The richness–heterogeneity relationship differs between heterogeneity measures within and among habitats

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The positive monotonic relationship between habitat heterogeneity and species richness is a cornerstone of ecology. Recently, it was suggested that this relationship should be unimodal rather than monotonic due to a tradeoff between environmental heterogeneity and population sizes, which increases local species extinctions at high heterogeneity levels. Here, we studied the richness–heterogeneity relationship for an avian community using two different environmental variables, foliage-height diversity and cover type diversity. We analyzed the richness–heterogeneity within different habitat types (grasslands, savannas, or woodlands) and at the landscape scale. We found strong evidence that both positive and unimodal relationships exist at the landscape scale. Within habitats we found positive relationships between richness and heterogeneity in grasslands and woodlands, and unimodal relationships in savannas. We suggest that the length of the environmental heterogeneity gradient (which is affected by both spatial scale and the environmental variable being analyzed) affects the type of the richness–heterogeneity relationship. We conclude that the type of the relationship between species richness and environmental heterogeneity is non-ubiquitous, and varies both within and among habitats and environmental variables.

The positive relationship between habitat heterogeneity and species richness is considered one of the most ubiquitous in ecology, especially in the case of avian communities (MacArthur and MacArthur 1961, Cody 1981). The mechanism behind this relationship derives from the idea of communities as collections of species assembled together according to the fit of their niche requirements to local habitat conditions. Whether variability occurs within- or among-habitats, heterogeneous areas consist of more niches and therefore support a higher diversity of species (MacArthur and MacArthur 1961).

Recently, the predominance of the positive relationship between richness and heterogeneity was challenged in a study that suggested that the general shape of that relationship is in fact unimodal (Kadmon and Allouche 2007, Allouche et al. 2012). The reasoning behind this hypothesis stems from the integration of species area relationships into the richness–heterogeneity relationship (Kadmon and Allouche 2007). Given a finite space, more heterogeneous areas comprise less area per habitat type. Consequently, each habitat can support smaller populations, and these populations become more prone to stochastic extinctions. The outcome of this area–heterogeneity tradeoff is manifested by a negative relationship between species abundance and heterogeneity, a positive relationship between extinction rates and heterogeneity, and a unimodal relationship between species richness and

heterogeneity. Allouche et al. (2012) reported, though, that in specific systems the shape of the relationship can be positive, negative, unimodal, or flat. These differences among systems emerge from species characteristics as well as the spatiotemporal scales of the analyses.

The challenges in studying the richness–heterogeneity relationships are twofold (assuming the estimation of richness is correct): quantifying heterogeneity in a way that is relevant to the taxa of interest, and conducting the analysis at the correct spatial scale (or scales). There are many different ways to quantify habitat heterogeneity, which are influenced by the choice of environmental heterogeneity variable quantified (e.g. elevation, habitat type, or habitat structure), followed by the heterogeneity measure being used (e.g. variance, range, or diversity). Examples from past studies include elevation range (Veech and Crist 2007, Allouche et al. 2012), variation in climate (Veech and Crist 2007), relative cover and diversity of landcover types (Jonsen and Fahrig 1997, Weibull et al. 2000, Culbert et al. 2012), and landscape metrics of the spatial pattern of woody vegetation (Bar-Massada et al. 2012). As for the effects of spatial (and to a lesser extent, temporal) scales on the relationships, multiple studies have shown that the spatial grain and extent of the area in which heterogeneity is quantified affects the richness–heterogeneity relationship (Kerr and Packer 1997, Rahbek and Graves 2001, Kent et al. 2011, Bar-Massada et al. 2012).

Here, we evaluated how different environmental variables as well as the hierarchical level of the analysis (within habitats or at the landscape scale) affect the shape of the richness–heterogeneity relationship in a grassland-savanna-woodland landscape mosaic in the Upper Midwest of the USA. Our specific objectives were: 1) to quantify the shape of the avian species richness–heterogeneity relationship based on two measures of habitat heterogeneity: 1] foliage height diversity, which is a measure of vertical vegetation structure; and 2] cover type diversity, which is a measure of abundance distribution of different habitat cover types; 2) to assess the type of the richness–heterogeneity relationship at two different hierarchical levels; within-habitats across the entire landscape.

