



# Effects of bird species-level environmental preference on landscape-level richness-heterogeneity relationships

Yoni Gavish<sup>a</sup>, Eric M Wood<sup>b</sup>, Sebastián Martinuzzi<sup>c</sup>, Anna M. Pidgeon<sup>c</sup>,  
Avi Bar-Massada<sup>a,\*</sup>

<sup>a</sup>Faculty of Natural Sciences, University of Haifa, Kiryat Tivon, Israel 36006

<sup>b</sup>Department of Biological Sciences, California State University – Los Angeles, Los Angeles, CA, United States 90032-8300

<sup>c</sup>SILVIS Lab, Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI, United States 53706

Received 21 March 2021; accepted 12 September 2021  
Available online 13 September 2021

## Abstract

The niche-based argument that species are filtered from environments in which they cannot sustain viable populations is the basis of the Richness-Heterogeneity Relationship (RHR). However, the multi-dimensionality of niches suggests that the RHR may take different shapes along different environmental axes, with potential confounding effects if filtering along the axes is not equally strong. Here, we explore how different structural and landscape variables drive the RHR as the accumulative outcome of environmental preferences at the species-level while considering the intercorrelation between heterogeneity levels along three niche axes. We used occurrence data of avifauna from 226 sites situated along a grassland-to-woodland gradient in a Midwestern USA study area. In each site, we quantified horizontal (habitat cover type), vertical (vegetation height structure), and spatial (habitat configuration) heterogeneity and explored the shape of the observed RHR at the landscape scale, as well as the correlations among heterogeneity levels at different axes. We then fitted species distribution models to environmental variables from the three axes separately and compared the stacked probabilities of occurrences of all species to the observed species richness. We found that predictions of richness patterns improved when more than one heterogeneity axis was included in RHR models, and that habitat suitability along different axes is not equally strong. Furthermore, a unimodal RHR along the vegetation height axis, which the species distribution models revealed to be a weak predictor for most species, may arise through intercorrelation with heterogeneity along the two other axes, along which we recorded stronger signals of environmental preference at the species level. Our results emphasize the importance of selecting relevant niche axes in studies of species richness patterns because ultimately, these patterns reflect the various environmental preferences of individual species.

© 2021 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

**Keywords:** Species richness; Heterogeneity; Habitat structure; Habitat suitability; Environmental filtering; Species distribution models

## Introduction

Environmental heterogeneity is a fundamental ecological pattern that plays a role in many ecological processes (Grinnell, 1917; Hutchinson, 1957). Along with area and

\*Corresponding author.

E-mail address: avi-b@sci.haifa.ac.il (A. Bar-Massada).

isolation, environmental heterogeneity is amongst the most influential drivers of species richness (Rosenzweig, 1995). Environmental heterogeneity can promote species coexistence in space (Chesson, 2000a) and time (Chesson, 1994) and has inherent effects on species co-occurrence patterns (Bar-Massada, 2015b; Heino, 2013). In addition, it affects the relative role of niche vs. dispersal assembly processes in generating ecological communities (Bar-Massada et al., 2014). Environmental heterogeneity plays a role in these phenomena because variation in environmental conditions across space (and time) enables species with different ecological requirements to establish and persist in sites (or periods) where (or when) they have distinctive advantages over heterospecifics (Chesson, 1994, 2000b; Hutchinson, 1957). In the absence of other processes, aggregating species-level occurrence in sites where required habitat elements exist gives rise to richness patterns at the community level.

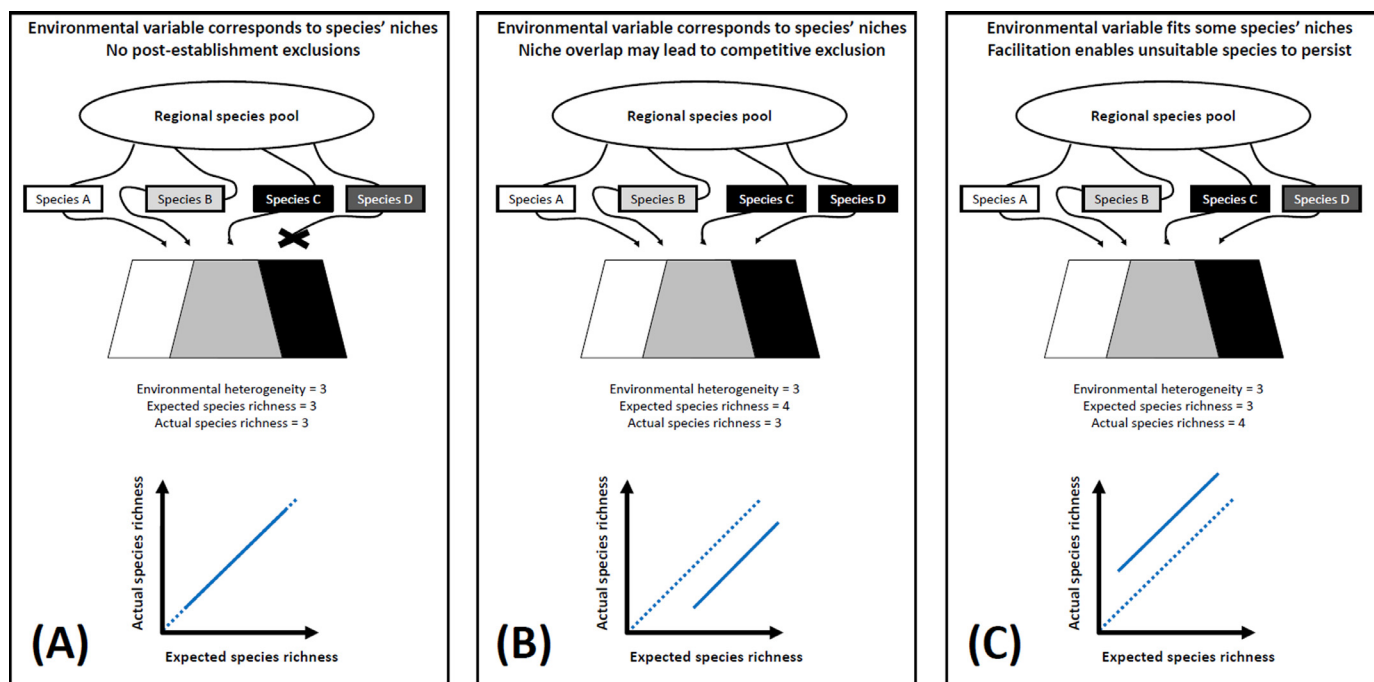
Both empirical and theoretical studies suggest that the relationship between species richness and environmental heterogeneity (the richness – heterogeneity relationship, RHR hereafter) may take multiple shapes (Allouche et al., 2012; Ben-Hur & Kadmon, 2020), including positive-monotonic (Bar-Massada & Wood, 2014; Stein et al., 2014), unimodal (Bar-Massada, 2015a; Bar-Massada & Wood, 2014; Chocron et al., 2015), and even negative-monotonic curves (Ben-Hur & Kadmon, 2020; Gazol et al., 2013; Laanisto et al., 2013). Positive RHRs are the manifestation of niche-based environmental filtering (Allouche et al., 2012), the process by which species arriving from the regional species pool can only establish in a locale if their niche preferences correspond with the biotic and abiotic conditions in the site (whereas species whose preferences do not fit are ‘filtered out’). The positive RHR is driven by environmental filtering because an increase in heterogeneity leads to more habitat types, which can support more species with specific habitat requirements (Hutchinson, 1957). Negative RHRs may arise if the increase in habitat heterogeneity occurs over a restricted and finite area, thereby making the amount of area covered by each combination of habitat conditions too small to support viable populations of specialist species (Flather & Bevers, 2002), thus increasing their likelihood of stochastic extinction (Kadmon & Allouche, 2007). Unimodal RHRs may arise if the range of heterogeneity covered is wide enough (i.e., from nearly homogenous environments to highly heterogeneous environments) to include both the positive RHR at relatively low heterogeneity values and the negative RHR that occurs at high heterogeneity (Allouche et al., 2012; Kadmon & Allouche, 2007). We note, however, that the particular shape of the RHR is not indicative of the strength of environmental filtering (or any other mechanism) as a species-selection process, as all shapes may arise under either strong or weak filtering, which is likely due to other processes unrelated to environmental filtering, such as area limitation (Chocron et al., 2015), spatial scale (Stein et al., 2014) or even fine-scale habitat fragmentation (Laanisto et al., 2013;

Tamme et al., 2010). If the negative RHR is related to area limitation, species must be first sorted into the habitat by an environmental filter and then become stochastically extinct due to area limitation (Kadmon & Allouche, 2007).

