

Title:

AVIFAUNAL RESPONSES TO BROAD-SCALE HABITAT HETEROGENEITY IN SAVANNA SYSTEMS

INTRODUCTION

Most of the world's biodiversity is threatened by anthropogenic land-use change. In particular, biodiversity continues to decline due to agricultural intensification, increasing resource demand, and globalization caused by a rapidly growing human population (Freedman 2014). Although area dedicated to nature reserves has increased 500% in the past three decades (Wittemyer et al. 2008), only 14% of terrestrial land is protected ("Terrestrial protected areas," 2016), while around 40% of land surface is occupied by croplands and pastures (Foley et al. 2005). The most dramatic land-use change is occurring in developing nations, where the human population increase is 2.8% per year (Pickett et al. 2012). These areas also tend to contain most of the world's biodiversity (Brashares et al. 2001) and are where humans rely most on ecosystem services for their survival (Mertz et al. 2007). Understanding how these changing landscapes affect biodiversity is a pressing research need.

The effects of converted land on biodiversity within functional ecosystems depend on the composition and arrangement of land cover types within a matrix (Child et al. 2009). There have been a variety of studies investigating the response of biodiversity to landscape heterogeneity (e.g. Watson et al. 2004; Seymour et al. 2015; Gregory et al. 2010). There has generally been support for the habitat heterogeneity hypothesis (Benton et al. 2003), which states that more complex landscapes support higher species richness and diversity by providing a greater density of niches. Nonetheless, studies that occur in different locations or use different biodiversity metrics, sampling designs, and habitat categorizations often demonstrate contradictory results (de Lima et al. 2013). Despite the general interest in the habitat heterogeneity hypothesis, there has been a surprising lack of tests of this hypothesis in developing nations with the fastest rates of agricultural land conversion in the world (Sirami & Monadjem 2012; Senyatso et al. 2013; Green et al. 2005).

The mechanisms behind the habitat heterogeneity hypothesis also warrant further investigation. Heterogeneity can be deconstructed into two components: composition, which refers to the diversity of land cover types, and configuration, which measures the complexity of the arrangement of cover types. The roles of landscape composition and configuration in heterogeneity-diversity relationships are poorly understood. Alternatively, the types and amounts of land cover types within a landscape have been shown to drive bird distributions (e.g. Verhulst et al. 2004, Piha et al. 2007). We consider whether land-use is a superior predictor of species diversity than habitat heterogeneity as an additional test of the viability of the habitat heterogeneity hypothesis.

Birds are one of the best taxonomic groups to use for understanding factors limiting biodiversity because they are diverse, well studied, sensitive to environmental gradients, and cost-effective to sample (de Lima 2013, Seymour 2015). A diversity of feeding guilds, body structures, and habitat and breeding requirements makes birds an excellent tool to study heterogeneity-diversity relationships. In addition, birds are the

least data-deficient taxon (IUCN 2015) because there are extensive existing inventories, national atlas data, and citizen science records (e.g. Griffioen & Clarke 2002; Senyatso et al. 2013). We can use existing information about birds to understand their relationships with habitat variables. Finally, birds are important contributors to ecosystem services (provisioning, regulating, cultural, and supporting) (Whelan et al. 2008).

In this study we examine the effect of broad-scale land cover heterogeneity on the diversity and community composition of birds within the Lowveld of Swaziland. This tropical savanna region is one of the most threatened terrestrial ecosystems, as it contains high levels of biodiversity and endemism while facing rapid land conversion for agriculture, grazing, and resource extraction (Steenkamp et al. 2006). The landscape is comprised of a mosaic of land uses, including subsistence farms, grazing lands, settlements, intensive agriculture, and conservation lands. A variety of landscape compositions and configurations presents a unique opportunity to investigate if and how savanna bird diversity responds to heterogeneity at a broad scale. Our investigation of heterogeneity-biodiversity relationships in a human-dominated savanna system will be vital to informing land management decisions with the ultimate goal to create working landscapes that maintain biodiversity and ecosystem functions.

HYPOTHESES

In accordance with the habitat heterogeneity hypothesis, we hypothesize that greater land cover composition and configuration at a large scale (12.5 km²) coincide with higher species richness and diversity. Alternatively, we tested the prediction that land-use alone (e.g. amount of agriculture, amount of savanna) is the strongest predictor of bird species richness and diversity.