Methods

Study area

We characterized the avian community and measured habitat characteristics at Fort McCoy, a military installation in southwestern Wisconsin which covers 24 281 ha (Fig. 1). The study area consists of three dominant habitat types that are available for civilian research: 1) grasslands, which are dominated by forb and grass and have low tree and shrub cover (< 5%); 2) oak savannas (hereafter savanna), which have 5–50% tree cover with variable shrub cover; and 3) oak

woodlands, which have higher tree cover than savannas (> 50% tree cover) and variable shrub cover, (Curtis 1959). The distribution of these habitats depends on edaphic features, elevation differences, slope and aspect induced microclimates, and both inadvertent and intentional military habitat management, which consists mainly of controlled burning and tree thinning. Dominant tree species in the savannas are black oak *Quercus velutina*, northern pin oak *Q. ellipsoidalis*, bur oak *Q. macrocarpa*, jack pine *Pinus banksiana*, and black cherry *Prunus serotina*; while in the woodlands red oak *Q. rubra*, and white oak *Q. alba* are the most common tree species. Dominant shrubs throughout the study area are American hazelnut *Corylus americana* and blueberry *Vaccinium angustifolium.* Dominant herbaceous species in the grassland and savanna include big bluestem *Andropogon gerardii* and little bluestem *Schizachyrium scoparium*, while in the woodlands, Pennsylvania sedge *Carex pensylvanica* is the most common ground cover species.

Surveys of the avian community and habitat characteristics

We conducted avian surveys annually from 2007 to 2009 that included 254 sample points, which were allocated using a stratified random sampling design, stratified completely within the boundaries of one of the three habitat
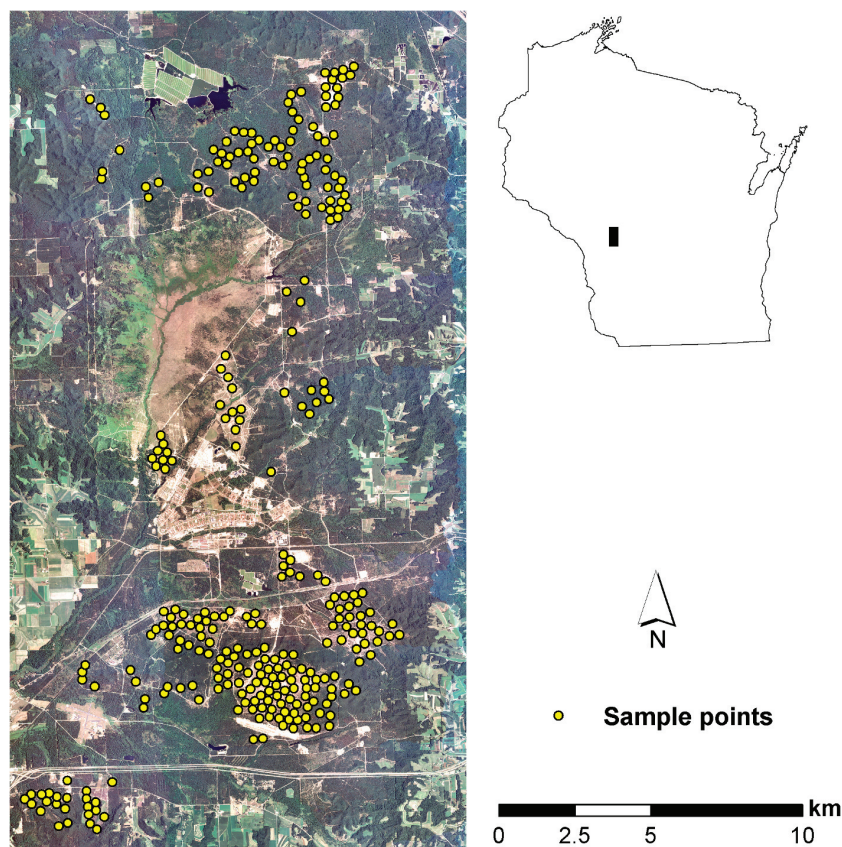

Figure 1. Aerial photo of the study area (left), its location in Wisconsin (top-right) and the locations of the sample points (yellow circles). Reprinted from Bar Massada et al. (2012).

types (Wood et al. 2011, 2013). Prior to sampling, we used digital topographic maps, leaf-on infrared aerial photos, and field visits to stratify habitats based on the proportional availability of each of the three habitat types (Wood et al. 2013). We surveyed 61 sample points in grassland, 122 in savanna, and 71 in woodland. At each sample point, we performed a five-minute point count documenting all bird species seen or heard (Ralph et al. 1995). We used laser rangefinders to estimate distance to each detected bird, and we truncated detections at 100 m to allow comparability of avian metrics among sample points. We visited sample points four times in 2007 and 2008 and three times in 2009 to increase detectability. Four trained observers completed counts in 2007 and 2008, and three observers completed counts in 2009. Based on the survey results, we quantified avian species richness in each sample point for each year, and average species abundance per year (mean number of individuals per species per point), to evaluate Allouche et al.'s (2012) suggestion that population sizes decrease at higher heterogeneity levels. We found no evidence of increasing species accumulation throughout our study period suggesting our sampling design adequately captured species diversity of our study area accounted for (Wood et al. 2013).