In addition to habitat filtering, the RHR is affected by any ecological process or methodological decision that alters our estimation of either richness and/or heterogeneity. In terms of ecological processes, for example, species richness is affected by species dispersal abilities (Bar-Massada, 2015a), interspecific biotic interactions (Bertness & Callaway, 1994), and ecological drift (Hubbell, 2001). Regarding methodological decisions, measures of environmental heterogeneity differ according to the variable type (categorical vs. continuous), the hierarchical level of the analysis (i.e., within habitats or across habitats), and the grain and extent of the spatial and temporal scales (Costanza et al., 2011; Li & Wu, 2004). Finally, environmental heterogeneity may be quantified for different habitat characteristics, such as elevation (Schmitz et al., 2002); food resources (Gazol et al., 2013); or woody cover (Ovalle et al., 2006).

On top of the ecological processes mentioned above, the multi-dimensionality of niches suggests that even within a single community and study system, the RHR may take different shapes along different environmental axes (Bar-Massada & Wood, 2014). In fact, in the absence of other ecological processes, the RHR results from the accumulation of many species-level environmental filtering processes (Kadmon & Allouche, 2007), potentially along multiple environmental axes.

Under the environmental filtering mechanism, if a species passes the filter of a given environmental axis, we expect its distribution to reflect that filtering, especially when biotic interactions or dispersal limitation have a relatively weak effect on its distributional patterns (Pottier et al., 2013). In such cases, and from a methodological standpoint, we would expect high predictive ability of Species Distribution Models (SDM) based on variables that together reflect and capture the heterogeneity along the given environmental axis (e.g., the cover of various habitat types reflecting habitat heterogeneity). We further expect that if an environmental axis is essential to many species, stacking the predicted likelihood of occurrence from their respective SDMs would provide an accurate and unbiased estimate of local species richness (Guillera-Arroita, 2017) (Fig. 1A). Alternatively, if environmental filtering along a specific axis is a weak process for a focal species (i.e., its ability to establish and persist in a site is unrelated to the site’s condition along this niche axis), we expect its distribution pattern to deviate from this axis (and in practice, we expect the SDM to have relatively lower predictive ability). Furthermore, if this axis is a weak filter for most species, the stacked likelihood of occurrence would not provide an accurate and unbiased estimate of local species richness. A weak agreement between the stacked likelihood of occurrence of many species and local species richness may also emerge if other processes besides environmental filtering affect species presence in a local



**Fig. 1.** A schematic representation of potential relationships between actual species richness, expected species richness (summed suitability), and environmental heterogeneity under different community assembly scenarios. Each trapezoid depicts a simple representation of a landscape, with shades of gray showing the values of an arbitrary environmental variable that acts as an environmental filter. Box colors depict species' environmental preferences. For simplicity, assume that all species are specialists that can only establish in a single habitat type, that there is no dispersal limitation, and that each sub-habitat type is small, so it can only support a viable population of a single species. In panel (A), species richness is related to environmental heterogeneity solely through environmental filtering. Consequently, actual richness and summed suitability are expected to correspond perfectly. In panel (B), pre- and post-establishment interaction processes among species also affect species richness. In this scenario, expected species richness based solely on species-level niche requirements in the absence of interspecific interactions is higher than actual richness. In panel (C), one species with unsuitable niche requirements can establish and persist due to facilitative processes. Hence actual species richness is higher than expected.

community, leading to either underestimation (e.g., due to dispersal limitation, predation, competition, Fig. 1B) or overestimation (e.g., due to rescue effects, mass effects, facilitation, Fig. 1C) of richness.

Finally, the shape of the RHR along a given niche axis may also indicate correlations among environmental variables whose role as environmental filters varies. For example, assume variable A is a strong environmental filter for many species and that species richness is positively related to its heterogeneity. In contrast, variable B is a weak filter for most species, but its heterogeneity value is negatively correlated with variable A. The RHR for variable B will be negative monotonic, not because of the ecological mechanism of limited area per species, but simply because of the statistical relationship between A and B and the strong response of many species to A. This possibility, which has been mostly ignored in the literature, highlights the need to analyze multiple niche axes and their interrelations in studies that aim to explain the RHR. This can be achieved by analyzing the effect of each environmental variable on the RHR independently while also considering the effects of different variables on species richness, environmental heterogeneity, and the RHR simultaneously. Our objective here was to explore

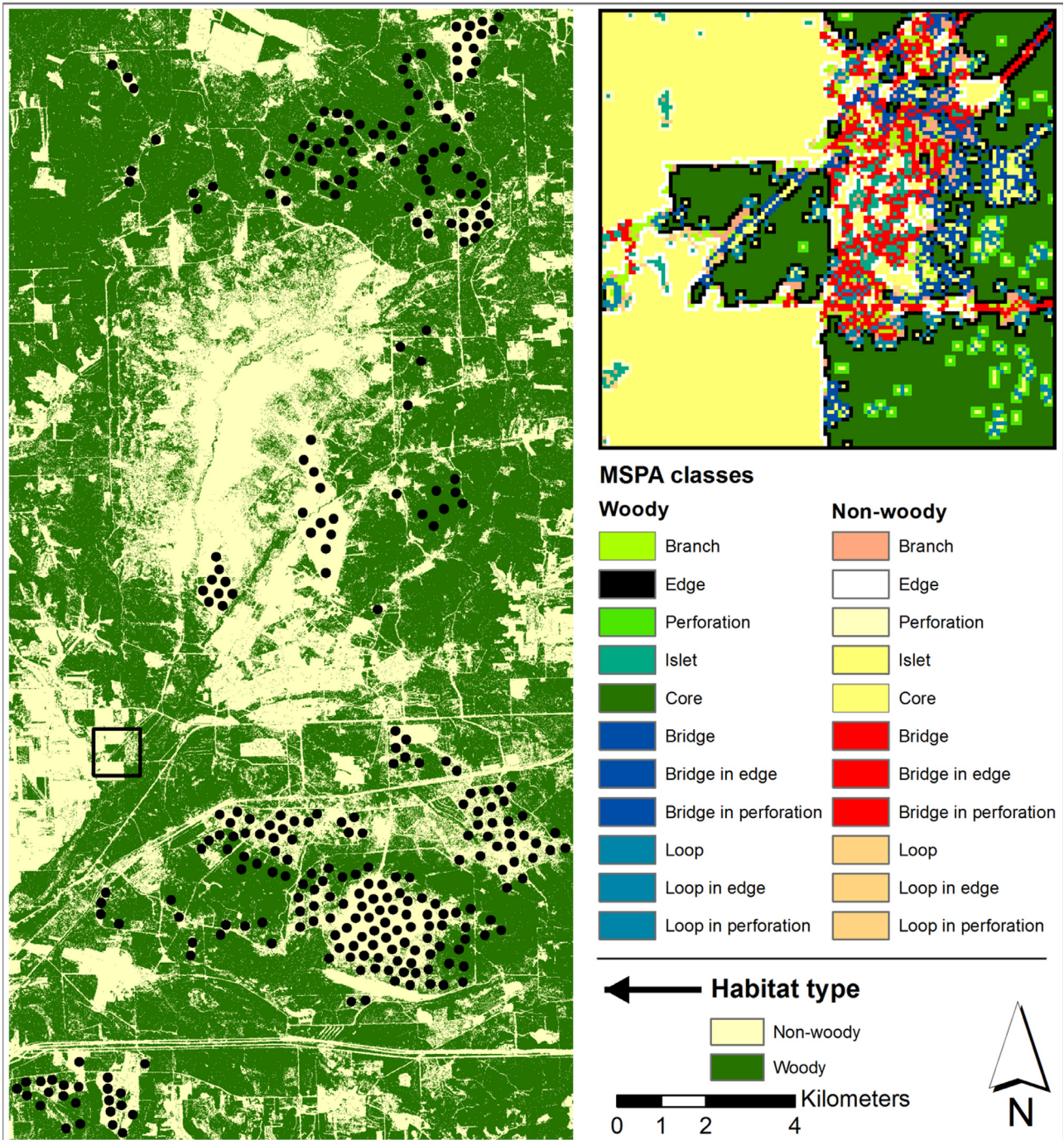
how different environmental variables that capture structural and habitat features in a landscape in central Wisconsin (including vegetation height, habitat cover, and habitat configuration; and subsequently, their heterogeneity) drive avian species richness patterns and the RHR. Specifically, we wanted to test if richness patterns and the RHR reflect the accumulative outcome of species-level habitat preferences along multiple axes (with habitat preference serving as a proxy for environmental filtering at the individual species level), which are captured by species distribution models (or habitat suitability models); and to analyze the RHRs that emerge from the predictions of these models.