METHODS

Study area

We will be working in Northeast corner of Swaziland, stationed at the Savannah Research Center located in Mbuluzi Nature Reserve (Figure 1). Our approximately 30 km x 100 km study area was chosen to encompass the lowveld region, a tropical savanna that is recognized for its high biodiversity and endemism. This is especially evident in avifaunal communities, as over 500 bird species and over 50 bird species endemic to Southern Africa have been recorded in Swaziland (Boycott et al. 2007). The average monthly temperature in the Swaziland lowveld is 18°C in July and 26°C in January, and the average annual rainfall is 550-725 mm (Goudie & Price Williams, 1983). The savanna within the study area is dominated by Acacias corresponding to basaltic soils in the east, while the granitic soils in the west support broad-leafed woodlands (Sweet & Khumalo, 1994). Widespread shrub encroachment has occurred throughout the area within the past 30 years (Sirami & Monadjem 2012).

The study area has experienced varying levels of resource extraction spatially and temporally, resulting in an intricate matrix of commercial sugarcane, subsistence farms, peri-urban development, and conservation lands. Hunters and gatherers first settled in Swaziland at least 30,000 years ago, though the lowveld landscape remained mostly

unchanged until the arrival of cattle ranchers around 100 years ago, followed by the commercial sugar cane industry in the 1980s. Thereafter, most land was converted into farms, ranches, and homesteads, while 2-3% of land was set aside or converted to protected areas with distinctive management regimes. Even within savannas, there exist different degrees and types of human impact, making our study region a good site to investigate the effects of human-dominated land-use heterogeneity.

Land-use mapping

To map land use, we obtained 30 m x 30 m land-cover data through supervised classification of Landsat 8 data in Google Earth Engine (Figure 1). The land cover was classified into five predominant land-use types: agriculture, riparian/forest, communal lands, closed savanna, and open savanna.

We used a moving-window analysis to quantify variation in landscape heterogeneity based on heterogeneity in landscape composition and configuration. To do so, within a 2 km radius of each savanna cell on the map, we measured compositional heterogeneity using the Shannon-Weiner Index of land-cover diversity and land-cover richness (number of land-cover types within the 2 km radius). For configurational heterogeneity, we calculated the total length of edge between land uses and the total number of patches to capture the degree of fragmentation of land-cover, and we calculated a 'largest patch' index, a metric of landscape subdivision (a metric that quantifies the probability that two randomly chosen pixels in the landscape are not situated in the same patch), and a 'patch cohesion index' (a metric that quantifies the connectedness of landcover) to capture potential connectivity of land-cover. The metrics were correlated, so we used principal components analysis (PCA) to derive a single compositional heterogeneity variable and a single configurational heterogeneity variable to guide our site selection process (see Site selection).

Site selection

To account for variability along a rainfall gradient, we stratified the study area into three regions longitudinally: North, Middle, and South. We identified 5 conditions surrounding savannas that comprise of combinations of high, low, and medium land-use composition and configuration (Table 1). Within each stratum, we randomly selected at least one area of savanna surrounded by each condition. All sampled points were restricted to be on accessible land and at least 1 kilometer apart.