In addition to the avian surveys, we characterized the habitat at each sample point using established breeding-bird monitoring protocols (Martin et al. 1997). At each sample point, an observer demarcated four 5-m radius sub-plots, with one at the center of the sample point, and one of each in the following sub-plot segments: 0–120°, 121–240°, and 241–359°, at a random distance between 20–80 m. We used the random distances to capture the variability of habitat characteristics of our study area. Within each sub-plot, two observers collected habitat and foliage-height diversity data. To quantify the habitat, we estimated percent cover of habitat characteristics at three defined height intervals, which captured the ground (<0.5 m), shrub (0.5–5 m), and tree layer (live trees >10 cm diameter at breast height (dbh) and >5 m). For the ground layer, we estimated percent cover of all grasses, forbs, litter (defined as any mixture of leaf and stick litter), rocks, and bare ground (defined as any mixture of dirt, sand, or moss cover). At each sub-plot, the combination of all ground layer variables totaled 100%. At the shrub layer, we estimated percent cover of true shrubs (e.g. American hazelnut) and tree shrubs (black oak <10 cm dbh and <3 m). In some cases, blueberry shrubs were not >0.5 m. But, we included them in the shrub layer. In the tree layer, observers stood at the center of each sub-plot, and used a densitometer to estimate percent cover of all live trees, identified to species. We averaged the cover data within each layer, for each habitat variable, among sub-plots for a sample-point averaged representation of habitat characteristics (Wood et al. 2012, 2013).

Additionally, we measured foliage-height diversity, which characterizes vertical vegetation structure (MacArthur and MacArthur 1961). At each sup-plot, we collected four foliage-height diversity measurements, with one five m from the sub-plot center point in each of the cardinal directions (N, E, S, and W), totaling 16 foliage-height diversity measurements at a sample point. At each of the foliage-height diversity measurement stations, an observer vertically placed a 10 m telescoping pole. A second observer tallied the total number of vegetation hits on the telescoping pole, partitioned within 30 cm intervals. If the canopy was taller than 10 m, the second observer used binoculars to estimate vegetation hits at 30 cm intervals.

Heterogeneity measures and statistical analysis

From on the data on habitat characteristics, we calculated two measures of habitat heterogeneity. The first was foliage height diversity (FHD), based on calculating Shannon's diversity measure on the results of the vertical vegetation structure (MacArthur and MacArthur 1961). The second heterogeneity measure was cover-type diversity (CDiv), which was based on calculating Shannon's diversity measure of the different fractions of the main cover types (i.e. conifers, hardwoods, tree-shrubs, shrubs, grasses, rocks, and ground) described in the previous section. Higher FHD and CDiv values denote higher habitat heterogeneity. We assumed that temporal changes in habitat structure were negligible within our study period (Wood et al. 2012), and thus in all subsequent analyses we used the same values of FHD and CDiv regardless of sampling year.

We generated univariate linear models and linear models with a quadratic term to quantify the relationships between mean species richness across sampling years and habitat heterogeneity per site. We also generated models for each sampling year separately, to assess whether there was a profound difference in the richness–heterogeneity relationships among different years. In landscape-scale models, which comprised data from all three habitat types, we added habitat type as a categorical explanatory variable to account for potential habitat–specific drivers of species richness that may not be related to within- and among habitat heterogeneity. We compared models with different combinations of explanatory variables based on their adjusted R^2 and Akaike's information criterion (AIC). We checked model assumptions of normality with (QQ-norm plots) and heteroscedasticity (with residuals versus fitted values plots), and found no evidence of violation of model assumptions. To evaluate whether spatial autocorrelation existed in our data, we computed and analyzed empirical variograms of the residuals of all of our models (Legendre and Fortin 1989). We found no evidence for significant spatial autocorrelation.

