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Research Article

Demography and dispersal influence the relationship between habitat suitability and population density

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A central goal of ecology is to understand spatial patterns of species densities. Habitat suitability estimates from species distribution models (SDMs) could be used to represent species density and overcome the scarcity of density data. However, there is mixed evidence that habitat suitability is a reliable descriptor of density, and it is suggested that local dynamics affect the relationship between habitat suitability and density. We simulated population dynamics for 200 virtual species considering different combinations of factors (demographic stochasticity, dispersal, and intraspecific competition) that affect population sizes and SDMs were trained using different sets of environmental predictors to evaluate when habitat suitability reflects densities. We also examined the generalities of these relationships in nature considering 200 North American bird species sampled by the Breeding Bird Survey. We found that even when population growth rate and demographic stochasticity were the only factors driving population dynamics and SDMs are trained with the two environmental factors that controlled population density, habitat suitability was not consistently related to virtual species densities. Incorporating dispersal dynamics and spatial differences in intraspecific competition had negative effects on the relationship between habitat suitability and density, showing that these factors influence these relationships. Similarly, habitat suitability could not explain the density of North American birds. Together, our results suggest that the use of habitat suitability estimates from SDMs to understand population densities should be avoided as habitat suitability does not relate to density under many scenarios.

Keywords: demographic stochasticity, dispersal, habitat suitability, intraspecific competition, population density, species distribution model

Introduction

The fundamental niche is a persistence threshold that defines the sets of environmental conditions that allows species to persist across geographic space (Hutchinson 1957, Pulliam 2000, Colwell and Rangel 2009). Several statistical methods that relate species occurrence data with environmental conditions have been developed to identify



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areas that are environmentally suitable for species occurrence (Peterson et al. 2011). These tools, frequently referred to as species distribution models (SDMs), are primarily used to estimate species geographic distributions and have been essential for answering macroecological and biogeographical questions as well as to aid conservation efforts (Cayuela et al. 2009, Calabrese et al. 2014, Biber et al. 2020). SDMs generate habitat suitability estimates where higher values represent more favorable conditions for species to occupy. These favorable conditions are usually assumed to support larger population sizes because of an increased survival and reproductive success of individuals occurring in these areas (Weber et al. 2017, Dallas and Hastings 2018, Lee-Yaw et al. 2022), leading to a potential positive relationship between habitat suitability and species abundance (Gomes et al. 2018). Although abundance is the term often used in these studies, hereafter we will use the term *density* (number of individuals per area) as oftentimes it is the only possible measure given that sampling is frequently done in a non-exhaustive way and it consists of the number of individuals observed in a specified area.

This putative relationship between habitat suitability and density has spurred an interest in using SDMs to predict species densities (Oliver et al. 2012, Acevedo et al. 2017, Monnier-Corbel et al. 2023). Estimating species density through sampling approaches is a difficult task, such that a lack of spatial and temporal density data, a shortcoming called the *Prestonian shortfall*, represents a major knowledge gap for most species (Hortal et al. 2015). Addressing this knowledge gap is important given that having information on species densities is crucial for understanding population dynamics (Santini et al. 2024). Using SDMs to predict species density is thus compelling given the more widespread availability of presence data that are often used in these models (Pearce and Boyce 2006, Bradley 2016). However, current evidence indicates that SDMs have limited efficacy in describing species density as most successful predictions come from cases where these relationships were assessed for single species whereas evaluations considering multiple species tend to be unsuccessful (Weber et al. 2017, Dallas and Hastings 2018, Lee-Yaw et al. 2022, Waldock et al. 2022). There is mixed evidence on the ability of habitat suitability estimates to reflect different demographic parameters that influence population sizes (Brambilla and Ficetola 2012, Pellissier et al. 2013, Aizpurua et al. 2017, Lee-Yaw et al. 2022, Şen et al. 2024). If habitat suitability is often unrelated to demographic parameters, then it is less likely that habitat suitability would reflect population density as demographic parameters directly affect population growth rates.

A lack of connection between habitat suitability and density could also occur because a species density in a given location is affected by factors that are often ignored in SDMs (Boulangéat et al. 2012). For example, spatial differences in the level of intraspecific competition, because of differences in resource availability, can lead to complex spatial patterns of population dynamics (Klomp 1964, Turnbull et al. 2007, Zhang et al. 2021). Dispersal can further affect observed population densities by allowing the persistence of populations

in unsuitable environments through source–sink dynamics (Pulliam 1988, 2000, Furrer and Pasinelli 2016). Moreover, when there are spatial differences in population growth rates and in intraspecific competition, dispersal can enhance population sizes and lead to larger than expected populations (Oksanen 1990, Zhang et al. 2021). When population sizes are small, demographic stochasticity plays an important role in driving population dynamics where these populations can face a higher extinction risk (Gabriel and Bürger 1992, Melbourne and Hastings 2008). Since SDMs are trained on binary data and often assume equilibrium dynamics (Lalechère et al. 2025), it can be particularly challenging for habitat suitability estimates to relate to species densities given the several factors, such as the ones outlined above, that affect population sizes.

