquatic (Barnes, 2022; Bijleveld et al., 2018) and terrestrial (Gaston et al., 1999; Webb et al., 2019) species. Despite being largely weak, intraspecific abundance-occupancy relationships are observed in many natural systems (reviewed in Borregaard & Rahbek, 2010; Gaston et al., 2000; Holt et al., 2002), suggesting the potential that species-level variation may influence the observed variation in relationship strength. However, we also find that these weak relationships were not strongly influenced by the incorporation of species-level differences in demographic rates, covariance between population growth rate and dispersal, or the structure of the spatial network. This is in contrast with the stronger support for interspecific abundance-occupancy relationships—supporting previous suggestions (Borregaard & Rahbek, 2010; Gaston et al., 2000)—as well as the positive effect of species-level variation in demographic rates, dispersal, and spatial network structure on abundance-occupancy relationships. The explanation for this likely relates to the large difference in the drivers of intra- versus interspecific patterns, as intraspecific relationships are measured as a function of time, predicated on the idea that when a species is more abundant in a given time (or a lagged time Manne & Veit, 2020), it will also be more widespread. This is likely due to temporal change in environmental conditions resulting in changes to demographic or dispersal parameters.

Abundance-occupancy relationships have received much empirical interest (Gaston et al., 2000), as well as some theoretical development (Holt et al., 2002). However, some of the theoretical development has criticized the relationships as being a statistical artifact (Hartley, 1998), and other theory has implicitly assumed a relationship between occupancy and abundance by modeling occupancy as a function of abundance. That is, if we assume that species abundance through time or across space is distributed as a Poisson random variable, then occupancy is simply $1-e^{-\mu}$, where μ is species abundance. The idea underlying this is that higher species abundance will result in higher occupancy, potentially due to the inherent issue of species detection when species densities are low. Models of this structure are useful but do not address how species demography, dispersal, and the structure of the landscape influence abundance-occupancy relationships. This work builds on other simulation studies attempting to explore how abundance-occupancy relationships may result from species-level differences. For instance, Martinez et al. (2017) explored interspecific abundance-occupancy relationships by generating simulated time series based on sampled fish communities and pointed to the importance of spatial processes, something which we demonstrate for interspecific abundance-occupancy relationships in our spatially explicit simulation model.

This study also highlights how model parameterization decisions can influence the resulting support for the relationship observed. One parameter in particular is worth discussing. The burn-in period considered was set at 10 generations, something that can readily be changed depending on the underlying dynamics the authors wish to capture. Interestingly, if we increased this burn-in period to remove potential transient dynamics as the system approaches equilibrium, we see a shift toward negative intraspecific abundance-occupancy relationships (Appendix S1: Figure S9). This is potentially due to the reachable states, in terms of mean abundance and occupancy, that the system can get to when the system is closer to equilibrium. We do not tend to observe negative intraspecific abundance-occupancy relationships in natural systems, either because of this proximity to equilibrium issue, or because of numerous other factors that are currently not incorporated into the modeling framework. This is an interesting area for future research to showcase the importance of the environment, species interactions, and evolution potentially altering abundance-occupancy relationships.

The spatially explicit nature of the simulation model allowed us to address how the distribution of habitat patches and dispersal dynamics of the species influenced resulting abundance-occupancy relationships. It is important to note that the spatial networks we used represent only a subset of potential spatial network configurations, as we opted to use a stochastic block model in an attempt to capture a range of modularity values. Future work exploring how abundance-occupancy relationships change as a function of other ecologically relevant network structures (e.g., a lattice) will likely strengthen the general results we observed. Furthermore, the model may allow for a null estimate of abundance-occupancy relationship strength in natural systems under different scenarios in terms of spatial network structure and assumptions of species neutrality and dispersal dynamics. From a theoretical perspective, our simulation model approach could be further explored and built upon by incorporating additional putative mechanisms and assumptions about abundance-occupancy relationships, for example, the importance of interspecific aggregation (Gaston et al., 1998; Hartley, 1998) and sampling process or scale (Steenweg et al., 2018). Importantly, our finding of a dependence of the role of spatial network structure (in terms of network size and dispersal connection variability) on the measured abundance-occupancy relationships when different demographic relationships are enforced (e.g., variation in initial occupancy, covariation between population growth rate, and dispersal ability) requires further theoretical and empirical testing. This interplay between species demographic variation and habitat network structure could have clear implications when thinking about how abundance-occupancy relationships will change through time as community composition shifts (for interspecific abundance-occupancy relationships) or as habitats become fragmented.

AUTHOR CONTRIBUTIONS

Tad A. Dallas performed the analysis. All authors contributed to manuscript writing.

ACKNOWLEDGMENTS

We thank several anonymous reviewers for their constructive feedback. This work has been supported by the National Science Foundation (NSF-DEB-2420769 and NSF-DEB-2017826).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Dallas et al., 2022) are available in Figshare at https://doi.org/10.6084/m9.figshare.17072759.v4.