## Materials and methods

### Study area and surveys of the avian community

We conducted the study in Fort McCoy, southwestern Wisconsin, USA, an active military installation covering 24,281 ha (Fig. 2). The installation is located within the Driftless Area, an unglaciated region of Wisconsin, Illinois, Iowa, and Minnesota, that harbors diverse habitat types,





**Fig. 2.** Locations of sampling sites (black circles) on the classified aerial image of the study area (10 m cell size). The inset shows an example of morphological spatial pattern analysis (MSPA) for a small subset of the image (black square in the main image), with colors representing MSPA classes. For visual simplicity, the colors of the bridge and loop sub-categories were merged. A full description of MSPA classes appears in: <https://forest.jrc.ec.europa.eu/en/activities/lpa/mspa/>. The color version of this figure appears in the online article.

including sparsely vegetated forb and grass-dominated grasslands, oak-dominated (*Quercus* spp.) savannas and woodlands, and mixed hardwood forests. These habitat types at Fort McCoy vary strongly in both structural and plant species composition and thus harbor distinct bird assemblages.

We conducted field surveys of the avian community from 2007 to 2009, encompassing the breeding period of the

majority of diurnally active landbirds in the study area. These surveys included 226 sites, in a stratified random design within the three dominant habitat types (grassland, oak savanna, oak woodland), and separated by at least 300 m. At each site, trained observers conducted a five-minute point count, during which all birds seen or heard were recorded (Hutto et al., 1986; Ralph et al., 1995). Observers

estimated the distance to each detected bird using laser rangefinders, and we truncated detections at 100 m. Sites were visited four times in 2007 and 2008 and three times in 2009. From the count data, we generated a presence/absence matrix by pooling data from all visits. We treat the data as presence/absence since each site was visited eleven times, and we have found no evidence of increasing species accumulation during our study period (Wood et al., 2013). Further, habitat conditions, including vegetation cover and plant composition at sites, remained relatively stable across years as there were no major disturbances during the three-year study.

### Niche axis 1 - horizontal habitat structure

At each site, we recorded the percent cover of 22 horizontal cover variables (e.g., % cover of hardwood, Table A.1) in five circular subplots of 5 m radius, located at the center and four corners of each site (i.e., 100 m from its center in the cardinal directions), following established breeding bird surveying protocols (Bar-Massada & Wood, 2014; Martin et al., 1997). We used these percent cover variables as the explanatory variables in the horizontal-variables SDMs (see below) and calculated the Shannon diversity of the 22 cover types as a measure of horizontal heterogeneity. This measure for land cover diversity is similar to classic metrics for animal species diversity (e.g., MacArthur & MacArthur, 1961), but with the relative abundance of different species replaced by the proportional cover of different land cover types. We omitted from all horizontal analyses four sites with extremely low heterogeneity values (2.5 standard deviations below the mean). All of these sites were located in grasslands. Yet, species richness in them did not differ significantly from the average species richness in the other 47 grassland sites, which we retained for subsequent analyses.

### Axis 2 - Vertical habitat structure

We collected data on vertical vegetation structure at each site at 16 points, four in each of the four corner subplots described in the previous section. At each point, we divided the vertical axis into 55 sections of 30 cm each and recorded the number of times any plant (regardless of individual identity) hit our measuring pole within each section, using a 12 m telescopic pole or estimated with rangefinders for sections higher than 12 m. We then summed the number of hits from all 16 points and used the 55 vertical height sections as explanatory variables in the vertical-variables SDMs. Next, we calculated the Shannon diversity index of these 55 variables as our measure of vertical heterogeneity (MacArthur & MacArthur, 1961; more details are in Wood et al., 2012).

### Axis 3 - Spatial configuration of the habitat

Spatial variables and their corresponding heterogeneity characterize the habitat configuration of woody and non-

woody vegetation in a 100 m radius around each site. We acquired a 1 m resolution color orthophoto of the study area taken in summer 2008 and used a supervised classification model to separate woody (“1”) from non-woody (“0”) vegetation (Fig. 2). We performed image classification using the maximum likelihood method and conducted all GIS analyses in ArcGIS 10.2. We calculated the percent cover of woody vegetation within a 100 m buffer around each site based on classification results. In general, the woody cover amount increases along a continuum among the three main habitat types in the study area (grasslands, savannas, and woodlands, Fig. 2).

Next, we resampled the binary map to 10 m resolution using a majority filter. Then we used Morphological Spatial Pattern Analysis (MSPA), implemented in GuidosToolbox 2.9 (<https://forest.jrc.ec.europa.eu/en/activities/lpa/gtb/>; last accessed 21/7/2021), to identify different spatial context units in the binary habitat map (Vogt et al., 2007). MSPA assigns each “1” cell to one of 11 landscape structural categories (core, edge, perforation, bridge, bridge in edge, bridge in perforation, loop, loop in edge, loop in perforation, islet, and branch; see details in: <https://forest.jrc.ec.europa.eu/en/activities/lpa/mspa/>; last accessed 21/7/2021) while setting all “0” cells as background. Given that bird species in the study area might view either woody or non-woody cells as preferred habitat, running MSPA only on one habitat type (woodland or non-woodland) does not provide insight into the spatial pattern of the other class. We, therefore, generated two different MSPA maps, once with the woody habitats as “1” and the other with the non-woody habitats as “1”. The two maps are complementary but different, with the “0” of one map assigned to the other map's eleven “1” categories. We combined the two maps to create a single map with 22 categories (Fig. 2 inset). We used the percent cover of each category in the 100 m buffer around each site as the explanatory spatial variables in the SDM. We calculated Shannon's diversity index of the percent cover of each MSPA category as our spatial heterogeneity measure. Fusing the two MSPA maps ensured spatial heterogeneity peaked at savanna habitat (i.e., sparse trees in a grass/forb matrix, Fig. A.1), where both tree-and grassland-affiliated species may find appropriate habitats (Wood et al., 2011).