Species tolerate different ranges of environmental conditions and use different types of resource, which could further lead habitat suitability estimates to be unrelated to density. For example, abundance–occupancy relationships describe the tendency for widespread species to be more locally abundant than restricted species, possibly because these widespread species are more generalist in terms of environmental conditions they tolerate or in the resources they use (Borregaard and Rahbek 2010, Ten Caten et al. 2022). For such generalist species, SDMs might not be able to detect important environmental variables that limit their distributions, making these models unable to differentiate suitable and unsuitable environments in these cases (Hernandez et al. 2006, van Proosdij et al. 2016, Harisena et al. 2021). Conversely, species with restricted distributions can still achieve high densities in locations they occupy depending on local resource availability (Komonon et al. 2009, Crisfield et al. 2024). As species might exhibit different types of specialization that can lead to complex patterns of geographic distributions and densities (Crisfield et al. 2024), SDMs might have difficulties distinguishing these types of specialization from occurrence data. Lastly, species can have performance curves (i.e. the relationship between how population growth rate changes along environmental conditions) with different characteristics that SDMs might also not be able to properly describe from occurrence data, which would ultimately render these models inappropriate for understanding densities (Lee-Yaw et al. 2022).

Here, we used a simulation framework to examine the effects of incorporating demographic stochasticity, dispersal, and intraspecific competition when modeling population dynamics across geographic space on the relationship between habitat suitability and density (Fig. 1). Simulated species had performance curves of different shapes and breadth to consider how species differences affect these relationships. To examine the generalities of these relationships in nature we also assessed how habitat suitability related to the density of 200 North American bird species. We found that habitat suitability was often positively correlated to density, but these relationships were highly variable and habitat suitability often explained $\approx 25\%$ and $\approx 5\%$ virtual species and North American birds densities, respectively. Demographic

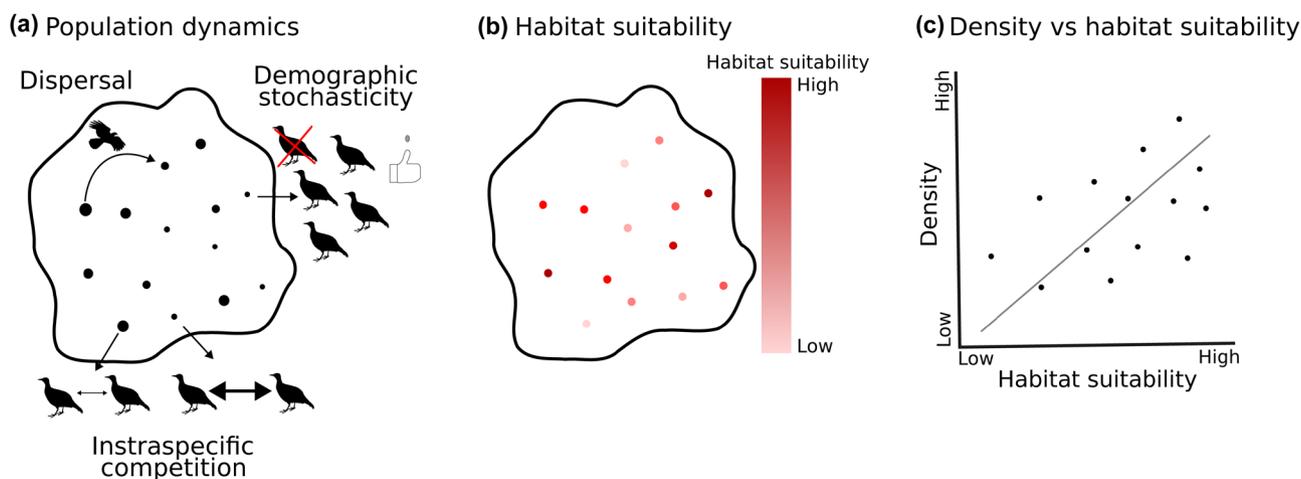


Figure 1. Populations of virtual species were simulated considering different local dynamics that affect species density (point sizes in a). Dispersal and demographic stochasticity did not vary across populations when they were considered in the models, but some population models included spatial differences in the strength of intraspecific competition (thicker double-headed arrow represents stronger intraspecific competition). Habitat suitability was estimated using species distribution models for sites where populations occurred (b) to explore the relationship (grey line) between habitat suitability and densities (c).

stochasticity, dispersal, and intraspecific competition had small negative effects on these relationships, and species differences and characteristics of the SDMs explained a small amount of the variability in these relationships across virtual species, suggesting that habitat suitability often does not reflect species densities.

Material and methods

Virtual species population dynamics

We simulated 200 virtual species occurring in a lattice representing the United States and Canada (spatial resolution of 20 minutes that had 25 207 cells; Supporting information) using population models that considered different factors that influence population dynamics (Fig. 1). A discrete time Ricker model was used to simulate population dynamics, where populations grew according to population growth rate R and intraspecific competition ($\alpha=0.005$) limited population sizes. The number of offspring was treated as a Poisson random variable with mean of R offspring per individual and survivorship was treated as a binomial random variable with probability $e^{-\alpha N_t}$, representing the effects of demographic stochasticity in our model.