Results

The shape of the richness–heterogeneity relationship across the entire landscape was directly affected by the type of heterogeneity measure (Fig. 2, top row; Table 1). Avian species richness had a significant unimodal relationship with FHD regardless if the model included or excluded a categorical habitat type variable, but the model which consisted of both was stronger ($R^2 = 0.44$) than the model that included habitat type only (ΔAIC $= 17.2$; $R^2 = 0.42$) and the quadratic model of FHD without habitat (ΔAIC $= 78.02$; $R^2 = 0.29$). The quadratic models of species richness versus FHD and habitat for specific years were significant as well,
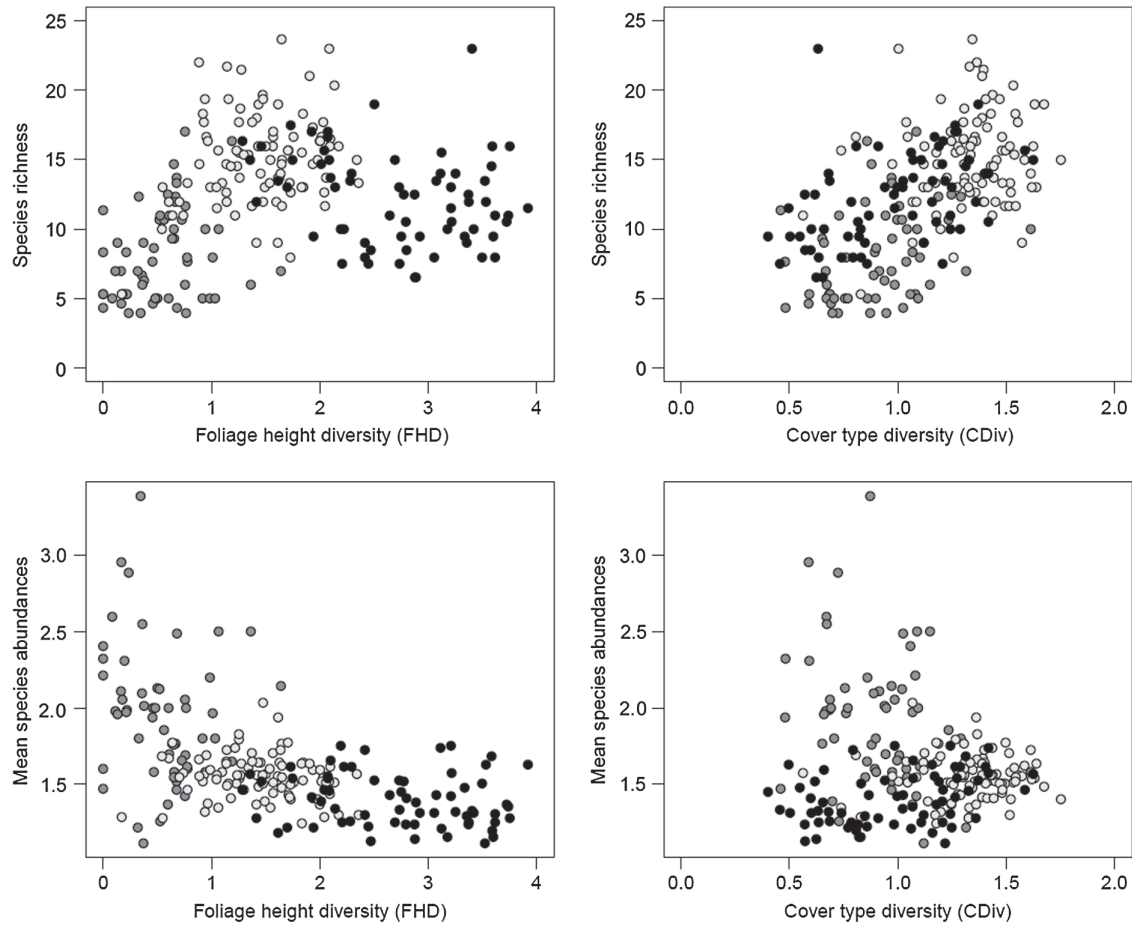
Figure 2. Relationships between avian species richness (top row) and abundance (bottom row, number of individuals per species averaged across species) and two measures of habitat heterogeneity. Left column: foliage height diversity (FHD); right column: cover type diversity (CDiv). Data is based on averaged richness and abundance values across all three study years. Circle colors denote habitat type (gray – grasslands, white – savannas, black – woodlands).

were consistently better than corresponding univariate linear models and models that included either FHD or habitat separately, and had R^2 values of 0.25, 0.41, and 0.39, for 2007, 2008, and 2009, respectively.