### Empirical estimation of models of RHR

At this stage, we had a set of explanatory variables that we could use to explore habitat preference at the species level (see next section) and a heterogeneity measure summarizing them to explore the RHR for each of the three niche axes. First, we quantified the relationships among all possible pairs of the three heterogeneity measures (horizontal heterogeneity, vertical heterogeneity, and spatial heterogeneity) using linear regression models with and without quadratic terms. Next, we quantified the RHR by fitting linear regressions with the observed species richness as the dependent variable and one of the three



heterogeneity measures as the predictor variable. We fit models using least-squares and built two models per heterogeneity variable: first with a linear term only and second with linear and quadratic terms to capture either the monotonic linear effect or a unimodal effect in the RHR expected by current ecological theory (Bar-Massada & Wood, 2014). In addition, we fit a model containing all three heterogeneity measures as predictors, with or without quadratic terms, to explore the benefit of accounting for multiple niche axes in the prediction of species richness. We compared the explained variances of the models adjusted for multiple predictors (adjusted  $R^2$ ) and their information content using Akaike's Information Criterion (AIC). Finally, we evaluated if models violated the assumption of independence via spatial-autocorrelation by visually inspecting the semi-variograms of model residuals and found no evidence for spatial-autocorrelation. We fit all models using R (R Core Team, 2013), generated the figures using the R package ggplot2 (Wickham, 2016), and generated semi-variograms using the R package gstat (Gräler et al., 2016).

### Estimation of environmental suitability at the species level

To assess the role of environmental preference at the individual species level on the richness patterns at the community level, we fitted SDMs using the random-forest algorithm (Breiman, 2001), implemented in the R package sdm (Naimi & Araújo, 2016). In doing so, we made an implicit assumption that SDMs can provide a proxy for the outcome of environmental filtering, as manifested by environmental preference. This assumption might break down in cases where the spatial distribution of a species reflects other processes besides filtering, including interspecific interactions, dispersal limitations and barriers, and demographic stochasticity. Nevertheless, we suggest that in our study system, these processes are less likely to considerably alter the distribution of any given species due to the lack of dispersal barriers and the large number of sample sites in each habitat type (grasslands, woodlands, and savannas), which increases the likelihood of the successful estimation of species-environment relationship even if interspecific interactions affect occurrence in some sites (Soberón, 2007). We restricted our analyses to 49 bird species (Table A.2; out of 71 bird species detected) that were present in ten sites or more (Hernandez et al., 2006), which occurred, on average, in 49.08 sites (range 10–146). We used the SDM procedure outlined below with three different variable sets per species; the 22 horizontal habitat cover variables, the 22 spatial configuration variables, and the 55 vertical vegetation structure variables. In a single SDM procedure, we first divided the sites into ten cross-validation sets, ensuring they all have similar relative proportions of presences and absences. Next, we fitted a random-forest model on nine of the cross-validation sets and made predictions for the set-aside one. After

fitting ten random-forest models, one for each cross-validation set, we assembled the predicted value for all sites, thus ensuring all our predicted values were based on set-aside sets that were not included in model training. We took the mean predicted value from the ten models per variable set as the habitat preference value and the mean area under the curve (AUC) of the receiver operator curve (ROC) over the ten runs as the model performance index.

We compared AUC values of the three axes for each species to explore if one of the environmental axes was consistently better at predicting species distribution patterns and, therefore, may signal a stronger filter for more species. Next, in each sampling site, we summed the suitability value of all species to yield the expected species richness values along each axis and compared the expected values to the actual species richness. When stacking species, we only took the subset of species with  $AUC > 0.6$ , thus minimizing the effect of statistical bias due to low predictive ability of the suitability models (by omitting species with low AUC we distilled the relationship between environmental filtering and the RHR because we only retained those species who responded to the three niche axes we accounted for). Therefore, the list of species we explored in each axis (for both observed and expected richness) differed slightly. If environmental filtering is the dominant mechanism behind the RHR along an axis, and the confounding factors highlighted at the beginning of this section are weak, then expected species richness should correspond well with actual species richness. We, therefore, fitted a linear regression model of the actual species richness against the expected richness (Piñeiro et al., 2008) and compared the slope and intercept to a unit slope and zero intercept, respectively. Furthermore, if a low correlation between observed and expected richness is due to poor predictive abilities of the SDMs, then we would not expect the difference between observed and expected richness to vary consistently along the values of the heterogeneity axis (i.e., the deviation between observed and expected richness will not depend on environmental heterogeneity). To explore this, we calculated the difference between expected and actual species richness and quantified its relationship with habitat heterogeneity (of the corresponding niche axis) using a linear regression model. We also included terms for percent woody cover and the interaction between heterogeneity and woody cover in the model to account for a potential confounding effect of habitat type (grassland, savanna, or woodland) on the relationship.

## Results

### The richness-heterogeneity relationships along the three axes

Horizontal heterogeneity had a significant unimodal quadratic relationship with vertical heterogeneity (linear effect:

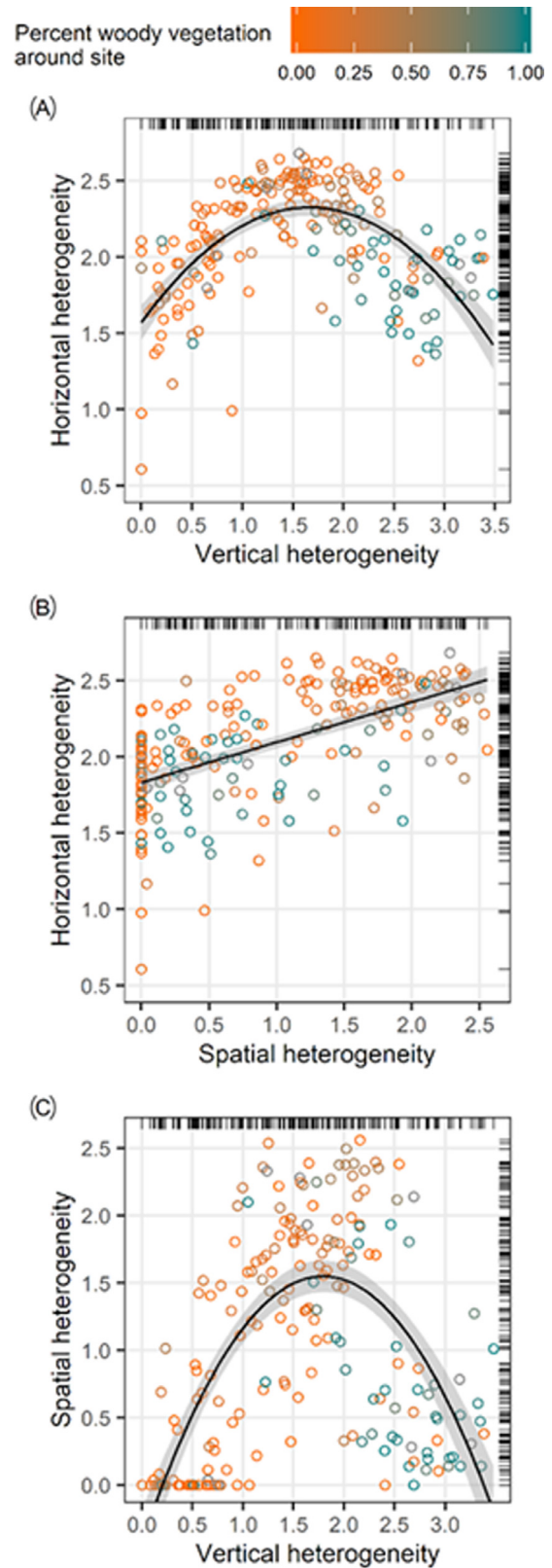
$0.8 \pm 0.07$ ,  $p < 0.001$ , quadratic effect:  $-0.24 \pm 0.02$ ,  $p < 0.001$ , adjusted  $R^2$ : 0.37; Fig. 3A), and a significant positive relationship with spatial heterogeneity (effect:  $0.23 \pm 0.02$ ,  $p < 0.001$ , adjusted  $R^2$ : 0.34; Fig. 3B). Spatial heterogeneity had a significant quadratic relationship with vertical heterogeneity (linear effect:  $2.24 \pm 0.17$ ,  $p < 0.001$ , quadratic effect:  $-0.62 \pm 0.05$ ,  $p < 0.001$ , adjusted  $R^2$ : 0.44; Fig. 3C).