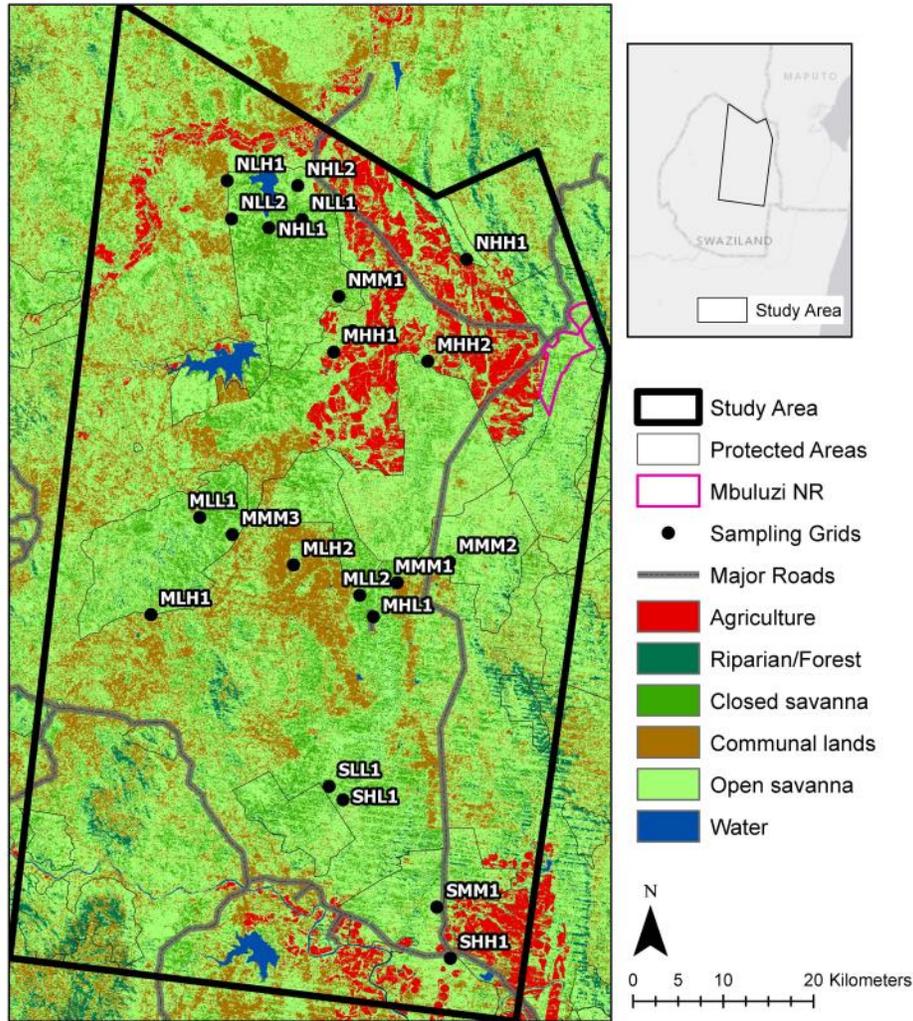


Figure 1: Map of the study site and sampling grids in the lowveld of Swaziland, illustrating protected areas and Mbuluzi Nature Reserve. The 30 m x 30 m land cover raster emphasizes large variation in the amount and arrangement of agriculture, forest, savanna, and rural homesteads.

Composition	Configuration	n
High	High	3
High	Low	3
Low	Low	3
Low	High	3
Medium	Medium	3
Total:		15 (+ Mlawula)

Table 1: Combinations and number of replicates of each land-use composition and configuration condition. Each region (North, Middle, South) contains at least one replicate of each combination.

Sampling design

To sample and compare communities at two scales, we used 550 m x 550 m sampling grids at each selected site. Each grid consists of five 50 m x 50 m plots at the four corners and center of the grid (Figure 2).

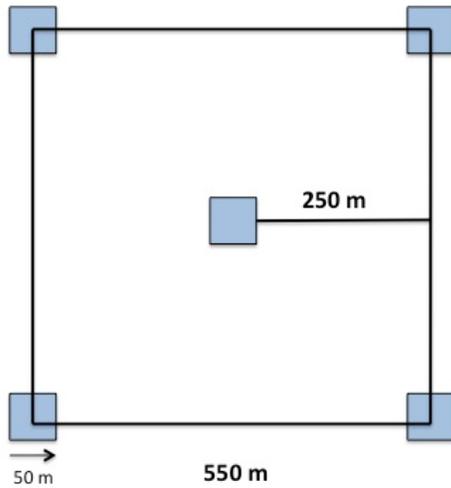


Figure 2: Grid sampling design with 5 50 m x 50m plots.

Avifaunal sampling

We sampled bird assemblages during the dry season (in June and July) of 2016. Point counts were replicated each day per plot in a 4-day period. Point counts of songbirds entail recording all birds seen or heard within a 50 m radius of the center of each plot within 10 minutes. Point counts occurred between dawn and 3.5 hours after sunrise, and were not conducted under rainy or windy conditions to maximize detection. The sampling order of plots was rearranged whenever possible so that each plot was sampled at different times. To eliminate observer bias, the same two experienced observers each conducted two point counts per plot.