ORCID

Tad A. Dallas https://orcid.org/0000-0003-3328-9958
Lauren A. Holian https://orcid.org/0000-0003-2627-378X
Cleber Ten Caten https://orcid.org/0000-0003-3788-3508

REFERENCES

Adler, P. B., D. Smull, K. H. Beard, R. T. Choi, T. Furniss, A. Kulmatiski, J. M. Meiners, A. T. Tredennick, and K. E. Veblen. 2018. "Competition and Coexistence in Plant Communities: Intraspecific Competition Is Stronger than Interspecific Competition." *Ecology Letters* 21: 1319–29.

Barabás, G., M. J. Michalska-Smith, and S. Allesina. 2016. "The Effect of Intra-and Interspecific Competition on Coexistence in Multispecies Communities." *The American Naturalist* 188: E1–E12.

Barnes, R. 2022. "Intraspecific Abundance–Occupancy–Patchiness Relations in the Intertidal Benthic Macrofauna of a Cool-Temperate North Sea Mudflat." *Estuaries and Coasts* 45: 827–838.

Bijleveld, A. I., T. J. Compton, L. Klunder, S. Holthuijsen, J. Ten Horn, A. Koolhaas, A. Dekinga, J. van der Meer, and H. W. Veer. 2018. "Presence-Absence of Marine Macrozoobenthos Does Not Generally Predict Abundance and Biomass." *Scientific Reports* 8: 1–12.

Blackburn, T. M., P. Cassey, and K. J. Gaston. 2006. "Variations on a Theme: Sources of Heterogeneity in the Form of the Interspecific Relationship between Abundance and Distribution." *Journal of Animal Ecology* 75: 1426–39.

Borregaard, M. K., and C. Rahbek. 2010. "Causality of the Relationship between Geographic Distribution and Species Abundance." *The Quarterly Review of Biology* 85: 3–25.

Brown, J. H., D. W. Mehlman, and G. C. Stevens. 1995. "Spatial Variation in Abundance." *Ecology* 76: 2028–43.

Chesson, P., and C. T. Lee. 2005. "Families of Discrete Kernels for Modeling Dispersal." *Theoretical Population Biology* 67: 241–256.

Cowley, M., C. Thomas, D. Roy, R. Wilson, J. León-Cortés, D. Gutiérrez, C. Bulman, R. Quinn, D. Moss, and K. Gaston. 2001. "Density–Distribution Relationships in British Butterflies. I. The Effect of Mobility and Spatial Scale." *Journal of Animal Ecology* 70: 410–425.

Dallas, T., C. T. Caten, and L. Holian. 2022. "Code and Data to Reproduce 'Landscape Structure and Species Life History Effects on Abundance-Occupancy Relationships'." figshare. Dataset. https://doi.org/10.6084/m9.figshare.17072759.v4.

Dallas, T., B. A. Melbourne, and A. Hastings. 2019. "When Can Competition and Dispersal Lead to Checkerboard Distributions?" *Journal of Animal Ecology* 88: 269–276.

Donald, P. F., and R. J. Fuller. 1998. "Ornithological Atlas Data: A Review of Uses and Limitations." *Bird Study* 45: 129–145.

Faust, K., and S. Wasserman. 1992. "Blockmodels: Interpretation and Evaluation." *Social Networks* 14: 5–61.

Fort, H. 2018. "On Predicting Species Yields in Multispecies Communities: Quantifying the Accuracy of the Linear Lotka-Volterra Generalized Model." *Ecological Modelling* 387: 154–162.

Freckleton, R., J. Gill, D. Noble, and A. Watkinson. 2005. "Large-Scale Population Dynamics, Abundance–Occupancy Relationships and the Scaling from Local to Regional Population Size." *Journal of Animal Ecology* 74: 353–364.

Freckleton, R. P., D. Noble, and T. J. Webb. 2005. "Distributions of Habitat Suitability and the Abundance-Occupancy Relationship." *The American Naturalist* 167: 260–275.

Fruchterman, T. M., and E. M. Reingold. 1991. "Graph Drawing by Force-Directed Placement." *Software: Practice and Experience* 21(11): 1129–64.

Gaston, K. J. 1996. "The Multiple Forms of the Interspecific Abundance-Distribution Relationship." *Oikos* 76: 211–220.

Gaston, K. J., T. M. Blackburn, J. J. Greenwood, R. D. Gregory, R. M. Quinn, and J. H. Lawton. 2000. “Abundance–Occupancy Relationships.” *Journal of Applied Ecology* 37: 39–59.

Gaston, K. J., T. M. Blackburn, and R. D. Gregory. 1999. “Intraspecific Abundance–Occupancy Relationships: Case Studies of Six Bird Species in Britain.” *Diversity and Distributions* 5: 197–212.

Gaston, K. J., T. M. Blackburn, and J. H. Lawton. 1998. “Aggregation and Interspecific Abundance–Occupancy Relationships.” *Journal of Animal Ecology* 67: 995–99.

Gaston, K. J., and J. Curnutt. 1998. “The Dynamics of Abundance-Range Size Relationships.” *Oikos* 81: 38–44.

