Anthropogenic and environmental influences on mammalian alpha and beta diversity in a hardwood forest landscape

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A R T I C L E   I N F O

A B S T R A C T

Species richness within a site (i.e., alpha diversity) and between sites (i.e., beta diversity) are important measurements of biodiversity utilized in wildlife research and management. However, novel occupancy modeling approaches, especially at large spatial scales and in conjunction with other analyses of biodiversity, remain scarce in studies of mammalian biodiversity across forested landscapes. We assessed alpha and beta diversity of mammals across a 16,058-km^2 region of southern Illinois, USA, between January and April of the years 2008–2010. We deployed camera traps, measured habitat variables, applied hierarchical occupancy modeling and meta-analysis techniques to investigate alpha diversity, and used partial redundancy analyses and partial Mantel tests to investigate beta diversity. We collected 86,486 photographic captures of mammals. Alpha diversity values ranged from 3 to 10; models incorporating Simpson's diversity index of patch types, distance to major road, and agriculture clumpiness index were most supported. Forest proximity and percentage forest cover explained minor variation in beta diversity, and we found weak, positive correlations between beta diversity and percentage forest cover and forest proximity index. Mammalian biodiversity was strongly influenced by generalist species and highest with (1) moderate levels of habitat heterogeneity, (2) low to moderate levels of anthropogenic influence, and (3) nearby forest cover. Anthropogenic influences and the presence of agriculture appeared to increase species richness by providing novel food resources and additional habitat that generalist species could exploit while also being tolerant of any accompanying landscape fragmentation or disturbance. While dominated by generalist species, our local mammalian community had an affinity for forest cover, reinforcing the importance of forested habitat to these species in hardwood forest systems. Our study demonstrates the usefulness of hierarchical modeling approaches and the importance of examining biodiversity through varying measurements.

1. Introduction

Species richness is a fundamental measurement of biodiversity used in ecological models and conservation plans (Gotelli and Colwell, 2001; Guillera-Arroita et al., 2019), allowing for quantitative analysis of biodiversity both within (i.e., alpha diversity) and between (i.e., beta diversity) communities. Environmental characteristics of an area is one of the most influential factors affecting such patterns at all scales (Pulliam, 1988; Carey and Johnson, 1995; Urquiza-Haas et al., 2009). By providing numerical values (Wilson

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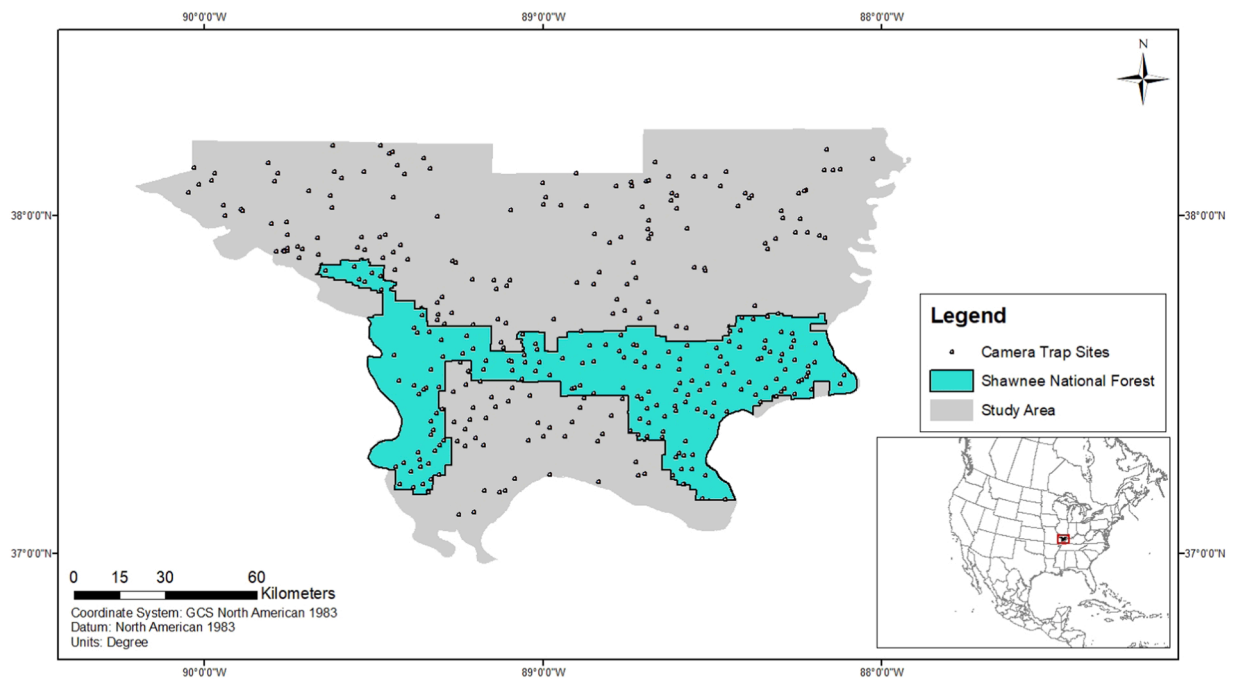
Fig. 1. Map of study area, Shawnee National Forest boundary, and locations of the 357 political sections (2.6-km^2) surveyed using camera traps in the 16 southernmost counties of Illinois, USA, between January and April of the years 2008–2010.

et al., 2012), species richness allows researchers to infer how biotic and abiotic variables influence alpha and beta diversity through comparison of differing sites and regions.