Avian species richness also had a significant positive relationship with CDiv, regardless of the inclusion of habitat as an explanatory variable in the model. The linear model consisting of both CDiv and habitat ($R^2 = 0.48$) was stronger than models with either CDiv ($\Delta AIC = 59.37$; $R^2 = 0.3$) or habitat ($\Delta AIC = 20.78$; $R^2 = 0.42$), and stronger than the quadratic model with FHD and habitat as explanatory variables. The linear models of species richness in specific years versus CDiv and habitat were consistent with the above results, as they were significant in all years, and consistently

Table 1. Model parameters for landscape scale analyses of the relationships between avian species richness and FHD, CDiv, and habitat type. Models are sorted according to ΔAIC (from best to worst). Significance terms for model coefficients are: $p \leq 0.05^*$, $p \leq 0.01^{**}$, $p \leq 0.001^{***}$.

Model terms	Coefficients						Model		
	FHD^2	FHD	CDiv^2	CDiv	Habitat (savanna)	Habitat (woodland)	p-value	R^2	ΔAIC
FHD^2 + FHD + CDiv + Habitat	−0.52*	2.40*		3.69***	4.17***	2.44*	<0.0001	0.48	0
CDiv + Habitat				4.27***	5.18***	3.78***	<0.0001	0.48	10.03
CDiv^2 + CDiv + Habitat			−2.94	10.43*	5.35***	3.85***	<0.0001	0.48	10.16
FHD^2 + FHD + Habitat	−0.85**	3.57**			5.29***	2.61*	<0.0001	0.44	13.61
FHD + Habitat		0.19			6.77***	3.62**	<0.0001	0.41	22.13
Habitat					7.01***	4.08***	<0.0001	0.42	30.81
CDiv				7.77***			<0.0001	0.3	69.4
FHD^2 + FHD	−1.99***	8.33***					<0.0001	0.29	91.63
FHD		1***					<0.0001	0.05	153.72

better than univariate models with either CDiv or habitat, or models where a quadratic term for CDiv was included as well.

While up until now we analyzed the effects of FHD and CDiv separately, including them both in a model (while retaining a quadratic term for FHD), together with habitat type, produced the best model of all of the alternatives ($R^2 = 0.48$; see Table 1 for ΔAIC for all subsequent models), which highlights the efficacy of both heterogeneity measures as predictors of species richness. Again, models for specific years yielded consistent findings, except for 2007 where neither CDiv nor habitat were significant predictors of richness when FHD and a quadratic term of FHD were included in the model.

At the landscape scale, mean species abundance (the average number of individuals per species per plot) had a negative significant relationship with FHD (Fig. 2, bottom left) ($R^2 = 0.29$, ΔAIC = 30.04). Yet when we added habitat as an explanatory variable in the model, FHD was not significant, but model performance increased ($R^2 = 0.39$). This model was slightly better than a model of mean abundance vs habitat type solely ($R^2 = 0.37$, ΔAIC = 4.18), implying that there is a weak relationship between FHD and avian abundance once habitat differences are accounted for. In contrast, we found no relationship between mean species abundance and CDiv (Fig. 2, bottom right), regardless of sampling year. The variation in species abundances per plot, denoted by their standard deviation, decreased significantly with increasing values of both FHD and CDiv, regardless of year, except for CDiv in 2009 where the standard deviation of abundance was not-related to CDiv.

The values of both FHD and CDiv differed significantly among habitats, and the variation in their values among habitats was significantly larger than their variation within habitats (ANOVA, $F_{2,212} = 278.1$, $p < 0.001$, and $F_{2,251} = 85.88$, $p < 0.001$, for FHD and CDiv, respectively) (Fig. 3). This implies that the gradient length in both heterogeneity measures was shorter within habitats compared to the gradient length at the landscape scale. In general, FHD increased as the cover of trees increased in habitats, from grasslands, through savannas (that mostly consist of a few tree species with varying understory vegetation), to woodlands that are characterized by multiple tree species, as well as varying understory vegetation. CDiv, in contrast,

was highest in savanna habitats, as they are horizontally patchy, containing a mixture of open and woody micro-habitats. Grasslands and woodlands, on the other hand, consist of more uniform horizontal cover of grasses and trees, respectively.