$$N_{t+1} = N_t R e^{-\alpha N_t} \quad (1)$$

In this model demographic stochasticity and population growth rate were the only factors causing changes in population sizes across generations. This model was expanded to also allow the occurrence of dispersal events between populations following a binomial random variable with probability d ($d=0.20$). Individuals dispersing from a focal population immigrated to new populations according to a negative

exponential dispersal kernel (Nathan et al. 2012) that was species-specific (Supporting information). The maximum dispersing distance (D_{max} ; in number of cells) was randomly chosen between 5 and 25 and the mean dispersal distance (D_{mean}) was a randomly chosen fraction between 0.1 and 0.6 of the maximum dispersal distance. Individuals could not disperse to cells outside the borders of the lattice (Supporting information). This model was further expanded to allow spatial variation in the strength of intraspecific competition (Zhang et al. 2021). We used data on productivity to inform the intensity of intraspecific competition as productivity limits population and community sizes of several taxa (Srivastava and Lawton 1998, Cerezer et al. 2021). We assumed a linear negative relationship between the productivity of a site and the level of intraspecific competition that a given population experienced ($\alpha=0.005-0.1$). We used the normalized difference vegetation index (NDVI) as a proxy for productivity and we obtained NDVI data for the first day of June of 2020 from MODIS through the R package 'MODISstp' (Busetto and Ronghetti 2016). Table 1 provides a summary of all parameters used, and their values, when simulating the population dynamics of the virtual species.

For each species, populations were simulated considering the following combination of factors: demographic stochasticity (considered our baseline model), demographic stochasticity and spatial intraspecific competition, demographic stochasticity and dispersal, and demographic stochasticity, spatial intraspecific competition, and dispersal, resulting in four population simulations per species (Table 2). Simulations started with all cells in the lattice occupied with 20 individuals from a given species and models ran for a total of 100 generations to allow population dynamics to reach equilibrium. By the end of the simulations, occupancy (fraction of occupied cells in the lattice) varied across species (0.38 ± 0.16), and we sampled 100–750 of those occupied cells to model

Table 1. Parameter values used to simulate the population dynamics (α , R , d , D_{\max} , D_{mean}) and the performance curve (H , m , r , p , s) of virtual species. α was either constant (0.005) or varied spatially (0.005–0.1) in population models. R varied from 0–3.3 across environmental conditions depending on species performance curves. d was set to 0.20 across all species. D_{\max} and D_{mean} varied across species and values (number of lattice cells) ranged from 5–25 and 1–15, respectively. H , the height of the species performance curves, which describes the maximum population growth rate species achieved under their optimum environmental conditions, was set to be the same (3.3) across all species. m varied across species and represented the temperature in which population growth rate was maximized. r represented the symmetry of species performance curves, and a value of zero represented perfectly symmetric curves whereas negative values represented asymmetric curves. p represented the kurtosis of the performance curves, and it was chosen to be 3 and 5.25 for symmetric and asymmetric performances, respectively. s varied across species and represented the breadth of performances in terms of temperature.

Parameter	Definition	Values
α	Intraspecific competition	0.005–0.1
R	Population growth rate	0–3.3
d	Dispersal probability	0.2
D_{\max}	Maximum dispersal distance	5–25
D_{mean}	Mean dispersal distance	1–15
H	Performance curve height	3.3
m	Species optimum temperature	–15 to 14
r	Symmetry of performance curve	0, –0.95
p	Kurtosis of performance curve	3, 5.25
s	Performance curve breadth	3–10

the distribution of virtual species. We chose this number of cells for the virtual species to be consistent with the number of sites that the North American bird species considered in our study occupied (below).

Two performance curves, a symmetric and an asymmetric, were simulated for each virtual species considering mean annual temperature in the United States and Canada (section ‘Environmental predictors and model structure’). We simulated performance curves considering mean annual temperature because there is significant spatial variation in temperature patterns in North America (Supporting information). Mean annual temperature values ranged –26 to 24.4°C, allowing the possibility of simulating species that tolerate different ranges of temperatures. Symmetric and asymmetric performance curves were used because several species have performance curves with these properties (Oksanen and Minchin 2002, Vasseur et al. 2014). These performance curves represent how species’ population growth rates change along temperature gradients (Table 1), and they were used to estimate R of each population occurring in a given location. We used the *sech* function available in the ‘*senlm*’ package (Anderson et al. 2022) to simulate symmetric and asymmetric performance curves. Across all species, maximum population growth (height, H parameter in *sech*) rate was 3.3 for symmetric and asymmetric performance curves. A species had the same optimum temperature (location of the maximum, m parameter) for both performance curves, and this optimum was randomly sampled between –15 and 14. However, curves differed in skewness (symmetry, r , parameter), where the skewness of the symmetric and asymmetric

Table 2. Processes (factors) considered in the Ricker models (population models) used to model the population dynamics of the virtual species. Populations resulting from these models were randomly sampled and transformed into presence data that were used in SDMs fit considering different sets of environmental predictors. The relationship between population density and habitat suitability was evaluated for the combinations of population models and SDMs showed below (i.e. a total of six assessments for the virtual species). Dem. stoch. represents demographic stochasticity, spatial α represents spatial differences in intraspecific competition, BIO1 represent mean annual temperature, BIO2 represents mean diurnal range in temperature, BIO4 represents temperature seasonality, BIO12 represents annual precipitation, BIO13 represents precipitation of the wettest month, BIO15 represents precipitation seasonality and PCA axes represent the first four axes from a PCA performed over the 19 bioclimatic variables available in WorldClim (see Material and methods for details).