Understanding the underlying processes affecting alpha and beta diversity at various scales has been a priority of scientists (Hawkins, 2001; Torres-Romero and Olalla-Tárraga, 2015) and studied across multiple biogeographical realms (Andrews and O'Brien, 2000; Badgley and Fox, 2000; Hawkins and Porter, 2003; Whittaker et al., 2007). Such studies hypothesized habitat and anthropogenic influences as plausible explanations for observed diversity patterns (Riem et al., 2012; Meyer et al., 2015; Li et al., 2018; Boron et al., 2019). Given habitat has a strong impact on occupancy of individual mammalian species (Scharine et al., 2011; Anile et al., 2020; Cassel et al., 2020), it is also likely to be important to all mammalian species present in an area (Kerr and Packer, 1997; McKinney, 2008; Kalies et al., 2012). However, studies examining anthropogenic influences on mammalian occupancy or biodiversity reported contrasting results (Torres-Romero and Olalla-Tárraga, 2015). Many studies report negative relationships between biodiversity (e.g., species richness, phylogenetic diversity) and anthropogenic influences causing habitat loss, fragmentation, or disturbance (McKinney, 2008; Murphy and Romanuk, 2013; Newbold et al., 2015; Buffa et al., 2018; Chaudhary and Mooers, 2018). However, other studies observed a positive relationship between biodiversity and anthropogenic influences, particularly when occurring at low to moderate levels (Racey and Euler, 1982; McKinney, 2002; Nielsen et al., 2019; Viljur et al., 2022), highlighting the complex relationship between anthropogenic influences and biodiversity.

Given the potential effect of habitat and anthropogenic influences on biodiversity patterns, numerous modeling approaches have been created to assess possible relationships (Balvanera et al., 2002; Legendre et al., 2005; MacKenzie et al., 2006; Carvahlo et al., 2013; Kéry and Royle, 2015). Measurements such as Sørensen or Jaccard indices of similarity or dissimilarity allow for quantification of biodiversity between locations or communities (Chao et al., 2012; Baselga and Leprieur, 2015). When these indices are used in canonical correspondence analyses (Balvanera et al., 2002), redundancy analyses (Qiao et al., 2015), or with Mantel tests (Legendre et al., 2005), they enable researchers to examine relationships in natural systems to explain biodiversity patterns. Furthermore, multiple occupancy modeling (MacKenzie et al., 2006) approaches have arisen as effective methods to investigate questions about ecological systems. A traditional occupancy modeling approach describes the raw detection and non-detection data of individual species as a function of predictors and estimates species richness via stacking the resulting models (Dorazio and Royle, 2005; MacKenzie et al., 2006; Calabrese et al., 2014), creating a "predict-first-stack-later" strategy. Recently, approaches that relate spatially replicated species counts directly to environmental predictors at survey sites (Ferrier and Guisan, 2006) and attempt to "stack--first-predict-later" have emerged (Guillera-Arroita et al., 2019). By simultaneously analyzing multiple species detection data, assessment of occupancy models becomes more efficient and capable of providing insight into how communities respond to environmental and other variables as a function of individual species' responses, in addition to metacommunity patterns (Kéry and Royle, 2015).

Despite the development of novel occupancy modeling methods, application of these extensions evaluating biodiversity via alpha (i.e., species richness) and beta diversity remain scarce in forest wildlife literature, especially when used in conjunction with other techniques (Rovero et al., 2014; Bowler et al., 2016; Boron et al., 2019). Furthermore, few studies investigated biodiversity patterns of

temperate forest wildlife at large scales (Li et al., 2018; Crego et al., 2020). Within North America, most species richness studies occur in non-forested landscapes (Wait et al., 2018; Rich et al., 2019) or examine how biodiversity of specific taxonomic groups respond to specific disturbances (Allen et al., 2018; Janousek et al., 2019). Moreover, knowledge of influential habitat variables is of great conservation import.

To address this gap in literature, we conducted camera-trapping surveys and applied novel modeling approaches to assess associations between habitat variables and alpha and beta diversity of forest mammals in southern Illinois, USA. We predicted agriculture would be negatively associated with alpha diversity (Lesmeister et al., 2015; Boron et al., 2019). We further predicted variables associated with anthropogenic influences (e.g., distance to roads, density of human structures; Trombulak and Frissell, 2001; Riem et al., 2012) would negatively impact alpha diversity and measurements of urbanization (e.g., urban patch density) would be correlated with beta diversity. Additionally, we predicted variables associated with larger, less compact forest patches (e.g., forest shape, forest proximity) and increased forest cover would increase alpha diversity and be positively correlated to beta diversity, as forest patches with these characteristics would more likely sustain a larger number of species (Saura et al., 2008). We predicted variables associated with patch size (e.g., edge length, patch area) would be correlated to beta diversity, as similarly sized patches would display similar alpha diversity due to limitations in available resources and habitat (Foster and Gaines, 1991).

2. Material and methods

2.1. Study area

We studied forest wildlife in the 16 southernmost counties of Illinois, USA (Fig. 1; 16,058 km^2; Lesmeister et al., 2015). The study area included 6 of the 14 natural land divisions in Illinois (Southern Till Plain, Wabash Border, Shawnee Hills, Ozarks, Lower Mississippi Bottomlands, and Coastal Plain; Schwegman, 1973; Neely and Heister, 1987). Light-colored Alfisols dominated the study area (Fehrenbacher et al., 1984) with highly dark-colored Mollisols in bottomland areas near the Ohio and Mississippi rivers. Entisols were found throughout the study area on slopes prone to erosion and in sandy floodplains along riparian zones (Barnhardt, 2010). Soil parent materials were mainly loess followed by alluvium and outwash (Fehrenbacher et al., 1967). Land cover of the central portion of the study area primarily consisted of closed-canopy mixed hardwood forests dominated by *Acer*, *Carya*, and *Quercus* spp. and was primarily within the Shawnee National Forest (Luman et al., 1996). Agricultural cropland with primary crop rotations of corn (*Zea mays*), soybeans (*Glycine max*), and winter wheat (*Triticum aestivum*) dominated the northern regions and areas along large rivers (Lesmeister et al., 2015). The remaining land cover of the study area comprised grasslands (primarily cattle pasture and hay fields), wetlands, open water, and urban (Anon, 1996). Human and road densities were 21.5 persons/km^2 and 1.5 road km/km^2, respectively (Lesmeister et al., 2015). The Shawnee National Forest (1075 km^2), Crab Orchard National Wildlife Refuge (178 km^2), Cypress Creek National Wildlife Refuge (61 km^2), along with 6 other Illinois State Parks and 15 other state managed public areas were found within the study area. Mean temperatures of 5.4 ± 0.4 °C and mean precipitation of 26.0 ± 2.0 mm/week (National Oceanic and Atmospheric Administration, 2010) were observed during the study period. The study area was classified as a humid subtropical temperate climate within the Köppen classification of climates (Ackerman, 1941).