All three heterogeneity measures and their combination were significantly associated with avian species richness (Table A.3). Individual heterogeneity axes explained (adjusted  $R^2$ ) between 33% (horizontal and vertical heterogeneity) and 44% (spatial heterogeneity) of the variation in species richness, while the model combining all three variables explained 49% of the variation in avian species richness (Table A.3). Also, the model with all variables had the lowest AIC (1009.16), compared to the spatial, vertical, and horizontal heterogeneity models (1046.81, 1053.72, and 1066.81, respectively). Yet, the nature of the richness-heterogeneity relationships differed markedly among the three axes. Horizontal heterogeneity had a significant positive effect on species richness (linear effect:  $7.07 \pm 0.71$ ,  $p < 0.001$ , adjusted  $R^2$ : 0.33; its unimodal term was non-significant; species richness increased monotonically with increasing horizontal heterogeneity) (Fig. 4A), while vertical heterogeneity (linear effect:  $8.77 \pm 0.86$ ,  $p < 0.001$ , quadratic effect:  $-2.49 \pm 0.25$ ,  $p < 0.001$ , adjusted  $R^2$ : 0.33) and spatial heterogeneity (linear effect:  $8.07 \pm 0.93$ ,  $p < 0.001$ , quadratic effect:  $-2.35 \pm 0.41$ ,  $p < 0.001$ , adjusted  $R^2$ : 0.44) had significant unimodal effects on avian richness (Fig. 4B and 4C, respectively, Table A.3) with inflection points at global maxima located within the data range (i.e., species richness increased at low-to-moderate heterogeneity levels, then levelled off, and eventually decreased at high heterogeneity levels). However, there was a strong decline in richness at high vertical heterogeneity values. In contrast, only a modest decline was observed for high values of spatial heterogeneity, as the curve's inflection point was closer to the maximal value of heterogeneity.

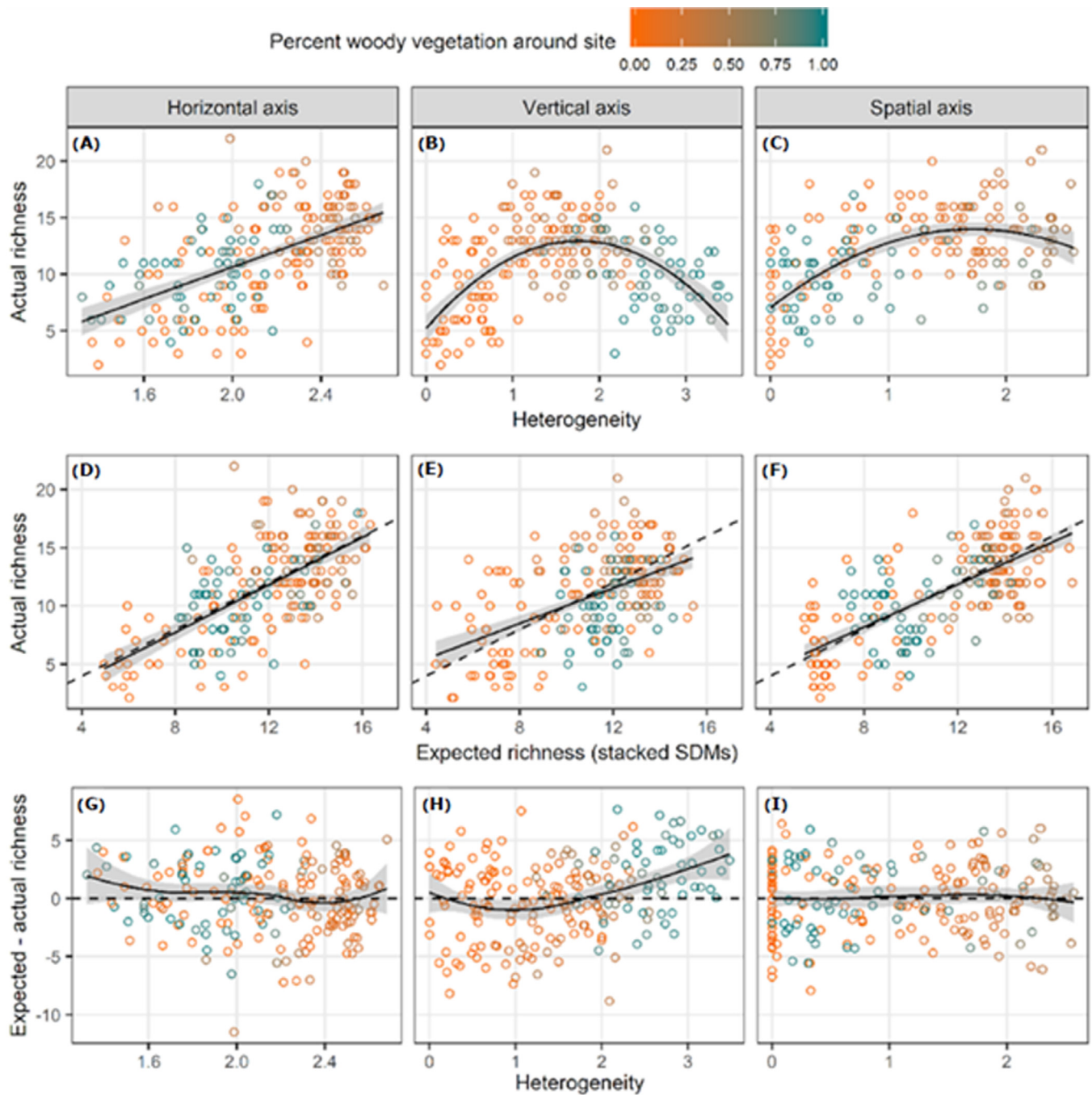
### Relationships between summed suitability and species richness

Across all three environmental variables (and their combination), the mean cross-validated AUC values of the random-forest models of bird species richness was 0.77 (standard deviation 0.10), 0.75 (0.12), and 0.73 (0.13) for the horizontal habitat cover variables, spatial configuration variables, and vertical structure variables, respectively. AUC values were generally higher with the horizontal variables than with spatial variables (Fig. A.2C), while the AUC with the vertical variables was lowest (Fig. A.2B, A.2D).

We excluded three, seven, and eight species with  $AUC < 0.6$  from the horizontal, spatial, and vertical heterogeneity analyses, respectively (Table A.2). After summing



**Fig. 3.** Relationships among the three heterogeneity variables. Each panel depicts a different pair of heterogeneity variables. Point colors represent the percent of woody cover (see also Fig. A.1). Small segments on the top and right axes depict the density of data points. The color version of this figure appears in the online article.