Factors (population models)	Environmental predictors (SDMs)
Dem. stoch.	BIO1 and NDVI
Dem. stoch. and spatial α	BIO1 and NDVI
Dem. stoch. and dispersal	BIO1 and NDVI
Dem. stoch., spatial α , and dispersal	BIO1 and NDVI
Dem. stoch., spatial α , and dispersal	BIO1, BIO2, BIO4, BIO12, BIO13, BIO15
Dem. stoch., spatial α , and dispersal	PCA axes

curves was 0 and –0.95, respectively. A negative value of skewness makes the performance curve have a broader left-hand tail while a value of 0 makes the performance curve symmetric (Anderson et al. 2022). Peakedness (peakedness, p , parameter) was chosen to be 3 and 5.25 for symmetric and asymmetric curves, respectively. The peakedness parameter controls the kurtosis of the performance curve and smaller values lead to flatter curves where population growth rates decrease more slowly away from the optimum environmental condition. Lastly, the spread (spread, s , parameter) of the asymmetric curves was 1/3 of the spread of symmetric curves. The spread represents the range of temperature values that a species could tolerate, and these values were randomly sampled between 3 and 10. Our goal was to evaluate whether the shape and the breadth of a species performance curve could affect the relationship between habitat suitability and density. The Supporting information shows an example of how a symmetric and an asymmetric performance curves change along the temperature gradient for a species.

North American bird density data

We used data on North American bird species to compare habitat suitability estimates from SDMs to the density of these species to explore the generality of these relationships for real species. Bird density data were obtained from the Breeding Bird Survey (BBS; Sauer et al. 2020). The BBS is a yearly standardized census of North American bird species that is performed by volunteers during the breeding season. In these surveys, routes of ≈ 50 km are sampled every 1 km for about three minutes through point counts where all birds seen or heard within a radius of 0.4 km are recorded. We used the data sampled from 1997–2019 to estimate the mean annual density and to model the distribution of 200 bird

species (see the Supporting information for species names) that were observed occurring in 100–750 locations. We chose this temporal extent to calculate mean annual density because a consistent number of sites (≈ 3000) have been continuously sampled by BBS since 1997, providing reliable estimates of population density for this time period. Incomplete sampling and detection probability could affect where species are recorded and their observed density and potentially influence the analyses of such data. However, incomplete sampling should not affect our study given the standardized nature of how the BBS data are collected, and also because there is limited evidence for potential biases influencing analyses of the BBS data across large spatial and temporal scales considering several species (Rosenberg et al. 2019). Moreover, the effects of detection probability are more prevalent when population sizes are small (Tanadini and Schmidt 2011, Bennett et al. 2024), such that both occurrence (used in SDMs to estimate habitat suitability) and density (used to relate to habitat suitability) data would be similarly affected by detection probability in these cases. This suggests that incomplete sampling or detection probability should have not influenced the relationship between habitat suitability and density that we observed for North American birds.

Environmental predictors and model structure

We obtained the 19 bioclimatic variables available in WorldClim 2.1 at a resolution of 10 min through the 'geodata' R package (Fick and Hijmans 2017, Hijmans et al. 2023). These variables include different measurements of temperature and precipitation patterns that are considered important determinants of species distributions (Barbet-Massin and Jetz 2014, Illán et al. 2014). For the North American bird species, we performed a PCA over the 19 bioclimatic variables covering North America and used the first four axes as predictors to model the species distributions given that they explained about 90% of the variation in the data (Kriticos et al. 2014). These environmental predictors were aggregated to have a resolution of 30 min when modeling the distribution of North American birds to match the spatial resolution in which the BBS data is sampled.

The distribution of virtual species were modeled using different sets of environmental predictors (Table 2). First, we modeled their distributions using mean annual temperature and NDVI as predictors. This represents a situation where there is a perfect knowledge about the environmental conditions that affect the population dynamics of species. SDMs were fitted using NDVI and mean annual temperature as predictors for the four population models that we considered. We also modeled species distributions using mean annual temperature, mean diurnal range in temperature, temperature seasonality, annual precipitation, precipitation of the wettest month, and precipitation seasonality (hereafter multiple environmental predictors). This exemplifies a situation where there is some knowledge about what variables potentially affect population dynamics, but unimportant predictors are also considered in the model. SDMs using these multiple environmental predictors were fitted for population

models that simultaneously considered demographic stochasticity, spatial intraspecific competition, and dispersal. Lastly, we performed a principal components analysis (PCA) over these 19 bioclimatic variables covering the United States and Canada and used the first four axes that explained about 90% of the variance of the data as predictors in the model. This constitutes a case where there is limited or no knowledge about the environmental factors that affect the population dynamics of a given species. SDMs using these PCA axes as predictors were also fitted for population models that simultaneously considered demographic stochasticity, spatial intraspecific competition, and dispersal. Thus, we were able to examine whether SDMs trained with uninformative environmental predictors had habitat suitability estimates that were less related to density. Environmental variables were aggregated to have a spatial resolution of 20 min when modeling the distribution of the virtual species to match the resolution in which their population dynamics were simulated.