2.2. Camera trapping

We conducted camera trapping surveys between January and April of the years 2008–2010, totaling about 12 months of sampling, following Lesmeister et al. (2015), and we used ArcGIS 9.3 (Environmental Systems Research Institute, Redland, CA) to conduct all GIS analyses. After identifying township and political boundaries (Illinois State Geological Survey, 2004a), we divided the study area into 2.6-km^2 political sections and surveyed sections via stratified random sampling. Land cover data from the United States Geological Survey's National Land Cover Database (USGS, 2007) was used to determine percentage forest cover for each political section. Study design for Lesmeister et al. (2015) was focused on mesocarnivores; given species of interest were unlikely to occupy areas with little forest cover (Nielsen and Woolf, 2002), political sections with < 11% forest cover were eliminated. The remaining political sections were stratified based on 10% forest cover increments, and 360 sections were randomly selected to proportionally represent the forest cover of the study area.

We surveyed 357 sections, and within each, we deployed 3–4 camera traps > 250 m apart to create a camera cluster (n = 1188 total camera locations and 357 camera cluster locations). At each camera trap location, we used 1 digital remote camera (Cuddeback Exicite [2.0 megapixel] or Capture [3.0 megapixel], Non Typical Inc., Park Falls, WI) with passive infrared sensors and incandescent flash, requiring both heat and motion to be detected to trigger a photographic event. Camera traps were placed opportunistically at each location ~0.5 m from the ground, aimed at a sardine and fatty acid scent disk (U.S. Department of Agriculture Pocatello Supply Depot, Pocatello, ID) placed ~2 m from the camera, and were set to be active 24 h each day with a 1-minute delay between photographs. During 2008, we surveyed 117 sections with 4 cameras in each section (n = 468 total camera locations). Preliminary analysis indicated that there was no difference in detection probability or variance between 3 and 4 camera locations/camera cluster (D. Lesmeister, Southern Illinois University, unpublished data). In 2009–2010, 240 sections were sampled with 3 camera traps in each cluster (n = 720 camera locations; Lesmeister et al., 2015). Each camera location was surveyed for 3 weeks with each, individual week acting as a single, independent survey session. Camera images were downloaded, and photographs identified to species. We considered wild mammals only in our analyses.

Table 1

Habitat variables calculated in FRAGSTATS 3.3 (McGarigal et al., 2002) for study of mammalian occupancy, alpha diversity, and beta diversity in the 16 southernmost counties of Illinois, USA, between January and April of the years 2008–2010.

Variable Acronym	Description
DIST MU	Distance (m) to nearest municipality
DIST MAJOR RD	Distance (m) to nearest major road (interstate highways and arterials)
DIST RD	Distance (m) to nearest minor paved road (collectors and local roads)
DIST STRUCT	Distance (m) to nearest human structure
MAJOR RD LENGTH	Length (m) of major road (interstate highways and arterials)/ha
RD LENGTH	Length (m) of minor paved roads (collectors and local roads)/ha
STRUCT	Number of human structures/ha
OWNERSHIP	Ownership (public or private) of camera location
URBAN PATCH	Patch area coefficient of variation: standard deviation/mean patch size (ha)
URBAN PERCENT	Percentage of camera-cluster buffer comprised of urban patches
PATCH AREA	Patch area coefficient of variation: standard deviation/mean patch size (ha)
EDGE	Total length (m) of patch edge/ha
FOREST SHAPE	Forest shape index; mean perimeter-to-area of patch, increases as patch becomes less compact
GRASS SHAPE	Grassland shape index; mean perimeter-to-area ratio of patch, increases as patch becomes less compact
STREAM LENGTH	Length (m) of stream/ha
WETLAND SHAPE	Wetland shape index; mean perimeter-to-area of patch, increases as patch becomes less compact
AG CLUMP	Agriculture clumpiness (fragmentation) index, range: − 1 (patch maximally disaggregated) to 1 (patch maximally clumped)
FOREST PROX	Forest proximity index; mean sum of forest patch size (ha) divided by the squared distance (m) from focal patch
GRASS PROX	Grassland proximity index; mean sum of grassland patch size (ha) divided by the squared distance (m) from focal patch
GRASS PERCENT	Percentage camera-cluster buffer comprised of grassland patches
SIMPSON	Simpson's diversity index of patch types; proportional abundance of each patch type
FOREST PERCENT	Percentage forest cover

2.3. Habitat variables

We considered the effects of 22 habitat variables on mammalian species richness (Table 1) at the camera-cluster scale. We measured distances (m) to nearest (1) municipality (Anon, 2006), (2) major road, (3) minor paved road (FHWA, 2000; ISGS, 2004a, 2004b), and (4) human structure (Anon, 2005). We calculated remotely sensed variables representing land cover; patch size (Anon, 1996); and density of (1) major roads, (2) minor paved roads, (3) human structures, and (4) streams (Anon, 1994), using FRAGSTATS 3.3 (McGarigal et al., 2002). These variables were calculated within 50 ha and 250 ha buffers at each individual camera location. Mean values of the camera location variables were assigned as the values of each camera cluster. Spearman's rank correlation (Hollander et al., 2014) was used to confirm all 22 habitat variables were only weakly correlated with correlation coefficient values $< |0.20|$ (Akoglu, 2018) and could be included in the hierarchical occupancy modeling and partial distance-based redundancy analyses. Data for all habitat variables were centered and normalized for model inclusion and comparison.