Data analysis

We used linear mixed models in the lme4 package (Bates et al. 2014) in R V. 3.2.4. (R Development Core Team 2016) to model the response of species richness and diversity as a function of landscape composition, landscape configuration, and land-use. Response variables were species richness and Shannon diversity. Large-scale land cover heterogeneity variables were Shannon diversity of land cover, edge length, land division, and land cohesion. (see Land-use mapping). The grid containing the plots were used as a random effect to account for spatial correlation between plots. Models with heterogeneity variables and models with land-use variables will be run independently to select the best predictors of species richness and diversity within each group. Then, combinations of the best predictors from each group were tested in models. The best models will be selected using the Akaike information criterion (AIC) to determine the strongest combination of

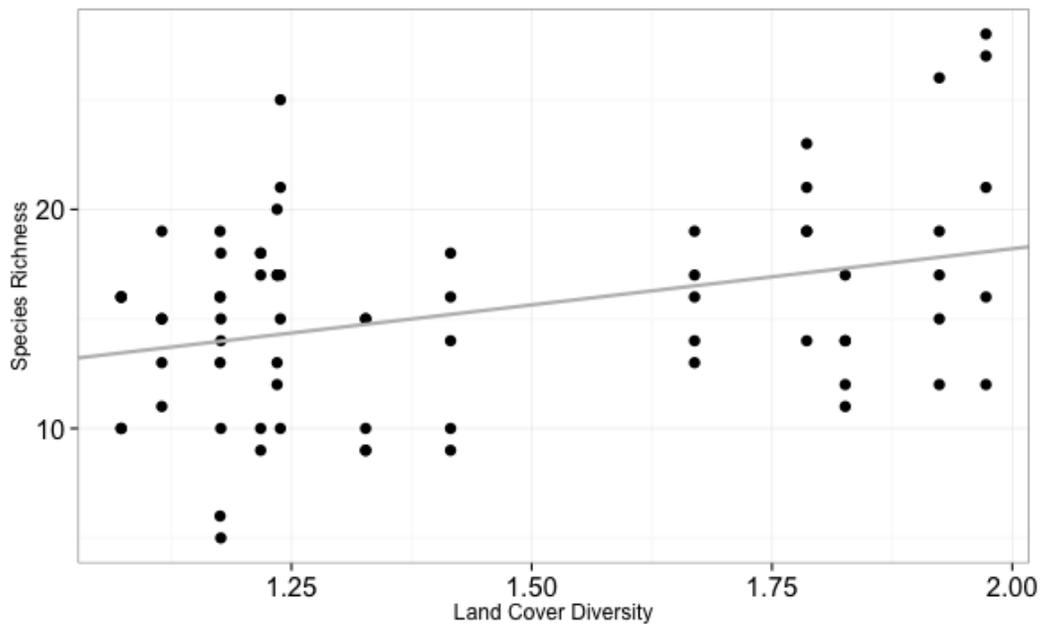
predictors of species richness and evenness. Model parameters were determined to be significant if the 95% confidence interval around the estimate did not contain zero.

RESULTS

We recorded 2755 individuals of 86 bird species during 320 10-minute point counts. 4 endemic and 2 near-endemic species were observed. The mean number of species registered within each plot was 14.9 (5.0 SD). The five most commonly detected species were dark-capped bulbul (*Pycnonotus tricolor*), white-bellied sunbird (*Cinnyris talatala*), chinspot batis (*Batis molitor*), red-faced mousebird (*Urocolius indicus*), and yellow-breasted apalis (*Apalis flavida*). Each of these species occurred in at least 60% of point counts.