Modeling and evaluating species distributions

The distribution of virtual and real species was modeled using MaxEnt, a widely used machine-learning method that requires presence and pseudo-absence data and that generally have good performance (Elith et al. 2010, Santini et al. 2021). Models were fit using default regularization coefficient values as these have been shown to perform well for a wide range of species and because fine tuning models individually for each species is impractical when considering several species as in our case (Phillips and Dudík 2008, Merow et al. 2013). To have a balanced dataset for modeling species distributions, we sampled as many pseudo-absences as the number of presences that species had, such that 50% of the data were presences and 50% were pseudo-absences (Senay et al. 2013, Iturbide et al. 2015). Pseudo-absences were randomly sampled from 400 km buffers surrounding presence points of virtual (i.e. the 100–750 sampled populations) and real species (i.e. the BBS routes where species were recorded). Sampling pseudo-absences from 400 km buffers surrounding presences allows enough variation in environmental conditions to be captured when fitting the SDMs while not being too general and considering environments that are not important for the species. Nonetheless, we also examined the effects of sampling pseudo-absences from the entire landscape when fitting SDMs for the virtual species in the Supporting information. We used a cross-validation procedure, where 75% of our dataset was used to train the models and the other 25% was used to test the models. This process was repeated 20 times to account for potential differences in the habitat suitability estimates that could arise from using specific sets of presences and pseudo-absences when training and testing the models. Models were evaluated using the area under the receiver operating characteristic curve (AUC) (Fielding and Bell 1997). AUC is a discrimination performance measure that assesses how well a model distinguishes between presences and pseudo-absences, where values closer to 1 suggests a model is good at differentiating presences from pseudo-absences and values around 0.5 indicates a random performance. Habitat

suitability estimates and AUC were averaged across species considering the 20 models that were fitted for each species. For the virtual species, we assessed whether habitat suitability estimates produced by SDMs could replicate their performance curves. Performance curves were rescaled to 0–1 and we compared, along the temperature gradient, the difference between observed mean habitat suitability produced by SDMs and the actual population growth rate in a given environment based on the performance curve of the species.

Assessing the relationship between habitat suitability and density

The presence data used to model species distributions were used to evaluate how habitat suitability related to population density. We extracted habitat suitability for presence points and we used the observed population size in those locations to represent species densities. The population density estimate used for the BBS data was the mean number of individuals recorded between 1997–2019 across routes occupied by species while for the virtual species population density was the number of individuals observed in a given cell in generation 100 (i.e. the last generation in the simulations where populations should have reached equilibrium). The relationship between habitat suitability and density was evaluated using Pearson's correlations. To examine how well habitat suitability explained density, we calculated the coefficient of determination, which is equal to the squared Pearson's correlation coefficient.

We fitted two linear mixed-effect models to evaluate the effects of different factors on the relationship between habitat suitability and density across species. In both LMMs, we used the correlation coefficient (r) between habitat suitability and density as the response variable and species were used as random effects, but different fixed effects were considered. In our first LMM, our goal was to understand how factors that contribute to local population dynamics affect the relationship between habitat suitability and density. We encoded dummy variables to assess how considering dispersal and spatial intraspecific competition in population models affected these relationships. Demographic stochasticity was present in all models and was considered our baseline case. Thus, we did not encode a dummy variable for demographic stochasticity. In this LMM, we also considered whether using multiple environmental predictors or PCA axes when training SDMs affected the relationship between habitat suitability and density by encoding dummy variables for these predictors. In our second LMM, we were interested in understanding how species differences and SDMs characteristics could affect the relationship between habitat suitability and density. Fixed effects considered were the breadth and the shape (i.e. symmetric or asymmetric) of species performance curves, the mean absolute difference between habitat suitability and population growth rate (estimated from presences), and the mean SDM performance. In this model, continuous predictors were in different scales and they were standardized to allow comparisons of their effects on the relationship between habitat suitability and density. LMMs were fit using the 'glmmTMB' R

package (Brooks et al. 2017) while model diagnostics (model assumptions were generally met; Supporting information) and goodness of fit (Nakagawa's conditional R^2) were estimated using the 'performance' R package (Lüdecke et al. 2021). This conditional R^2 takes fixed and random effects into account when estimating the model goodness of fit.

Results

Do demographic stochasticity, dispersal, and intraspecific competition affect the relationship between habitat suitability and density?

Correlations between habitat suitability and density were often significant and positive, but the strength of these relationships varied considerably across species within the different models of population dynamics (Fig. 2a), and habitat suitability explained $\approx 25\%$ of the variation in species density (Fig. 2b). Habitat suitability was not consistently related to density even when population dynamics were driven solely by population growth rates and demographic stochasticity and SDMs were trained with the two environmental factors that affected the density of species. We found that in the baseline case (the intercept) of our first LMM, the average correlation between habitat suitability and density was 0.48. This correlation is reduced to 0.45 for population models that considered dispersal ($r_{\text{intercept}-\beta} = 0.45$; $\beta = -0.027$, $p < 0.01$) and to 0.41 for models that considered spatial differences in intraspecific competition ($r_{\text{intercept}-\beta} = 0.41$; $\beta = -0.069$, $p < 0.01$) (Fig. 2c). Nakagawa's conditional R^2 was 0.28, indicating that this LMM had a relatively limited explanatory power. The performance of SDMs widely varied across virtual species, such that these models tended to have lower performance for species that have broader performance curves (Supporting information).

As expected, SDMs were more consistently able to identify the important environmental predictor that drives population growth rate when they were trained with mean annual temperature and NDVI than when multiple environmental predictors were considered (Supporting information). However, using multiple environmental predictors had no effect on the correlation between habitat suitability and density, while using PCA axes as predictors negatively affected these relationships ($r_{\text{intercept}-\beta} = 0.38$; $\beta = -0.099$, $p < 0.01$; Fig. 2c). This suggests that having no information on environmental factors that affect population dynamics may lead to habitat suitability estimates that are less related to species densities.

What explains the high variability in the relationship between habitat suitability and density?