2.4. Hierarchical modeling

We performed hierarchical modeling using 3 models (null, month effect, year effect) that utilized a process model and subsequent observation model following Kéry and Royle (2015) and used Just Another Gibbs Sampling (JAGS; Plummer, 2003) software to model occupancy and alpha diversity. Due to violations of the closure assumption for occupancy modeling, we used the following 3 models to account for potential bias in detection and occupancy rates:

Null model.

Process model: z_{ik}~Bernoulli(ψ_k)

Observation model: $ysum_{ik}|z_{ik}$~$(J_i, z_{ik}p_k)$

Month model variant.

Process model: $z_{ik} \sim Bernoulli(\psi_k)$

Observation model: $ysum_{ik} | z_{ik} \sim Binominal(J_i, z_{ik}p_k) + \alpha_i$ Survey Month

Year model variant.

Process model: $z_{ik} \sim Bernoulli(\psi_k)$

Observation model: $ysum_{ik} | z_{ik} \sim Binominal(J_i, z_{ik}p_k) + \alpha_s$ Survey Year

where J_i was the number of surveys indexed by camera cluster i, and the detection frequency data, $ysum_{ik}$, for species k at camera cluster i was fit to models using latent variables z. We modeled each species as fixed effects with detection and occupancy probabilities calculated from detection histories for individual species. This approach accommodates imperfect detection, allows each species to differ in detection and occupancy probability, and yields an estimate of camera cluster-specific species richness (i.e., alpha diversity).

For each model, 3 parallel chains were run using 150,000 iterations, a thinning rate of 10, and a burn in of 50,000 iterations. Deviance information criterion (DIC) values were used to compare models, with lower DIC values indicating a model would best predict a replicate dataset having the same structure as the observed data (Spiegelhalter et al., 2002). Similar to the node deviance monitored by WinBUGS, the deviance included within DIC was defined as.

$$-2 * \log(p(y|\Theta))$$

where all normalizing constants were included, with y comprising all stochastic nodes assigned values from the input data and Θ comprising the immediate stochastic parents of y. Stochastic parents are defined as the stochastic nodes upon which the distribution of y depends, when collapsing over all logical relationships (Spiegelhalter et al., 2002). This metric was used when calculating the effective number of parameters (pD):

$$pD = Dbar - Dhat$$

Dbar was the posterior mean of the deviance, and Dhat was a point estimate of the deviance obtained by substituting the posterior means (Spiegelhalter et al., 2002). These allowed for the calculation of DIC:

$$DIC = Dbar + pD = Dhat + 2 * pD$$

These metrics are particularly useful when the posterior distributions of the models were obtained via MCMC. DIC acts as a hierarchical generalization of the Akaike information criterion (AIC; Tomohiro, 2007), and pD helps when selecting for parsimony through fewest estimated number of parameters (Hooten and Hobbs, 2015).

We used the camera cluster, community occupancy estimates from models with lower DIC values than the null model in subsequent meta-analyses to relate model estimates to the 22 habitat variables (Table 1) following Kéry and Royle (2015), using a regression model with 2 residual components. The first residual estimated uncertainty among the community model analysis by utilizing the posterior standard deviation of the community size estimate at the site. The second residual component influenced the lack of fit, allowing individual data points to lie off the modeled relationship. For each model, 3 parallel chains were run using 20,000 iterations, a thinning rate of 10, and a burn in of 5000 iterations. Weakly informative model priors were selected and were set from 0 to 10 to provide minimal influence on inferences, while still allowing for calculation of posterior distributions (Syversveen, 1998).

Convergence of model MCMC iterations was determined when Rhat values were all within 0.1 of 1.00 (Kéry, 2010). Models ≤ 5 DIC of the lowest ranked model were considered to be informative (Spiegelhalter et al., 2002), and further assessed for parsimony using pD (Hooten and Hobbs, 2015). The estimated relationships between habitat variables and species richness for the models with lowest DIC and pD values were plotted. We created models examining each habitat variable individually and each possible combination of 2 habitat variables. Due to parameter constraints and model instability, models incorporating ≥ 3 habitat variables were unable to be created.

2.5. Partial distance-based redundancy analysis

Beta diversity was measured using Jaccard's dissimilarity index through the R package vegan (Oksanen et al., 2020) in R (R Core Team, 2022):

$$C_j = 1 - j/(a + b - j)$$

where j is the number of species shared by 2 sites, a is the number of species at site 1, and b is the number of species at site 2 (Magurran, 1988). Jaccard's dissimilarity index ranges from 0 to 1, with a minimum value of $C_j = 0$ indicating complete compositional similarity among a pair of sites, and a maximum value of $C_j = 1$ indicating no shared species between the 2 sites. Jaccard's dissimilarity index was selected due to its effectiveness in providing a pairwise comparison of sites using presence/absence data (Hao et al., 2019).

Dissimilarity between sites was investigated using a partial distance-based redundancy analysis with first- and second-degree terms of explanatory variables using methods described by Borcard et al. (2018) and conducted in R package vegan. A partial redundancy analysis removes the effect of explanatory variables from a set of response variables before conducting a standard redundancy analysis, and we used a distance-based approach to assess 22 habitat variables (Table 1) potentially influencing dissimilarity between sites. We allowed for both first- and second-degree terms, accounting for potential linear relationship or non-linear relationships respectively, between the explanatory variables and dissimilarity matrix. We applied a square root transformation to the Jaccard's dissimilarity matrix and computed a principal coordinate analysis of the dissimilarity matrix. We ran a redundancy analysis of the computed principal coordinates, acting as the response data, while constraining explanatory variables. This modelling approach is a multivariate equivalent of a partial regression analysis, enabling us to determine the amount of variation explained in the Jaccard's dissimilarity matrix by matrices of variables while holding geographic location, mean temperature, and mean precipitation constant. This approach accounted for potential variation caused by spatial autocorrelation between sites and seasonal differences between survey periods. We ran a permutation test of terms with 999 permutations to test the significance of the environmental measures at both first- and second-degree terms with α = 0.05. A forward selection function was applied to all constrained and conditional variables to identify which variables accounted for the most variation in beta diversity and estimate how much of the total variation was accounted for.