When we analyzed the community data within habitats (Table 2; Fig. 2 top left, different colors denote different habitats) we found that the unimodal richness–FHD relationship was only retained in savannas, where the best among all alternative models consisted of a significant quadratic term of FHD. In grasslands, the best model, which included FHD, did not have a significant quadratic term. A univariate linear model with FHD was significant ($p = 0.05$) with a positive slope, indicating a weak positive relationship between richness and FHD. In woodlands, while the quadratic term of the FHD model was significant, its coefficient value was positive, indicating a minimum inflection point. Since this contradicts ecological theory (which predicts a global maximum inflection point), we attribute this result to a statistical artifact, and therefore suggest that the richness–FHD relationship in grasslands is negative-linear.

We found that the positive richness–CDiv relationship which we found at the landscape scale was also retained within grasslands and woodlands (Table 2). In contrast, we found no significant relationship between richness and CDiv in savannas. These results were mostly consistent across sampling years, except for 2007, where all the models of richness vs CDiv were non-significant. Finally, we did not find linear models with quadratic terms that significantly explained the richness vs. CDiv relationship, regardless of habitat type or sampling year (Table 2).

Analyzing abundance data within habitats, we found that the negative relationship between mean species abundance and FHD which we found at the landscape scale was retained only for grasslands in 2009 ($\beta = -0.81$, $p < 0.001$, $F_{1,46} = 7.17$, $R^2 = 0.13$). Similar to the landscape scale, we found no relationships between mean species abundance and CDiv within habitat types.

Discussion

The positive relationship between species richness and habitat heterogeneity has been considered one of ecology's
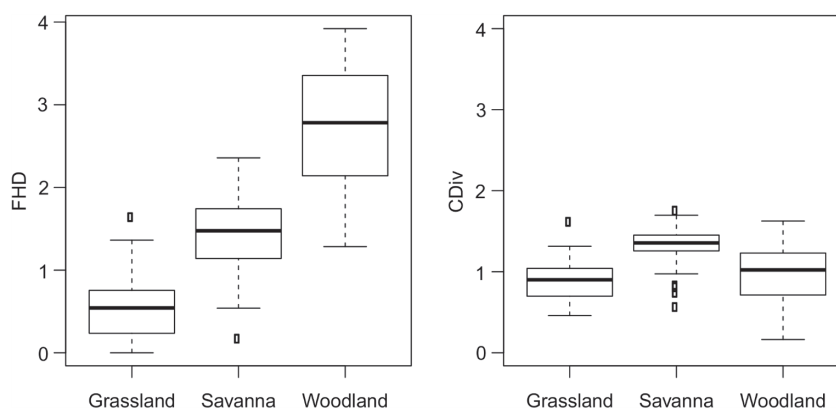

Figure 3. Boxplots of foliage height diversity (FHD, left, modified from Wood et al. (2012)) and cover type diversity (CDiv, right) in different habitats.

Table 2. Model parameters for within-habitat analyses of the relationships between avian species richness FHD, and CDiv. Models are sorted according to ΔAIC (from best to worst within habitat type). Significance terms for model coefficients are: $p \leq 0.05^{*}$, $p \leq 0.01^{**}$, $p \leq 0.001^{***}$.

Habitat	Model terms	Coefficients				Model		
		FHD^2	FHD	$CDiv^2$	CDiv	p-value	R^2	ΔAIC
Grasslands	$FHD^2 + FHD + CDiv$	−3.71	6.4		3.27	0.02*	0.12	0
	$FHD^2 + FHD$	−4.44	8.07*			0.02*	0.09	0.86
	FHD		2.37			0.053	0.05	2.59
	CDiv				4.92**	0.009**	0.1	5.30
	$CDiv^2 + CDiv$			−0.79	6.41	0.03*	0.08	7.27
Savannas	$FHD^2 + FHD$	−3*	10.06**			0.006**	0.08	0
	$FHD^2 + FHD + CDiv$	−2.86*	9.58*		0.69	0.016*	0.08	1.83
	FHD		1.72*			0.025*	0.04	3.33
	CDiv				2.51	0.13	0.01	6.15
	$CDiv^2 + CDiv$			−4.85	14.45	0.2	0.01	7.14
Woodlands	$FHD^2 + FHD + CDiv$	1.15	−6.49		4.16**	$<10^{-3***}$	0.20	0
	CDiv				5.1***	$<10^{-4***}$	0.20	2.39
	$CDiv^2 + CDiv$			−0.25	5.6	$<10^{-3***}$	0.19	4.42
	$FHD^2 + FHD$	1.87*	−11.07*			0.011*	0.10	6.57
	FHD		−1.18*			0.04*	0.04	9.76