**Fig. 4.** Top row: relationships between avian species richness and three habitat heterogeneity measures. Curves depict the linear (A) or quadratic (B, C) fit of linear regression models (Table A.3). Panels (A) and (B) depict results that were reported in Bar-Massada and Wood (2014), which we re-analyzed here. Middle row: relationships between actual species richness in sites and expected species richness when stacking SDMs based on habitat cover type (D), vertical habitat structure (E), and spatial configuration (F). The solid line depicts a linear model fit to the data, whereas the dashed line depicts the 1:1 line. Deviations between the solid and dotted lines correspond with a weaker effect of habitat preference at the species level on species richness at the landscape scale. Bottom row (G, H, I): relationships among the difference between actual and expected species richness and the corresponding heterogeneity measure. The solid lines are loess curves, while dashed lines highlight the zero-difference line. Note that the figure column is aligned per the heterogeneity axis. Point colors depict the percent of woody cover. The color version of this figure appears in the online article.

in each site the predicted habitat suitability measures from the random-forest models across the remaining species, their relationship with actual species richness varied among

environmental axes (Fig. 4D, 4E, 4F). The relationship between actual richness and expected richness did not differ from 1:1 when stacking the horizontal habitat cover SDMs



(slope =  $1.02 \pm 0.08$ , intercept =  $-0.42 \pm 0.98$ ) and only slightly differed when stacking the spatial configuration variables SDMs (slope =  $0.91 \pm 0.06$ , intercept =  $0.9 \pm 0.84$ ). The horizontal cover and spatial configuration models predicted 43.30% and 49.71% of the variation in actual species richness, respectively (Fig. 4D, 4F). In contrast, stacked vertical structure SDMs significantly differed from the unity line (slope =  $0.75 \pm 0.08$ , intercept =  $2.41 \pm 1.00$ ) and explained just 26.15% of the variation in actual species richness (Fig. 4E).

In the stacked horizontal cover SDMs and spatial configuration SDMs, the differences between expected and actual species richness were not significantly affected by horizontal heterogeneity and spatial heterogeneity, respectively (Fig. 4G, 4I), nor by their interactions with the proportion of woody cover. In contrast, for the stacked vertical structure SDMs, the difference between expected and actual species richness was significantly affected by woody cover and its interaction with vertical heterogeneity (Fig. 4H; effect size of woody cover =  $-5.21 \pm 2.28$ ,  $p = 0.02$ ; effect size of interaction between vertical heterogeneity and woody cover =  $2.72 \pm 0.87$ ,  $p = 0.002$ ; effect size of vertical heterogeneity is non-significant ( $p = 0.84$ )). An analysis of the interaction reveals a strong overestimation of species richness in sampling plots with high woody cover (blue circles in Fig. 4H). In contrast, in plots with low-to-intermediate woody cover (orange and red circles in Fig. 4H), there was better correspondence between expected and actual richness. The sites in which over-estimation occurs are the same ones that drive the unimodal relationship between species richness and vertical heterogeneity (Fig. 4B).

## Discussion

### General findings and caveats

In this study, we shed light on the role of environmental preferences at the individual species level as an important driver of the RHR of the avian community at a local scale. Most empirical explorations of the RHR either focus on the phenomenological shape of the relationship (Stein et al., 2014) or partition the variance in species richness explained by various heterogeneity axes (Chocron et al., 2015). Although much can be learned from such approaches, here, we adopted a bottom-up approach. Each species' environmental preference along each of the three axes was first quantified using SDM, and the RHR is then explored as the accumulation of species-level responses. While our approach cannot quantify the relative importance of environmental filtering versus other processes in driving species richness, or allow for the direct quantification of filtering existence or strength, it allows exploring if the cumulative environmental preferences of multiple individual species are a significant driver of the RHR. Since the SDMs were based on variables that captured the horizontal composition,

vertical structure, and spatial configuration (or heterogeneity) of our study system, our approach also approximates the relative role of environmental preferences across these environmental axes. With that in mind, we found that different axes of heterogeneity may be correlated in complex ways to one another (Fig. 3). First, more than one heterogeneity axis is needed to improve the predictions of richness patterns (Table A.3). Second, the shape of the RHR varies among axes (Fig. 4, A-C), and third, environmental preference along different axes may not be equally strong (Fig. 4, D-I). We caution that the approach we applied here might not be suitable for all study settings, as it benefited from the unique characteristics of our study area, which likely minimized the effect of confounding factors on our results. These were lack of dispersal barriers, similar climatic conditions across sites, and strong species – environment relationships, which led to moderately strong SDM performance across all niche axes. Another caveat to our conclusions is that they are difficult to generalize because our analysis focused on one taxonomic group in a single landscape. Finally, the general notion about the difficulty of inferring ecological processes from community patterns holds here as well: it is impossible to directly deduce the strength or even the presence of environmental filtering (or any assembly process) from empirical community data (Münkemüller et al., 2020). Yet given the specific characteristics of our study system (mentioned above), it is likely that our results provide a reasonable approximation to the differential effect of environmental filtering across different niche axes on the RHR.

### Environmental filtering across multiple niche axes

Species-specific niche preferences are the root causes of environmental filtering. According to niche theory, each species can survive and reproduce only under a restrictive set of conditions. Thus, under environmental filtering (Kraft et al., 2015), species would only be found in locations where suitable conditions prevail. Of course, the environment may still affect species distribution patterns even in the absence of environmental filtering through its effects on population growth rates (Chesson, 2000a) or biotic interactions (Bar-Massada & Belmaker, 2017; Chesson, 2000b; Kraft et al., 2015). Thus, even under weak environmental filtering, we expect species to be absent in locations where unfavorable biotic and abiotic conditions prevail. Nonetheless, niches are multi-dimensional and species-specific, implying that filtering may act differently along different axes on different species in the community. Indeed, in our study, we found that a combination of all three heterogeneity variables increases the explanatory power of the richness-heterogeneity model (Table A.3). Although the adjusted  $R^2$  increase was not substantial, it does highlight the benefit of accounting for multiple niche axes in attempts to explain the relationships between community patterns and

environmental variables, in line with Hutchinson's classic prediction (Hutchinson, 1957).

In the case of the avian communities in our study area, the results of the stacked SDMs suggest that both horizontal habitat composition and the spatial configuration of the habitat may act as stronger habitat filters compared to the vertical composition of the habitat (Fig. 4, Fig. A.2). It seems reasonable that horizontal habitat composition will act as a stronger habitat filter than the habitat's vertical composition because habitat composition represents the available sub-habitat types (e.g., trees, shrubs, grass, or bare soil), which many bird species tend to select, strongly, at the microsite scale (Roth, 1976). The other variable which served as a strong habitat filter, spatial configuration (based on MSPA units), is likely informative because it reflects the spatial context of habitat patches in the site and differentiates among core woodland, woodland/grassland edge, and core grassland. Bird species have specific affinities for resources within habitats, which differ in their proportions across landscapes at different successional stages or disturbance histories (Imbeau et al., 2003; Pfeifer et al., 2017). In contrast, vertical habitat composition, which we found to provide a relatively weaker habitat filter, may only act as a strong filter to woodland specialist species, playing a minor role in the presence and absence of other species in the regional pool.

In general, the models of the RHR for the three heterogeneity axes had similar (and only moderate) explanatory power (Table A.3). This suggests that other processes besides environmental filtering per se affect the number of bird species in these communities. Such processes include species interactions and dispersal limitation, which are generally related to habitat conditions (Bar-Massada & Belmaker, 2017; Bertness & Callaway, 1994). The lack of a strong signal of environmental filtering on the RHR is aligned, to some degree, with the suggestion of recent studies that environmental filtering has an overall weak role in structuring communities (Cadotte & Tucker, 2017; Kraft et al., 2015). Yet it is also likely that our findings were affected by the local spatial scale of the analysis. Stronger RHRs are expected to be found at relatively coarser spatial scales compared to the local scale of our analysis (Chocron et al., 2015). This is because at moderate spatial scales, the length of the heterogeneity gradient will be greater (Chocron et al., 2015), allowing for increased differentiation between habitat types, thereby increasing the potential role of environmental filtering in structuring the community. Hypothetically, the signal of environmental filtering might be more pronounced if analyzed at coarser scales because niche differentiation (and habitat differences) will be greater at broader scales. Yet, simultaneously, the role of dispersal limitation in structuring meta-communities will also expand (Heino, 2011), possibly obscuring the effect of filtering per se. Hence it will be interesting to repeat our approach across a larger geographic area to see if our findings of the role of environmental filtering on the RHR are also expressed beyond the level of a single meta-community in one landscape.