Hanski, I. 1982. “Dynamics of Regional Distribution: The Core and Satellite Species Hypothesis.” *Oikos* 38: 210–221.

Hartley, S. 1998. “A Positive Relationship between Local Abundance and Regional Occupancy Is Almost Inevitable (but Not All Positive Relationships Are the Same).” *Journal of Animal Ecology* 67: 992–94.

He, F., and K. J. Gaston. 2003. “Occupancy, Spatial Variance, and the Abundance of Species.” *The American Naturalist* 162: 366–375.

Holt, A. R., K. J. Gaston, and F. He. 2002. “Occupancy-Abundance Relationships and Spatial Distribution: A Review.” *Basic and Applied Ecology* 3: 1–13.

Hubbell, S. P. 1997. “A Unified Theory of Biogeography and Relative Species Abundance and its Application to Tropical Rain Forests and Coral Reefs.” *Coral Reefs* 16: S9–S21.

Karnatak, R., and S. Wollrab. 2020. “A Probabilistic Approach to Dispersal in Spatially Explicit Meta-Populations.” *Scientific Reports* 10: 22234.

Komonen, A., J. Päivinen, and J. S. Kotiaho. 2009. “Missing the Rarest: Is the Positive Interspecific Abundance–Distribution Relationship a Truly General Macroecological Pattern?” *Biology Letters* 5: 492–94.

Manne, L. L., and R. R. Veit. 2020. “Temporal Changes in Abundance–Occupancy Relationships over 40 Years.” *Ecology and Evolution* 10: 602–611.

Martinez, C. M., D. E. Duplisea, R. M. Cerrato, and M. G. Frisk. 2017. “Exploration of Trends in Interspecific Abundance-Occupancy Relationships Using Empirically Derived Simulated Communities.” *PLoS One* 12: e0170816.

May, R. 1973. “Stability and Complexity in Model Ecosystems.” *Monographs in Population Biology* 6: 1–235.

Melbourne, B. A., and A. Hastings. 2008. “Extinction Risk Depends Strongly on Factors Contributing to Stochasticity.” *Nature* 454: 100–103.

Picard, N., and C. Favier. 2011. “A Point-Process Model for Variance-Occupancy-Abundance Relationships.” *The American Naturalist* 178: 383–396.

Steenweg, R., M. Hebblewhite, J. Whittington, P. Lukacs, and K. McKelvey. 2018. “Sampling Scales Define Occupancy and Underlying Occupancy–Abundance Relationships in Animals.” *Ecology* 99: 172–183.

Symonds, M. R., and C. N. Johnson. 2006. “Range Size-Abundance Relationships in Australian Passerines.” *Global Ecology and Biogeography* 15(2): 143–152.

Ten Caten, C., L. Holian, and T. Dallas. 2021. “Weak but Consistent Abundance-Occupancy Relationships across Taxa, Space, and Time.” *Global Ecology and Biogeography* 31(5):13472.

Tovo, A., M. Formentin, S. Suweis, S. Stivanello, S. Azaele, and A. Maritan. 2019. “Inferring Macro-Ecological Patterns from Local Species’ Occurrences.” bioRxiv 387456.

Venier, L. A., and L. Fahrig. 1996. “Habitat Availability Causes the Species Abundance-Distribution Relationship.” *Oikos* 76: 564–570.

Verberk, W. C., G. Van Der Velde, and H. Esselink. 2010. “Explaining Abundance–Occupancy Relationships in Specialists and Generalists: A Case Study on Aquatic Macroinvertebrates in Standing Waters.” *Journal of Animal Ecology* 79: 589–601.

Webb, M. H., R. Heinsohn, W. J. Sutherland, D. Stojanovic, and A. Terauds. 2019. “An Empirical and Mechanistic Explanation of Abundance-Occupancy Relationships for a Critically Endangered Nomadic Migrant.” *The American Naturalist* 193: 59–69.

Webb, T. J., R. P. Freckleton, and K. J. Gaston. 2012. “Characterizing Abundance–Occupancy Relationships: There Is no Artefact.” *Global Ecology and Biogeography* 21: 952–57.

Webb, T. J., D. Noble, and R. P. Freckleton. 2007. “Abundance–Occupancy Dynamics in a Human Dominated Environment: Linking Interspecific and Intraspecific Trends in British Farmland and Woodland Birds.” *Journal of Animal Ecology* 76: 123–134.

Wright, D. H. 1991. “Correlations between Incidence and Abundance Are Expected by Chance.” *Journal of Biogeography* 18: 463–66.

Yonatan, Y., G. Amit, J. Friedman, and A. Bashan. 2022. “Complexity–Stability Trade-Off in Empirical Microbial Ecosystems.” *Nature Ecology & Evolution* 6(6) : 693–700.

SUPPORTING INFORMATION

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

How to cite this article: Dallas, Tad A., Lauren A. Holian, and Cleber Ten Caten. 2025. “Landscape Structure and Species Life History Affect Abundance-occupancy Relationships.” *Ecology* 106(11): e70258. https://doi.org/10.1002/ecy.70258