We found that the high variability in the relationship between habitat suitability and density observed across virtual species could be explained by some of the factors that we considered in our second LMM. The baseline case (the intercept) of this LMM had an average correlation between habitat suitability and density of 0.39. Habitat suitability tended to relate

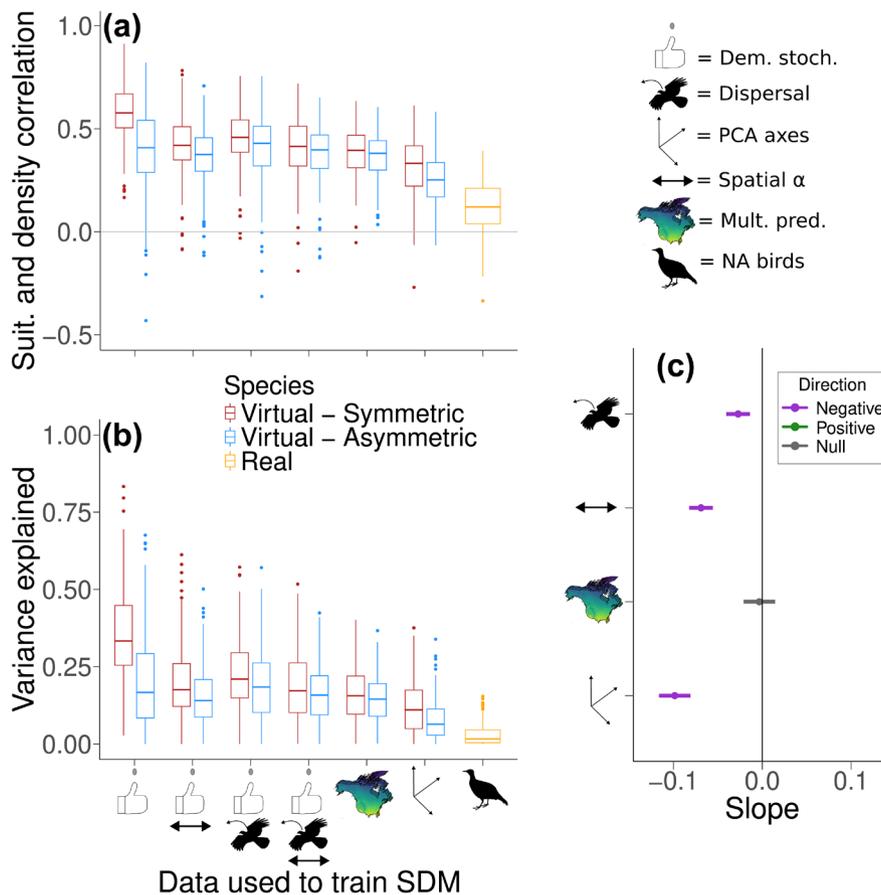


Figure 2. Observed correlations between habitat suitability (Suit.) and density for virtual species with symmetric (red color) and asymmetric (blue color) performance curves and for North American birds (NA birds). There was a general positive correlation between habitat suitability and density across all scenarios considered (a), but these relationships were highly variable and had low explanatory power (b), suggesting that habitat suitability cannot be used reliably to understand species density. Population models for the virtual species were simulated considering different combinations of demographic stochasticity (Dem. stoch.), spatial variation in the strength of intraspecific competition (Spatial α) and dispersal (Dispersal). SDMs were trained using mean annual temperature and NDVI as predictors, or multiple environmental conditions (Mult. pred.) or PCA axes (PCA axes) as predictors when specified. (c) Shows the results (slopes) from our first LMM, where purple and green colors represent significant negative and positive effects, respectively, of a predictor while grey color represents non-significant effect. We found that dispersal and spatial differences in intraspecific competition negatively affect the correlation between habitat suitability and density. Using multiple environmental predictors in SDMs did not affect these relationships while using PCA axes had negative effects on the observed correlations (c).

less to the density of species that had broader performance curves ($r_{\text{intercept} - \beta} = 0.35$; $\beta = -0.039$, $p < 0.01$; Fig. 3a, e) or when habitat suitability poorly reflected population growth rates ($r_{\text{intercept} - \beta} = 0.33$; $\beta = -0.061$, $p < 0.01$; Fig. 3b, e). SDMs performance and the shape of species performance curves did not affect the relationship between habitat suitability and density (Fig. 3c–e). Nakagawa's conditional R^2 was 0.20, also suggesting that this LMM could not explain most of the variation in the relationship between habitat suitability and density across species. Although SDMs trained with pseudo-absences sampled from the entire landscape had higher performance than models trained using pseudo-absences sampled from buffers for virtual species (Supporting information), the correlation between habitat suitability and density was similar regardless of how pseudo-absences were sampled (Supporting information). This further suggests that

SDMs that have high performance do not necessarily produce habitat suitability estimates that better reflect population density.

What is the relationship between habitat suitability and density for North American birds?