## The various shapes of the RHR

When exploring the shape of the RHR curves in our study, we found a unimodal curve for two niche axes: vertical and spatial (Fig. 4B, 4C). For spatial configuration, the expected number of species was similar to the actual number of species (Fig. 4F), and the residuals were not dependent upon spatial heterogeneity (Fig. 4I). Thus, we cannot rule out an area effect (in which the RHR becomes negative at high heterogeneity values) as predicted by the area-heterogeneity tradeoff hypothesis (Allouche et al., 2012). Yet the most spatially heterogeneous sites (which portray a negative relationship with richness) also have a low cover of core habitat (either woody or non-woody) and high cover of edge habitat; thus, bird species that cannot cope with edge-effects, or those that require large core habitat may have avoided such sites. Therefore, the unimodal RHR pattern we observed is more likely to arise through habitat selection instead of stochastic extinction as expected if the area effect was strong (Chocron et al., 2015).

In contrast, for vertical heterogeneity, the higher part (on the horizontal axis) of the RHR curve corresponds to sites with high woody cover (i.e., woodland sites). These are the exact sites in which, presumably, environmental filtering along this axis was at its weakest, as summed suitability across individual-species models predicted a much larger number of species than the actual number of species found in those sites (Fig. 4H). As these woodland sites are the least diverse in our study area in terms of plant species richness (E.M. Wood, unpublished data), it is expected that they will support a smaller number of bird species (Rotenberry, 1985). Hence the gap between expected and observed avian richness in woodland sites may be driven by the composition of the plant community, despite the high vertical diversity of those habitats in terms of structure.

Alternatively, the analysis of the relationships between different heterogeneity variables revealed that woodland sites with high vertical heterogeneity are characterized by low horizontal and spatial heterogeneity (Fig. 3), both associated with low species richness (Fig. 4A, 4C). Therefore, we propose that the 'missing' species in the higher parts of the vertical RHR curve might be those that could not establish because of missing horizontal and/or spatial sub-habitat types. In other words, the strong quadratic relationships between vertical heterogeneity and both horizontal and spatial heterogeneity suggest that the RHR in the vertical niche axis is not driven by strong environmental filtering, as predicted by the AHTO. Instead, the unimodal curve is more likely to be a statistical artifact that arises from the inter-relationships among the heterogeneity measures of different environmental axes. If filtering along the vertical axes were stronger than filtering along the horizontal axes, we would most likely observe a unimodal trend for the richness-horizontal heterogeneity curve.

## Conclusion

Our results suggest that the role of different ecological processes in driving the RHR depends on the environmental or niche axis to which most species in the community respond. Given the plethora of observed types of this relationship across different taxa, scales, and regions (Stein et al., 2014), what can we learn from our results that will enable future studies to understand this relationship better? We suggest that if the RHR is evaluated as a pattern driven by a bottom-up process, ideally, the choice of the environmental variable whose heterogeneity will serve as a predictor of species richness should reflect a niche axis known to affect species habitat selection in the first place. We presented an approach to evaluate this congruence. Yet, a single measure of environmental heterogeneity will likely not suffice to adequately explain variation in species richness across space (and time). Curiously, most studies seem to ignore the inherent relationship between environmental heterogeneity and species' niches and consequently rely on single heterogeneity measures, ignoring variation in species' environmental preferences and potential inter-relationships among different environmental variables. Here, we highlight the diverse effects of different environmental variables, their heterogeneity, and the ecological processes that they trigger on the richness patterns of avian communities and suggest that future studies account for the many faces of environmental heterogeneity when attempting to understand its roles in driving ecological phenomena.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgments

We thank our field assistants, C. Rockwell, A. Nolan, B. Summers, H. Llanas, S. Grover, P. Kearns, and A. Derose-Wilson, for their help in collecting the bird and habitat data. T. Wilder and S. Vos provided logistical field support. Ronen Kadmon provided insightful comments on an early version of this manuscript. We are grateful for support from the Strategic Environmental Research and Development Program (SERDP) and Prairie Biotic Research, Inc.

## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.baec.2021.09.002](https://doi.org/10.1016/j.baec.2021.09.002).

## References

- Allouche, O., Kalyuzhny, M., Moreno-Rueda, G., Pizarro, M., & Kadmon, R. (2012). Area–heterogeneity tradeoff and the diversity of ecological communities. *Proceedings of the National Academy of Sciences*, *109*, 17485–17500. doi:10.1073/pnas.1208652109.
- Bar-Massada, A. (2015a). Immigration rates and species niche characteristics affect the relationship between species richness and habitat heterogeneity in modeled meta-communities. *PeerJ*, *3*, e832. <https://doi.org/10.7717/peerj.832>
- Bar-Massada, A. (2015b). Complex relationships between species niches and environmental heterogeneity affect species co-occurrence patterns in modelled and real communities. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1813), 20150927. doi:10.1098/rspb.2015.0927.
- Bar-Massada, A., & Belmaker, J. (2017). Non-stationarity in the co-occurrence patterns of species across environmental gradients. *Journal of Ecology*, *105*(2), 391–399. doi:10.1111/1365-2745.12713.
- Bar-Massada, A., Kent, R., & Carmel, Y. (2014). Environmental heterogeneity affects the location of modeled communities along the niche-neutrality continuum. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20133249.
- Bar-Massada, A., & Wood, E. M. (2014). The richness–Heterogeneity relationship differs between heterogeneity measures within and among habitats. *Ecography*, *37*, 528–535.
- Ben-Hur, E., & Kadmon, R. (2020). Heterogeneity–diversity relationships in sessile organisms: A unified framework. *Ecology Letters*, *23*(1), 193–207. doi:10.1111/ele.13418.
- Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, *9*(5), 191–193. doi:10.1016/0169-5347(94)90088-4.
- Breiman, L. (2001). Random Forests. *Machine Learning*, *45*(1), 5–32. <https://doi.org/10.1023/A:1010933404324>
- Cadotte, M. W., & Tucker, C. M. (2017). Should Environmental Filtering be Abandoned? *Trends in Ecology & Evolution*, *32*(6), 429–437. doi:10.1016/j.tree.2017.03.004.
- Chesson, P. (1994). Multispecies Competition in Variable Environments. *Theoretical Population Biology*, *45*(3), 227–276. doi:10.1006/tpbi.1994.1013.
- Chesson, P. (2000a). Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and Systematics*, *31*(1), 343–366. doi:10.1146/annurev.ecolsys.31.1.343.
- Chesson, P. (2000b). General Theory of Competitive Coexistence in Spatially-Varying Environments. *Theoretical Population Biology*, *58*(3), 211–237. doi:10.1006/tpbi.2000.1486.
- Chocron, R., Flather, C. H., & Kadmon, R. (2015). Bird diversity and environmental heterogeneity in North America: A test of the area-heterogeneity trade-off: Bird diversity and environmental heterogeneity. *Global Ecology and Biogeography*, *24*(11), 1225–1235. doi:10.1111/geb.12353.
- Costanza, J. K., Moody, A., & Peet, R. K. (2011). Multi-scale environmental heterogeneity as a predictor of plant species richness. *Landscape Ecology*, *26*(6), 851–864. doi:10.1007/s10980-011-9613-3.
- Flather, C. H., & Bevers, M. (2002). Patchy Reaction-Diffusion and Population Abundance: The Relative Importance of Habitat Amount and Arrangement. *The American Naturalist*, *159*(1), 40–56. doi:10.1086/324120.