near ubiquitous truths, despite some system specific findings of alternative types of relationships (e.g. negative relationships between breeding birds richness and both habitat and climate heterogeneity; (Veech and Crist 2007). Here, we found that the picture may be less clear, as the type of the relationship is both context specific (what kind of habitat heterogeneity is studied) and habitat specific (in which habitat we utilize a given heterogeneity metric). We show that both the traditional, positive monotinic richness–heterogeneity relationship (Cody 1981, Benton et al. 2003), as well as the unimodal relationship (Kadmon and Allouche 2007, Allouche et al. 2012) can be found in the same landscape, depending only on the specific type of habitat heterogeneity that is measured. Moreover, we show that when the richness–heterogeneity relationships are quantified within different habitats in the same area, the type of the relationship can change. These results expand our findings in a previous study (Bar-Massada et al. 2012), in which we showed that the structure of the richness–heterogeneity relationship (the coefficients of the relationship curve, not its type) is affected by the spatial scale of the analysis. Here, the unimodal relationship that was prominent at the landscape scale disappeared completely in woodlands and grasslands when analyzed within habitats, and was mostly replaced by the more common positive relationship (or a negative relationship in the case of FHD in woodlands). A possible explanation for this difference is the much shorter range of FHD values within specific habitats, which prevents species richness levels to reach the inflection point suggested by Allouche et al. (2012). In contrast, the positive relationship between richness and CDiv we found at the landscape scale was retained within different habitats. This suggests that different metrics will exhibit different richness–heterogeneity relationships depending whether these relationships are analyzed within habitats or at the landscape scale. While we did not have sufficient data to assess scale effects on the richness–FHD relationship at spatial extents broader than our study area, results from another study suggest that the

avian richness–CDiv relationship at a regional scale is positive-monotonic. Culbert et al. (2012) quantified richness–habitat relationships for avian communities in the Upper Midwestern United States. For the Eastern Broadleaf Forest ecoregion province, which contains our study area, they found a positive and significant relationship between avian species richness and habitat heterogeneity, based on a habitat-diversity measure which is analogous to CDiv. However, since they did not fit quadratic relationships to their data, because they mostly exhibited linear trends (P. D. Culbert pers. comm.), we cannot rule out the existence of unimodal relationships at broader spatial extents.

Our results mostly support the theory on area–heterogeneity tradeoff (Kadmon and Allouche 2007, Allouche et al. 2012). When we used FHD as the measure of habitat heterogeneity, not only did we find a unimodal richness–heterogeneity relationship as expected by their theory, but we also found a negative relationship between mean species abundance and habitat heterogeneity, which complies with their second prediction. By using FHD, which is a direct descriptor of avian habitat (rather than using elevation range, which is the indirect measure of habitat heterogeneity that was used in many previous studies) our results are non-sensitive to some of the criticism towards the analysis of Allouche et al. (2012), namely the confounding effect of the unimodal richness–elevation relationship on the richness–heterogeneity relationship (Hortal et al. 2013). Unfortunately, our data did not span a sufficient time-period to test the third prediction of Allouche et al. (2012), of a positive relationship between extinction rates and environmental heterogeneity. However, we still caution that the unimodal richness–heterogeneity may not be as general as Allouche et al. (2012) suggest, given that we found equivalent support for the traditional positive relationship between species richness and CDiv in the same study area when data were analyzed at the landscape scale. However, we cannot rule out the possibility that the positive relationship between richness and CDiv within habitats and at the landscape

scale is an outcome of the scale-sensitivity of CDiv, as it is possible that at even broader spatial scales it will, too, exhibit a unimodal relationship with richness. Therefore, the question of which factors determine the predominance of a specific type of richness–heterogeneity relationship for different taxa, in specific habitats, and at different spatial scales remains a major theoretical challenge.

Given our contrasting findings when heterogeneity was measured for different habitat variables (foliage height diversity and habitat cover types), there is probably no universal richness–heterogeneity relationship which exists at all scales, just as species–environment associations vary with variables and scales (Wiens et al. 1987, Cushman and McGarigal 2004). The common features of the relationships we found were that for low to intermediate levels of habitat heterogeneity, increased heterogeneity tends to be associated with more species, regardless if it is analyzed within habitats or at the landscape scale. Then, depending perhaps on the lowest threshold on stable population sizes, richness can either increase with further heterogeneity, or reach an inflection point and decrease due to the system's inability to support stable populations (Allouche et al. 2012). In our study area, the latter happened only in savannas when we analyzed data from individual habitats. In grasslands and woodlands the relationship did not reach an inflection point, possibly because the length of the heterogeneity gradient within them is too short, and richness levels do not reach the inflection point.