We found that habitat suitability and density were positively correlated for 54% of the North American birds, while negative and non-significant relationships were observed for 5.5 and 40.5% of the species, respectively (Fig. 2a). Despite finding these positive relationships, habitat suitability rarely explained over 5% of the variation in density of North American birds (Fig. 2b). These results showed that habitat suitability is less often related to the density of real species compared to virtual species, and significant correlations could only explain a particularly small fraction of the variation in

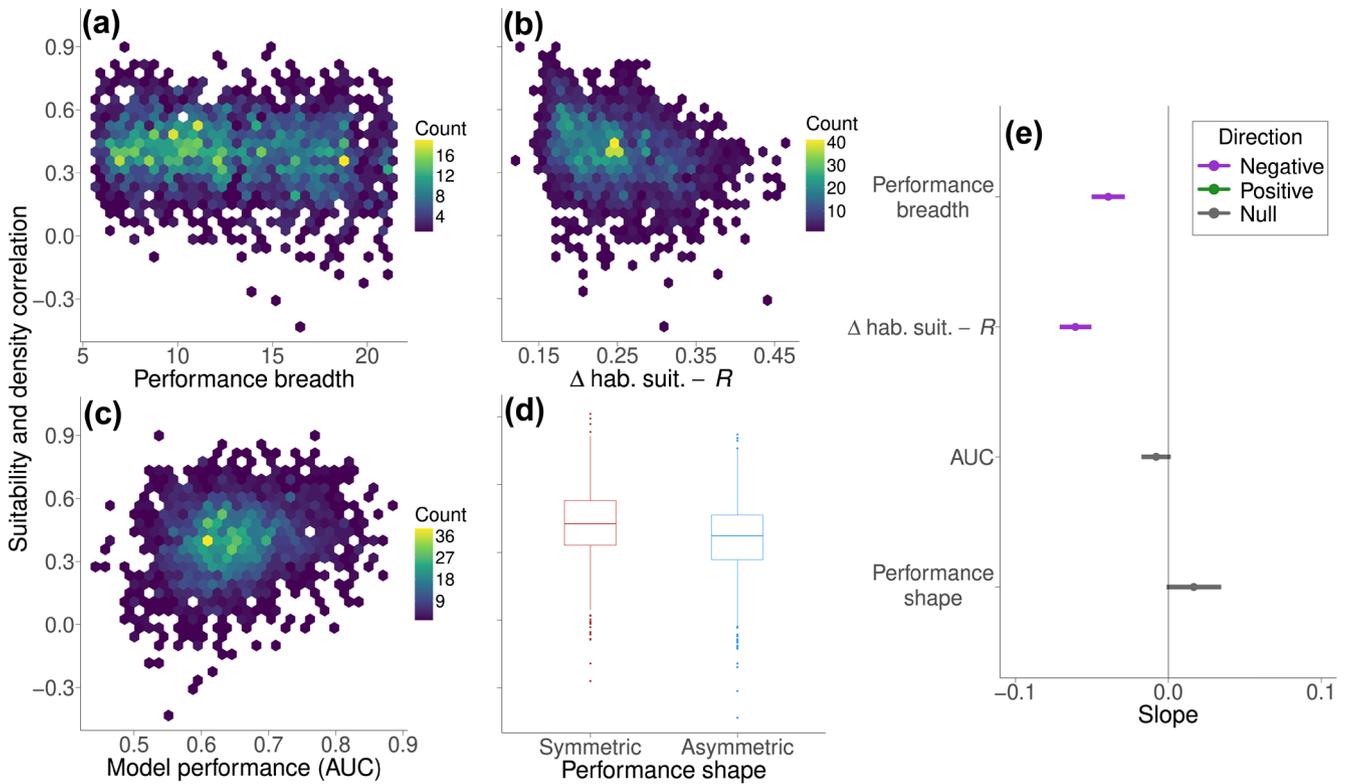


Figure 3. Hexagonal heat map showing how the correlation between habitat suitability and density is affected by the species performance breadth (a), the ability of habitat suitability estimates to accurately represent population growth rates (Δ hab. suit. - R , b), the average SDM performance (Model performance (AUC), c) and a boxplot showing the differences in those correlations between symmetric (red color) and asymmetric (blue color) performance curves (Performance shape, d) for virtual species. Cell color refers to the number of species within that bin in the hexagonal heat maps. (e) Shows the results (slopes) from our second LMM, where purple and green colors represent significant negative and positive effects, respectively, of a predictor while grey color represents non-significant effects. It is possible to see that broader performance breadths and habitat suitability estimates that poorly reflected population growth rates negatively impacted the relationship between habitat suitability and density. SDM performance and the shape of the species performance curve did not affect the correlation between habitat suitability and density.

density of North American birds. Nevertheless, SDMs performed relatively well for North American birds (Supporting information). Overall, our results highlight a general disconnect between habitat suitability and species densities for virtual species and North American birds.

Discussion

We found that habitat suitability is often positively correlated to density, but these relationships were widely variable across species and had low explanatory power, indicating that habitat suitability estimates might be unreliable for understanding species densities. The disconnect between habitat suitability and density often reported for real species is usually attributed to the fact that several factors, such as dispersal dynamics or resource limitation, acting at the local scale could lead to complex spatial patterns of density that habitat suitability would be unable to capture (Weber et al. 2017, Dallas and Hastings 2018, Jiménez-Valverde et al. 2021). We showed that even when population growth rates and demographic stochasticity were the only factors influencing

population sizes, habitat suitability estimates were still not consistently related to species densities. This indicates that including a stochastic component when simulating population dynamics may be enough to negatively impact the potential relationship between habitat suitability and density (Osorio-Olvera et al. 2019). Incorporating dispersal dynamics and spatial intraspecific competition to our models had small negative effects on these relationships, showing that these factors influenced the relationship between habitat suitability and density. However, these findings also suggest that demography and dispersal may not be the main factors responsible for the weak link between habitat suitability and density.