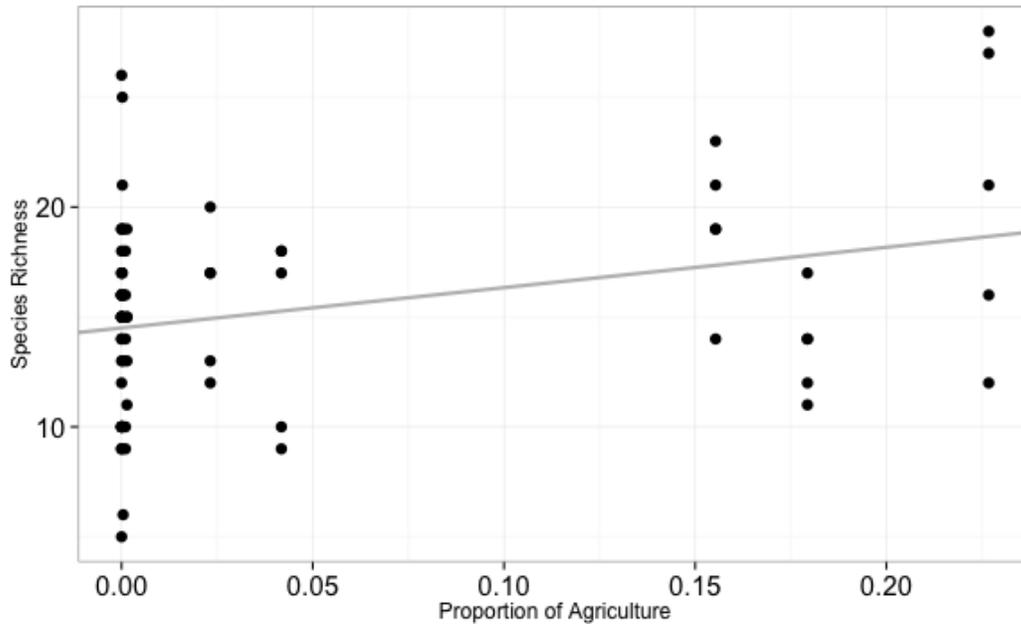
Effect of landscape heterogeneity

Four candidate models fell within two AICc values of the top model investigating the effects of Shannon diversity of land cover, Simpson diversity of land cover, land cohesion, and edge length on bird species richness. In species diversity models, three candidate models fell within two AICc values of the top model. Species richness and diversity were significantly positively correlated with landscape composition (higher land cover Shannon and Simpson diversity). Adding patch cohesion as a predictor in addition to landscape composition metrics improved models, though the 95% confidence interval around the estimate for patch cohesion contained zero in all cases. There was a negative correlation between patch cohesion and species richness and diversity, while edge length had no significant effect.



Effect of land use

In candidate models including the effects of amount of each land use type (savanna, agriculture, communal lands, riparian areas, and water) on bird species richness, three models fell within two AICc values of the top model. Those models include the effects of agriculture, which had a positive relationship with species richness, and the effects of savanna, which had a negative effect. In candidate models for species diversity, no models were considered superior to the null model. Four models fell within two AICc values of the top model, including the null model. The confidence interval of the best estimator of species diversity, amount of agriculture, contained zero. There were no significant effects of amount of communal lands, riparian areas, or water.



Combined effect of landscape heterogeneity and land use

When testing subsets of the best predictors of species richness from the heterogeneity suite and the land use suite, three models fell within two AICc values of the top model, which is a model using only Simpson land cover diversity as a predictor. Using the same method for species diversity models, two models fell within two AICc values of the top model, which contained only Shannon land cover diversity as an explanatory variable.

Heterogeneity Suite				
Response	Best Predictor	$\beta \pm SE$	Confidence Interval	
			2.5%	97.5%

Species Richness	Simpson Composition	.0793 ± .0362	.008	.150
Species Diversity	Shannon Composition	.0805± .0362	.014	.156

Land-use Suite		$\beta \pm SE$	Confidence Interval	
Response	Best Predictor		2.5%	97.5%
Species Richness	Amount of Agriculture	1.41 ± .577	.279	2.54
Species Diversity	Amount of Agriculture	.0713 ± .0364	-.00004	.143

Landscape Suite, Species Richness

Model	K	AICc	$\Delta AICc$	AICc(wt)	Cum(wt)	LL
Simp	4	411.8201	0	0.1518	0.1518	-201.6024
SW	4	412.3309	0.5108	0.1176	0.2695	-201.8577
SW+Coh	5	413.3767	1.5566	0.0697	0.3392	-201.2196
Simp+Coh	5	413.409	1.5889	0.0686	0.4078	-201.2357
Simp+Edge	5	414.1418	2.3218	0.0476	0.6349	-201.6022
Simp+Edge	6	414.5996	2.7795	0.0378	0.7558	-200.6331
SW+Edge	5	414.6513	2.8312	0.0369	0.8299	-201.8569
SW+Edge	6	415.3541	3.534	0.0259	0.8924	-201.0104
Simp*Coh	6	415.5227	3.7026	0.0238	0.9162	-201.0947
Shan*Coh	6	415.5421	3.722	0.0236	0.9398	-201.1044
Edge	4	415.892	4.0719	0.0198	0.9597	-203.6383
Coh+Edge	5	416.0839	4.2638	0.018	0.9777	-202.5732
Null	3	416.5119	4.6918	0.0145	0.9922	-205.0742

Abbreviations: Simp, Simpson diversity of land cover; SW, Shannon Weiner diversity of land cover; Coh, patch cohesion; Edge, total edge length.