A major challenge in the study of the richness–heterogeneity relationship is to find and use the most suitable heterogeneity measures. These, ideally, should correspond with the habitat requirements of the taxon of focus, as well as the relevant spatial scales at which it interacts with its environment. Here, we used two different measures of heterogeneity which we assume are ecologically meaningful to avian species, as they reflect the vertical (FHD) and horizontal (CDiv) distribution of microhabitats that are utilized by birds. Throughout the world, including grassland and desert scrublands (Wiens et al. 1981), temperate woodlands (Estades et al. 1997), and tropical forests (Karr et al. 1971), avian species diversity has been linked to fine-resolution variations in vertical vegetation structure, as characterized by foliage-height diversity. Horizontal vegetation structure is also associated with species diversity, though often to a lesser degree than vertical vegetation structure. For example, in a grassland-scrubland steppe environment, variations in horizontal vegetation structure are associated with increased shrub habitat heterogeneity leading to higher diversity of shrub affiliated species (Rotenberry and Wiens 1980). Though, this relationship was not found for grasslands and grassland affiliated species (Rotenberry and Wiens 1980). Other factors affecting species habitat use, such as floristic diversity, food availability, and presence of competitors and predators (Cody 1981) are not captured by the habitat heterogeneity measures of our study. The woodlands of our study area are structurally diverse but relatively homogenous with vegetation species composition. This may impact food resources and ultimately habitat selection by breeding birds (Cody 1981), leading to lower avian diversity. Furthermore, landscape composition also affects avian

species diversity (Turner 1989). For example, in a Mediterranean savanna-woodland landscape of Spain, variability in landscape heterogeneity is associated with higher avian species diversity (Atauri and de Lucio 2001). The grassland and woodland habitats of our study are situated among fairly large patches of similar habitat, only disrupted by occasional roads. On the other hand, the savanna habitats are situated on the border of both grassland and woodland habitats, and thus act as an ecotone situated between the two larger and predominante habitats of the area. Ecotones support higher species diversity (Risser 1995), and the savanna habitats of our study indeed support both grassland and woodland avian species, as well as birds affiliated with sparse-canopy habitats (Wood et al. 2011). Thus, both fine and broad scale factors not captured by our habitat heterogeneity measures affect species richness patterns of our study. Nonetheless, our findings support that avian species richness was best explained by a combination of both horizontal and vertical habitat heterogeneity together with intrinsic habitat characteristics within- and among-habitats.

The other consideration when determining the best heterogeneity measures to use when studying the richness–heterogeneity relationship is the scale at which a measure was quantified. We used plot-level measures of vertical and horizontal vegetation structure derived from ground-collected data. However, it is far more difficult to characterize variations in vertical and horizontal structure at broad spatial extents, thus making broad scale studies of avian communities difficult (Culbert et al. 2012). Yet, recent advances in remote sensing methodology are beginning to make this possible. For example, light detection and ranging (LiDAR) (Vierling et al. 2008) and Synthetic Aperture Radar (SAR) (Bergen et al. 2009) can capture fine resolution variations in vegetation height at broad spatial extents, and image texture can capture data on horizontal vegetation structure (Wood et al. 2012), which allows for their use in avian species diversity studies (Imhoff et al. 1997, Clawges et al. 2008, St-Louis et al. 2009, Wood et al. 2013). This is a welcomed advance, because attempts to quantify habitat heterogeneity often rely on simplistic plot-level measures of vertical and horizontal vegetation structure due to limited spatial data. Our results reveal that answers to the fundamental question of the relationship between species diversity and environmental diversity can differ according to the heterogeneity measure that is being used, and the spatial scale at which the heterogeneity measure is quantified. We suggest that future studies attempt to account for multiple types of heterogeneity and scales when addressing this question.

To conclude, we found that the same landscape can exhibit different relationships between avian species richness and habitat heterogeneity, depending on the environmental variable of choice as well as whether it is analyzed within habitats or at the landscape scale. Our results suggest that within relatively homogeneous habitats (i.e. where the range of heterogeneity gradient is short, e.g. grasslands and woodlands), the positive richness–heterogeneity relationship predominates regardless of the way heterogeneity is measured. In more diverse habitats (i.e. savannas) and at broader spatial scales, where the study area comprises several

different habitats, both unimodal and positive richness–heterogeneity relationships exist, depending on the type of environmental variable whose heterogeneity is calculated, as well its variation among different habitat types.

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