Table 2

Photographs collected during the study of occupancy and species richness in the 16 southernmost counties of Illinois, USA, between January and April of the years 2008–2010. Camera locations refers to individual camera traps, and camera cluster refers to a site with 3–4 camera traps.

Common name	Species name	Family name	Order name	Total photographic captures	Percentage of camera locations observed	Percentage of camera clusters observed
Bobcat	*Lynx rufus*	Felidae	Carnivora	412	15%	47%
Coyote	*Canis latrans*	Canidae	Carnivora	1397	39%	79%
Eastern cottontail	*Sylvilagus floridanus*	Leporidae	Lagomorpha	760	16%	38%
Eastern gray squirrel	*Sciurus carolinensis*	Sciuridae	Rodentia	1986	42%	81%
Fox squirrel	*Sciurus niger*	Sciuridae	Rodentia	1323	24%	49%
Gray fox	*Urocyon cinereoargenteus*	Canidae	Carnivora	546	8%	22%
Mouse	*Peromyscus* sp.	Cricetidae	Rodentia	467	5%	15%
Raccoon	*Procyon lotor*	Procyonidae	Carnivora	40,029	85%	99%
Red fox	*Vulpes vulpes*	Canidae	Carnivora	149	5%	16%
Southern flying squirrel	*Glaucomys volans*	Sciuridae	Rodentia	708	5%	14%
Striped skunk	*Mephitis mephitis*	Mephitidae	Carnivora	2467	22%	48%
Virginia opossum	*Didelphis virginiana*	Didelphidae	Didelphimorphia	26,643	77%	93%
White-tailed deer	*Odocoileus virginianus*	Cervidae	Artiodactyla	8607	83%	99%

Table 3

Estimated occupancy (ψ) and detection (p) rates with standard error for mammalian species estimated from the month effect *N*-fold community occupancy model, using data collected from remote camera surveys in the 16 southernmost counties of Illinois, USA, between January and April of the years 2008–2010.

Species	Detection (p)	Occupancy (ψ)
Bobcat	0.300 ± 0.002	0.483 ± 0.004
Coyote	0.531 ± 0.100	0.781 ± 0.002
Eastern cottontail	0.616 ± 0.003	0.200 ± 0.001
Eastern gray squirrel	0.630 ± 0.001	0.794 ± 0.002
Fox squirrel	0.618 ± 0.002	0.438 ± 0.002
Gray fox	0.627 ± 0.003	0.121 ± 0.001
Mouse *sp.*	0.620 ± 0.004	0.071 ± 0.001
Raccoon	0.898 ± 0.001	0.974 ± 0.001
Red fox	0.566 ± 0.005	0.070 ± 0.001
Southern flying squirrel	0.659 ± 0.001	0.068 ± 0.000
Striped skunk	0.593 ± 0.002	0.267 ± 0.002
Virginia Opossum	0.847 ± 0.001	0.910 ± 0.001
White-tailed deer	0.853 ± 0.000	0.987 ± 0.001

2.6. Partial mantel test

The effects of habitat variables selected through the forward selection function on beta diversity were further assessed and quantified using a partial Mantel test, while accounting for geographic location, and conducted through R package ecodist (Goslee and Urban, 2007). While a simple Mantel test is the correlation between 2 dissimilarity matrices, a partial Mantel test incorporates additional matrices, so the Mantel statistic describes the partial correlation of 2 dissimilarity matrices given all other explanatory variables. Distance matrices describing the pairwise differences in selected variables and geographic location between any 2 sites were calculated. Number of permutations was set to 9999, and number of iterations used for bootstrap confidence intervals was set to 5000 and α = 0.05, while all other function arguments were set to default values.

3. Results

3.1. Camera trapping

We recorded 86,486 photographic captures of 13 different mammal species or mammal groups over 29,988 camera days at 1188 camera locations (357 camera clusters). Photographic captures of species or species-groups included bobcat (*Lynx rufus*), coyote (*Canis latrans*), eastern cottontail (*Sylvilagus floridanus*), eastern gray squirrel (*Sciurus carolinensis*), fox squirrel (*Sciurus niger*), gray fox (*Urocyon cinereoargenteus*), mouse (*Peromyscus* sp.), raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*), southern flying squirrel (*Glaucomys volans*), striped skunk (*Mephitis mephitis*), Virginia opossum (*Didelphis virginiana*), and white-tailed deer (*Odocoileus virginianus*), and

Table 4

The deviance information criterion (DIC) and effective number of parameters (pD) for the month effect model relating estimated mammalian alpha diversity values at camera clusters to habitat variables, using data collected from remote camera surveys in the 16 southernmost counties of Illinois, USA, between January and April of the years 2008–2010. Habitat variables are defined in Table 1.