- Gazol, A., Tamme, R., Price, J. N., Hiiesalu, I., Laanisto, L., & Pärtel, M. (2013). A negative heterogeneity–diversity relationship found in experimental grassland communities. *Oecologia*, *173*(2), 545–555. doi:10.1007/s00442-013-2623-x.
- Gräler, B., Pebesma, E., & Heuvelink, G. (2016). Spatio-Temporal Interpolation using gstat. *The R Journal*, *8*(1), 204–218.
- Grinnell, J. (1917). The niche-relationships of the California Thrasher. *Auk*, *34*, 427–433.
- Guillera-Aroita, G. (2017). Modelling of species distributions, range dynamics and communities under imperfect detection: Advances, challenges and opportunities. *Ecography*, *40*(2), 281–295. doi:10.1111/ecog.02445.
- Heino, J. (2011). A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology*, *56*(9), 1703–1722. doi:10.1111/j.1365-2427.2011.02610.x.
- Heino, J. (2013). Environmental heterogeneity, dispersal mode, and co-occurrence in stream macroinvertebrates. *Ecology and Evolution*, *3*(2), 344–355. doi:10.1002/ece3.470.
- Hernandez, P. A., Graham, C. H., Master, L. L., & Albert, D. L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*, *29*(5), 773–785. doi:10.1111/j.0906-7590.2006.04700.x.
- Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.
- Hutchinson, G. E. (1957). Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, *22*(0), 415–427. doi:10.1101/SQB.1957.022.01.039.
- Hutto, R. L., Pletschet, S. M., & Hendricks, P. (1986). A Fixed-Radius Point Count Method for Nonbreeding and Breeding Season Use. *The Auk*, *103*(3), 593–602.
- Imbeau, L., Drapeau, P., & Mönkkönen, M. (2003). Are Forest Birds Categorized as “Edge Species” Strictly Associated with Edges? *Ecography*, *26*(4), 514–520 JSTOR.
- Kadmon, R., & Allouche, O. (2007). Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: A unification of island biogeography and niche theory. *The American Naturalist*, *170*(3), 443–454. doi:10.1086/519853.
- Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, *29*(5), 592–599. doi:10.1111/1365-2435.12345.
- Laanisto, L., Tamme, R., Hiiesalu, I., Szava-Kovats, R., Gazol, A., & Pärtel, M. (2013). Microfragmentation concept explains non-positive environmental heterogeneity–diversity relationships. *Oecologia*, *171*(1), 217–226. doi:10.1007/s00442-012-2398-5.
- Li, H., & Wu, J. (2004). Use and misuse of landscape indices. *Landscape Ecology*, *19*(4), 389–399. doi:10.1023/B:LAND.0000030441.15628.d6.
- MacArthur, R. H., & MacArthur, J. W. (1961). On Bird Species Diversity. *Ecology*, *42*(3), 594–598. doi:10.2307/1932254.
- Martin, T. E., Paine, C. R., Conway, C. J., Hochachka, W. M., Allen, P., & Jenkins, W. (1997). *Montana Cooperative Wildlife Research Unit, University of Montana. BBIRD Field Protocol*.
- Münkemüller, T., Gallien, L., Pollock, L. J., Barros, C., Carboni, M., Chalmandrier, L., Mazel, F., Mokany, K., Roquet, C., Smyčka, J., Talluto, M. V., & Thuiller, W. (2020). Dos and don'ts when inferring assembly rules from diversity patterns. *Global Ecology and Biogeography*, *29*(7), 1212–1229. doi:10.1111/geb.13098.
- Naimi, B., & Araújo, M. B. (2016). sdm: A reproducible and extensible R platform for species distribution modelling. *Ecography*, *39*(4), 368–375. doi:10.1111/ecog.01881.
- Ovalle, C., Del Pozo, A., Casado, M. A., Acosta, B., & de Miguel, J. M. (2006). Consequences of Landscape Heterogeneity on Grassland Diversity and Productivity in the Espinal Agroforestry System of Central Chile. *Landscape Ecology*, *21*(4), 585–594. doi:10.1007/s10980-005-3498-y.
- Pfeifer, M., Lefebvre, V., Peres, C. A., Banks-Leite, C., Wearn, O. R., Marsh, C. J., Butchart, S. H. M., Arroyo-Rodríguez, V., Barlow, J., Cerezo, A., Cisneros, L., D’Cruze, N., Faria, D., Hadley, A., Harris, S. M., Klingbeil, B. T., Kormann, U., Lens, L., Medina-Rangel, G. F., ... Ewers, R. M. (2017). Creation of forest edges has a global impact on forest vertebrates. *Nature*, *551*(7679), 187–191. doi:10.1038/nature24457.
- Piñeiro, G., Perelman, S., Guerschman, J. P., & Paruelo, J. M. (2008). How to evaluate models: Observed vs. predicted or predicted vs. observed? *Ecological Modelling*, *216*(3), 316–322. doi:10.1016/j.ecolmodel.2008.05.006.
- Pottier, J., Dubuis, A., Pellissier, L., Maiorano, L., Rossier, L., Randin, C. F., Vittoz, P., & Guisan, A. (2013). The accuracy of plant assemblage prediction from species distribution models varies along environmental gradients. *Global Ecology and Biogeography*, *22*(1), 52–63. doi:10.1111/j.1466-8238.2012.00790.x.
- Core Team, R (2013). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Ralph, C. J., Droege, S., & Sauer, J. R. (1995). Managing and monitoring birds using point counts: Standards and applications. *United States Geological Survey* (pp. 161–175). <http://www.treesearch.fs.fed.us/pubs/31755>.
- Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge University Press. doi:10.1017/CBO9780511623387.
- Rotenberry, J. T. (1985). The role of habitat in avian community composition: Physiognomy or floristics? *Oecologia*, *67*(2), 213–217. doi:10.1007/BF00384286.
- Roth, R. R. (1976). Spatial Heterogeneity and Bird Species Diversity. *Ecology*, *57*(4), 773–782. doi:10.2307/1936190.
- Schmitz, M., Platt, W., & DeCoster, J. (2002). Substrate heterogeneity and number of plant species in Everglades savannas (Florida, USA). *Plant Ecology*, *160*(2), 137–148. doi:10.1023/A:1015848300802.
- Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, *10*(12), 1115–1123. doi:10.1111/j.1461-0248.2007.01107.x.
- Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, *17*(7), 866–880. doi:10.1111/ele.12277.
- Tamme, R., Hiiesalu, I., Laanisto, L., Szava-Kovats, R., & Pärtel, M. (2010). Environmental heterogeneity, species diversity and co-existence at different spatial scales. *Journal of Vegetation Science*, *21*(4), 796–801. doi:10.1111/j.1654-1103.2010.01185.x.
- Vogt, P., Riitters, K. H., Estreguil, C., Kozak, J., Wade, T. G., & Wickham, J. D. (2007). Mapping Spatial Patterns with Morphological Image Processing. *Landscape Ecology*, *22*(2), 171–177. doi:10.1007/s10980-006-9013-2.
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis* (Second edition). Springer. doi:10.1007/978-3-319-24277-4.

- Wood, E. M., Pidgeon, A. M., Gratton, C., & Wilder, T. T. (2011). Effects of oak barrens habitat management for Karner blue butterfly (*Lycæides samuelis*) on the avian community. *Biological Conservation*, 144(12), 3117–3126. doi:[10.1016/j.biocon.2011.10.010](https://doi.org/10.1016/j.biocon.2011.10.010).
- Wood, E. M., Pidgeon, A. M., Radeloff, V. C., & Keuler, N. S. (2012). Image texture as a remotely sensed measure of vegetation structure. *Remote Sensing of Environment*, 121, 516–526. <https://doi.org/10.1016/j.rse.2012.01.003>
- Wood, E. M., Pidgeon, A. M., Radeloff, V. C., & Keuler, N. S. (2013). Image Texture Predicts Avian Density and Species Richness. *PLoS ONE*, 8(5), e63211. doi:[10.1371/journal.pone.0063211](https://doi.org/10.1371/journal.pone.0063211).

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)

**ScienceDirect**