Heterogeneity Suite, Species Diversity

Model	K	AICc	$\Delta AICc$	AICc(wt)	Cum(wt)	LL
SW	4	38.7339	0	0.1583	0.1583	-15.0593
Simp	4	38.8817	0.1478	0.147	0.3053	-15.1331
SW+Coh	5	40.6981	1.9642	0.0593	0.446	-14.8803

Simp+Coh	5	41.0475	2.3137	0.0498	0.6039	-15.055
SW+Edge	5	41.0521	2.3183	0.0497	0.6536	-15.0573
Simp+Edge	5	41.2009	2.467	0.0461	0.6997	-15.1317
Edge	4	41.2218	2.4879	0.0456	0.7453	-16.3032
Null	3	41.2816	2.5477	0.0443	0.7896	-17.459

Land-use Suite, Species Richness

Model	K	AICc	Δ AICc	AICc(wt)	Cum(wt)	LL
Ag+Sav	5	413.0211	0	0.3355	0.3355	-201.0418
Ag	4	413.7723	0.7512	0.2305	0.566	-202.5785
Sav	4	413.8162	0.7951	0.2255	0.7914	-202.6004
Null	3	416.5119	3.4908	0.0586	0.85	-205.0742

Abbreviations: Ag, amount of agriculture; Sav, amount of savanna.

Land-use Suite, Species Diversity

Model	K	AICc	Δ AICc	AICc(wt)	Cum(wt)	LL
Ag	4	39.7974	0	0.2416	0.2416	-15.591
Sav	4	40.1395	0.3421	0.2036	0.4452	-15.7621
Ag+Sav	5	40.564	0.7666	0.1647	0.6099	-14.8133
Null	3	41.2816	1.4842	0.115	0.7249	-17.459

Combined Suite, Species Richness

Model	K	AICc	Δ AICc	AICc(wt)	Cum(wt)	LL
Simp	4	411.8201	0.8806	0.1941	0.4956	-201.6024
Simp+Ag	5	413.5232	2.5837	0.0828	0.8156	-201.2929
Ag	4	413.7723	2.8328	0.0731	0.8887	-202.5785
Simp*Ag	6	415.6545	4.7149	0.0285	0.9814	-201.1606
Null	3	416.5119	5.5724	0.0186	1	-205.0742

Combined Suite, Species Diversity

Model	K	AICc	Δ AICc	AICc(wt)	Cum(wt)	LL
SW	4	38.7339	0	0.2446	0.2446	-15.0593
Ag	4	39.7974	1.0635	0.1437	0.5449	-15.591
SW+Ag	5	40.9271	2.1932	0.0817	0.8653	-14.9948
null	3	41.2816	2.5477	0.0684	0.9337	-17.459

DISCUSSION

Evaluating the validity and mechanisms behind the habitat heterogeneity hypothesis is crucial for its application to land management decisions. We tested this hypothesis at a

landscape level and contrasted it to the effectiveness of land use as a predictor of bird species richness and diversity. Relationships between landscape heterogeneity and species diversity were stronger than those between land use and species diversity. Our findings that greater land cover diversity leads to higher species diversity support the habitat heterogeneity hypothesis at a broad scale. Finally, we show that within landscape heterogeneity, composition is a stronger driver of species richness and diversity than configuration.

Support for the habitat heterogeneity hypothesis

Our results build on the support of the habitat heterogeneity hypothesis from previous studies of heterogeneity in different biomes (e.g. Belisle et al. 2001, Radford et al. 2005, Villard et al. 1998). However, most studies examine the effect of land use and landscape configuration, and do not consider a land cover diversity metric as a factor. Our finding that land cover diversity is a strong factor determining bird species richness and diversity is a notable supplement to other studies investigating the drivers of bird distributions. Though we also found a negative effect of patch cohesion on species diversity, landscape composition was stronger than configuration effects in predicting species diversity.

Our finding that amount of agriculture affects species richness and diversity also supports the habitat heterogeneity hypothesis because proportion of agriculture was positively correlated with land cover diversity (correlation = .78). Because the AIC values for the land cover diversity models are lower than that of the models with agriculture, the relationship between land cover diversity and species diversity is stronger than the relationship between amount of agriculture and species diversity.

Conservation implications

We determined that land-use changes in an agricultural matrix affect diversity within natural areas. Our results support the habitat heterogeneity hypothesis at a broad scale, and we show that species diversity can be maintained or even may increase with an addition of agriculture to a landscape. We advise further investigation into the threshold at which additional agriculture becomes detrimental.

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