Model	DIC	pD
SIMPSON+AG CLUMP	1090.8	320.9
STRUCT+DIST MU	1090.9	323.1
STRUCT+FOREST PROX	1091.6	321.8
SIMPSON+FOREST PERCENT	1092.1	323.1
PATCH AREA+DIST MAJOR RD	1093.3	323.8
EDGE+URBAN PERCENT	1093.9	325.0
DIST STRUCT+FOREST PERCENT	1094.0	323.8
PATCH AREA+SIMPSON	1094.7	326.0
AG CLUMP+DIST MU	1095.0	325.9
GRASS PROX+DIST MU	1095.7	325.7
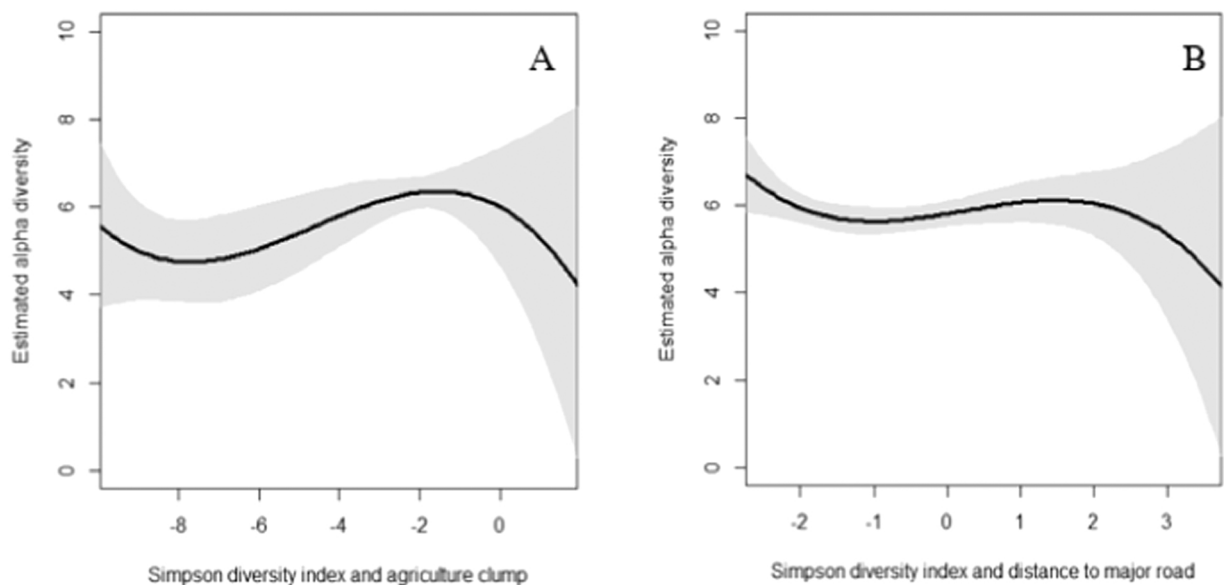
Fig. 2. Regression model predicting mammalian species richness values in relation to (A) Simpson diversity index of patch types and agriculture fragmentation index using month effect occupancy estimates and (B) Simpson's diversity index of patch types and distance to major road using year effect occupancy estimates. Black line indicating the regression model when propagating the uncertainty for *N* estimates and using normalized and centered data collected from camera clusters in the 16 southernmost counties of Illinois, USA, between January and April of the years 2008–2010. Grey area indicates 95% credible interval.

total captures of species or species-group used in subsequent analyses ranged from 149 (red fox) to 40,029 (raccoon; Table 2). The percentage of camera locations where study animals were recorded varied from 5% (red fox, southern flying squirrel, and mouse sp. separately) to 85% (raccoon), while percentage of camera clusters where study animals were recorded ranged from 14% (southern flying squirrel) to 99% (raccoon and white-tailed deer separately; Table 2). Camera cluster alpha diversity ranged from 3 to 10 ($\bar{x}$ = 6.6 ± 0.1 [SE throughout]).

3.2. Hierarchical modeling

Detection and occupancy rates from the month effect model ranged from 0.300 (bobcat) to 0.898 (raccoon) and 0.068 (southern flying squirrel) to 0.987 (white-tailed deer), respectively (Table 3), and were similar to the detection and occupancy rates from the year effect model (Table A.1). Ten month effect models and 3 year effect models had DIC values > 5 and were most parsimonious according to pD values. The highest DIC ranked and most parsimonious month effect model incorporated Simpson's diversity index of patch types and distance to major road (DIC=1090.8; pD=320.9; Table 4), and the highest DIC ranked and most parsimonious year effect model incorporated Simpson's diversity index of patch types and agriculture clumpiness index (DIC=1090.7; pD=322.3; Table A.2). Agriculture clumpiness index had a polynomial relationship with alpha diversity; with highest alpha diversity estimates when agriculture

Table 5

Explanatory variables with degree terms identified as significant by the part distance-based redundancy test using data collected from remote camera surveys in the 16 southernmost counties of Illinois, USA, between January and April of the years 2008–2010. Habitat variables are defined in Table 1.

Variable	Degree term	*P*
GRASS PERCENT	First-degree	0.001
FOREST PROX	Second-degree	0.005
EDGE	First-degree	0.008
AG CLUMP	First-degree	0.025
FOREST PERCENT	First-degree	0.025
SIMPSON	Second-degree	0.034

was randomly dispersed (Fig. 2A). Simpson's diversity index of patch types had both a polynomial (Fig. 2A) and decreasing cubic relationship (Fig. 2B) with alpha diversity, such that alpha diversity estimates were higher with moderate levels of Simpson's diversity index of patch types. Distance to major road had a decreasing cubic relationship with mammalian alpha diversity, with alpha diversity estimates declining as distance to major road increased (Fig. 2B).

3.3. Partial analyses

Values for Jaccard's dissimilarity index between camera sites ranged from 0.111 to 1.000. The partial distance-based redundancy analysis indicated model results were significant ($F_{1, 352} =1.232$, $P < 0.001$), but only explained a small amount of the variation observed between sites. Constrained matrices and conditional matrices accounted for 13.1% and 4.8% of variation in beta diversity, respectively. Six terms assessing the relationship between explanatory variables and the dissimilarity matrix were identified as significant when the permutation test was applied to all terms (Table 5). The forward selection function identified 2 terms as significant: (1) second-degree term for forest proximity index ($F=2.8244$, $P = 0.002$), and (2) first-degree term for percentage forest cover ($F=10.716$, $P < 0.001$). The second-degree term for forest proximity index and the first-degree term for percentage forest cover explained 4.6% and 3.8% of beta diversity variation, respectively. The partial Mantel test indicated differences in beta diversity were weakly and positively correlated with forest proximity index ($r_s=0.130$, $P < 0.001$) and percentage forest cover ($r_s=0.130$, $P = 0.001$).