The general disconnect between habitat suitability and density could occur because the presence data used to train SDMs might not contain the necessary information to describe densities. Occurrence data may be sampled opportunistically and not capture the range of environmental conditions that affect species occurrence (Phillips et al. 2009, Lee-Yaw et al. 2022). Further, high habitat suitability might suggest high probability of occurrence, but not of density, as environmental conditions can differently affect species occurrence and

density (Bradley 2016). Although SDMs that have better performance may produce habitat suitability estimates that better reflect population density (Jiménez-Valverde et al. 2021), we observed that model performance did not influence the relationship between habitat suitability and density. This suggests that a model that is suitable for estimating occurrences does not necessarily translate into a model that is suitable for estimating densities. SDMs that produced habitat suitability estimates that more properly reflected population growth rates led to stronger correlations between habitat suitability and density across species. This occurs because these models provide a more accurate description of how species performances, and consequently the potential population size in a given area, change along environmental gradients. This suggests that if habitat suitability describes demographic parameters, then the use of SDMs to understand population density may be more promising though habitat suitability is not consistently related to species demographic parameters in nature (Pellissier et al. 2013, Aizpurua et al. 2017, Şen et al. 2024). However, SDMs might be particularly unable to describe performance curves of species that tolerate a wide range of environmental conditions because these models often cannot discriminate suitable from unsuitable environments for such generalist species (Hernandez et al. 2006, Franklin et al. 2009, van Proosdij et al. 2016). This would explain why habitat suitability is less related to the density of species that have broader performance curves.

When assessed for a large number of mammals and plant species, the relationship between habitat suitability and density is often non-significant or is in contrasting directions (Dallas and Hastings 2018, Santini et al. 2019, Sporbert et al. 2020). We also observed variable relationships between habitat suitability and density for the 200 North American birds species that we considered. The positive relationship between habitat suitability and density found for about half of the species we considered could be occurring because these birds might have higher dispersal ability and are more capable of tracking suitable environments across geographic space and over time (Tingley et al. 2009, Zurell et al. 2018). This may occur through informed dispersal behavior where individuals would be more likely to disperse to good habitat patches (Clobert et al. 2009, Oro et al. 2021). Alternatively, our simulations did not consider informed dispersal, which led to the occurrence of source–sink dynamics by allowing individuals to occupy unsuitable sites (Pulliam 1988, 2000, Furrer and Pasinelli 2016). This could explain why dispersal had a negative effect on the relationship between habitat suitability and density of virtual species. Nonetheless, habitat suitability was still not able to explain most of the variation in the density of North American birds. This could be occurring because areas predicted to be of high environmental suitability can have populations of either low or high density (VanDerWal et al. 2009, Acevedo et al. 2017, Braz et al. 2020, Jiménez-Valverde et al. 2021). Moreover, populations occurring in locations with low habitat suitability can still have positive growth rates (Thuiller et al. 2014, Csörgő et al. 2017), and potentially reach high densities, which could further obscure

any potential relationship between habitat suitability and density.

Demographic stochasticity, dispersal, and intraspecific competition affect local densities (Melbourne and Hastings 2008, Furrer and Pasinelli 2016, Zhang et al. 2021), but these factors seem to have played a limited role in driving the disconnect between habitat suitability and density in our simulations given their relatively small negative impacts on these relationships. These small negative effects are possibly due to the already weak relationship between habitat suitability and density in models without dispersal and spatial differences in intraspecific competition. As a result, dispersal and intraspecific competition are more likely to have limited impacts on these relationships. However, the relationship between habitat suitability and density is likely to further deteriorate as more factors that influence population dynamics are considered when modeling populations. Such interplay between multiple factors that affect population dynamics could explain the generally weaker, or even absent, relationship between habitat suitability estimates and density observed for real species. For example, biotic interactions (e.g. interspecific competition and mutualism) and environmental stochasticity affect population densities (May 1973, Robertson 1996) and could be interacting with the factors that we considered in our study to influence these relationships even more for real species (Santini et al. 2019, Braz et al. 2020). The presence of sampling biases in the occurrence data that are often used to fit SDMs (Inman et al. 2021, Bowler et al. 2023), alongside with the use of environmental conditions that might not be related to the population dynamics of species, such as PCA axes, may further increase the disconnect between habitat suitability and density for real species.

Using SDMs to predict species densities is compelling because the presence data used in these models are more readily available than density data (Pearce and Boyce 2006, Hortal et al. 2015, Bradley 2016), but our findings suggest that SDMs should not be used for these purposes as they fail to describe different aspects of population dynamics under a wide range of scenarios. SDMs can still be useful for predicting species occurrences (Lee-Yaw et al. 2022), but there is a growing body of evidence showing that their use to estimate densities should be avoided. Population densities in a given location is affected by a myriad of factors and using demographic models that are tailored specifically to predicting densities is a more productive path forward (Dallas and Hastings 2018, Lee-Yaw et al. 2022). Citizen-science databases that have count data could be used, for example, to test the predictions made by these demographic models and it could improve our understanding of population trends (Dennis et al. 2017, Fink et al. 2020).

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Author contributions

Cleber Ten Caten: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Tad Dallas:** Conceptualization (equal); Funding acquisition (lead); Methodology (equal); Supervision (lead); Writing – review and editing (equal).

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Data availability statement

R code and data to reproduce the analyses are available on figshare at <https://doi.org/10.6084/m9.figshare.26940301> (Ten Caten and Dallas 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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