4. Discussion

We used novel modeling extensions to provide insight into the complex relationships between anthropogenic influences, habitat heterogeneity, and species richness of forest mammals at a large scale. Sites with moderate levels of habitat heterogeneity, represented by Simpson's diversity index of patch types, had highest alpha species richness. Furthermore, anthropogenic influences on the landscape, represented by distance to nearest major road and agriculture clumpiness index, appeared to increase alpha species richness by providing novel food resources and additional habitat for the generalist species that dominated our study. Forest-related variables were also influential on beta diversity, as expected (Joly and Meyers, 2001; Dechen Quinn et al., 2012; Lesmeister et al., 2015).

Detection and occupancy rates for study species partially agreed with previous research in southern Illinois; variation among studies may have been influenced by differing (1) scales of analysis (Wilson and Schmidt, 2015), (2) use of bait (Buyaskas et al., 2020; Randler et al., 2020), and (3) modeling approaches (Kéry and Royle, 2015). Pease et al. (2019) observed lower occupancy and detection rates for white-tailed deer, eastern gray squirrel, and raccoon, but this study was conducted across a much smaller portion (i. e., <20 km²) of southern Illinois. Cameras were not baited by Pease et al. (2019), which may have resulted in lower detection rates of raccoons compared to studies using baited camera stations. Furthermore, previous studies used single-species or 2-species co-occurrence occupancy modeling approach and reported higher occupancy rates for mesocarnivore species (Lesmeister et al., 2015; Morin et al., 2018). Alternatively, we used community occupancy modeling; Kéry and Royle (2015) noted different modeling approaches can provide widely differing results and yield new insights about relationships within the same system.

Our study was dominated by generalist species with the ability to thrive in diverse habitat types and resilience to fragmentation or disturbance. Ten of 13 study species (77% of total community composition) were considered generalists: bobcat (Nielsen and Woolf, 2002; Kolowski and Nielsen, 2008; Newbury and Hodges, 2018), coyote (Feldhamer et al., 2003; Thibault and Ouellet, 2005; Franklin et al., 2019), eastern cottontail (Feldhamer et al., 2003; Crawford et al., 2018), eastern gray squirrel (Williams, 2011; Amspacher et al., 2019), mouse sp. (Elliott and Root, 2010), raccoon (Rollins and Carroll, 2001; Kirby et al. 2016; Louppe et al., 2019), red fox (Kutschera et al., 2013; Reshamwala et al., 2018), striped skunk (Verts, 1967; Lesmeister et al., 2015; Amspacher et al., 2021), Virginia opossum (Allen et al., 1985; Magle et al., 2016; Greenspan et al., 2018; Walsh and Tucker, 2018), and white-tailed deer (Anstedt, 2016; Peebles-Spencer, 2016; Berry et al., 2019). Two study species (15% of total community composition) were considered forest specialists: gray fox (Feeney, 2000; Allen et al., 2021; Morin et al., 2022) and southern flying squirrel (Taulman, 2006; Rexroad, 2021). One study species (8% of total community composition) was considered an edge specialist: fox squirrel (Allen, 1982; Edwards et al., 1998; Amspacher et al., 2019). Despite their generalist behavior, forest cover is important to most of our study species. Gray squirrels can live in urban environments (Larson and Sander, 2022) but are often associated with denser forest cover (Edwards et al., 1998). White-tailed deer will opportunistically select habitat (Anstedt, 2016; Peebles-Spencer, 2016) but prefer forested habitat for thermal and escape cover (Harlow, 1984; Miranda and Porter, 2003). Contrastingly, the specialists within our community occasionally exploit habitat and

Table A1

Estimated occupancy (ψ) and detection (p) rates with standard error for mammalian species estimated from the year effect *N*-fold community occupancy model, using data collected from remote camera surveys in the 16 southernmost counties of Illinois, USA, between January and April of the years 2008–2010.

Species	Detection (p)	Occupancy (ψ)
Bobcat	0.299 ± 0.002	0.484 ± 0.004
Coyote	0.531 ± 0.001	0.782 ± 0.002
Eastern cottontail	0.658 ± 0.003	0.203 ± 0.002
Eastern gray squirrel	0.630 ± 0.001	0.795 ± 0.002
Fox squirrel	0.618 ± 0.002	0.438 ± 0.002
Gray fox	0.627 ± 0.003	0.121 ± 0.001
Mouse *sp.*	0.618 ± 0.004	0.070 ± 0.001
Raccoon	0.898 ± 0.001	0.974 ± 0.001
Red fox	0.565 ± 0.005	0.071 ± 0.001
Southern flying squirrel	0.660 ± 0.004	0.068 ± 0.000
Striped skunk	0.593 ± 0.001	0.268 ± 0.002
Virginia Opossum	0.847 ± 0.001	0.910 ± 0.001
White-tailed deer	0.853 ± 0.001	0.987 ± 0.000

Table A2

Deviance information criterion (DIC) and effective number of parameters (pD) for the year effect model relating estimated mammalian alpha diversity values of camera clusters to different habitat variables, using data collected from remote camera surveys in the 16 southernmost counties of Illinois, USA, between January and April of the years 2008–2010. Habitat variables are defined in Table 1.

Model	DIC	pD
SIMPSON+DT MAJOR RD	1090.7	322.3
RD LENGTH+DIST MU	1093.1	324.1
GRASS SHAPE+DIST MAJOR RD	1093.8	324.4

resources outside of their known preferences. Gray foxes, a highly forest-adapted species (Feeney, 2000; Allen et al., 2021; Morin et al., 2022), use forest edges near grasslands when hunting prey (Cooper et al., 2012; Cole, 2020), and fox squirrels, an edge specialist (Allen, 1982; Edwards et al., 1998; Amspacher et al., 2019), uses trees in dense forests for food and nesting.

Given the behavior and ecology of the mammalian community we sampled, our results were strongly affected by detection and occupancy of generalist species. Given many of these species were distributed ubiquitously across the study area, understanding relationships between occupancy, species richness, and habitat was difficult (MacKenzie et al., 2006), as widespread detection across varying sites with different habitats can cause underlying patterns about species richness to be obscured. However, we interpreted 3 and 6 habitat variables that were related to with alpha diversity and beta diversity, respectively. These variables were categorized into the following presumed influences on either alpha diversity or beta diversity: (1) habitat heterogeneity (i.e., Simpson's diversity index of patch types, percentage grassland area, and edge index), (2) anthropogenic influences (i.e., distance to major roads and agriculture clumpiness index), and (3) forest-related (i.e., forest proximity index and percentage forest cover).

Habitat heterogeneity, represented by Simpson's diversity index of patch types, has impacted mammalian diversity both positively (Bowland and Perrin, 1993; Medellin and Equihua, 1998; Ceballos et al., 1999; Tews et al., 2004) and negatively (August, 1983; Sullivan et al., 2000). Simpson's diversity index of patch types represents the probability that any 2 pixels selected at random would-be different patch types, where a patch is defined as an area of relatively homogeneous environmental conditions (McGarigal et al., 2002). In our study, a patch consisted of the same cover type (e.g., forest cover). Models incorporating this variable suggested moderate levels of habitat heterogeneity can positively influence alpha diversity, particularly for generalist species. Coyote (Riley et al., 2003), white-tailed deer (Dechen Quinn et al., 2012), Virginia opossum (Feldhamer et al., 2003), striped skunk (Amspacher et al., 2021), and eastern cottontail (Chapman et al., 1980) have all been positively associated with habitat heterogeneity; as sites with varying cover types and patches enable such generalist mammals to exploit different resources, while being tolerant to landscape fragmentation or disturbance (Devictor et al., 2008). As Simpson's diversity index of patch types occurred in both top models examining alpha diversity and was identified as a significant variable by the partial distance-based redundancy test, this variable likely exerts a strong influence on diversity across multiple metrics.

Edge index (Yates et al., 1997; Lidicker, 1999; Rosa et al., 2017) and percentage grassland area (Rich et al., 2016) have influenced mammalian diversity. Edge index is the total length (m) of patch edge/ha, where 0 indicates an entire landscape consists of a single patch (McGarigal et al., 2002); this variable is related to habitat heterogeneity, as it measures the relative size of the focal patch. Our hypothesis that variables related to patch size (e.g., edge index) would be correlated to beta diversity was supported. Edge index was identified as a significant variable influencing beta diversity. Given that many of our species were edge specialists, such as fox squirrel (Allen, 1982; Edwards et al., 1998; Amspacher et al., 2019), and generalists who use edge habitats, such as white-tailed deer (Dechen Quinn et al., 2012; Erb et al., 2012), eastern cottontail (Bertolino et al., 2011), striped skunk (Lesmeister et al., 2015; Amspacher et al., 2021), and Virginia opossum (Feldhamer et al., 2003), it is unsurprising that beta diversity would influenced by the amount of forest

edge present. Edge habitats provide varying cover and patches these species can exploit for different resources. Similarly, grasslands can provide additional habitat and cover, particularly for prey species, and thereby also attract predator species pursuing prey. For example, red foxes have been affiliated with grasslands (McDonald et al., 2008), as prey species, such as eastern cottontail, use grasslands (Fa et al., 1992; Crawford et al., 2018). Coyote abundance was higher in areas with grassland due to prey presence (e.g., white-tailed deer fawns; Rohm et al., 2007; Cherry et al., 2016), and grassland cover has been informative for modeling bobcat habitat statewide in Illinois (Woolf et al., 2002). As percentage grassland cover and edge index were only significant in 1 analysis, these variables appear to exert only minor influences on mammalian diversity in southern Illinois.

Anthropogenic influences, represented by agriculture clumpiness index and distance to major roads, are also known to positively (Racey and Euler, 1982; McKinney, 2002; Santini et al., 2018) or negatively (Riem et al., 2012, Newbold et al., 2015; Buffa et al., 2018) impact mammalian alpha diversity. However contrary to our hypothesis, both variables indicated low to moderate levels of anthropogenic influences increased mammalian alpha diversity. Agriculture clumpiness index was informative in a month effect model; this variable indicates the level of clustering among agricultural patches (McGarigal et al., 2002), and suggested randomly dispersed agriculture positively influenced mammalian alpha diversity. This was contrary to our original hypothesis that alpha diversity would be negatively related to agriculture. Rather, agriculture can provide additional resources for generalist mammals (Murphy et al., 1985; Beasley and Rhodes, 2010), or recreate edges and habitats such species were evolved to use (Koprowski, 1994). Within a matrix of largely natural habitat, agriculture can promote habitat heterogeneity and provide access to novel food resources or foraging opportunities (Santini et al., 2018). Occupancy of fox squirrels (Rizkalla et al., 2009), raccoons (Dijak and Thompson, 2000; Wilson and Nielsen, 2007), Virginia opossum (Blumenthal and Kirkland, 1976), and eastern cottontail (Swihart and Yahner, 1982) is positively linked with agricultural edges, while striped skunk occupancy has been positively related to higher levels of agriculture present (Lesmeister et al., 2015). Furthermore, mouse species are known to use tree lines, shelterbelts, and fencerows in agricultural habitats (Rizkalla et al., 2009). Therefore, agriculture that is present but not dominant at a site would likely attract many of our study species. Similarly, roads may also create heterogeneity that attracts mammalian species as our top year effect model examining alpha diversity identified distance to nearest major road as influential on biodiversity with lowest diversity furthest from major roads. Roads also provide foraging opportunities and potential corridors for white-tailed deer (Erb et al., 2012) and coyotes (Tigas et al., 2002), thus attracting these species to sites closer to roads. Additionally, densities of small mammals can be higher near roads given low risk of mortality due to (1) low movement rates across roads and (2) road avoidance by predators (Adams and Gies, 1983; Fahrig and Rytwinski, 2009). Both agriculture clumpiness index and distance to major road were highest ranked and part of the most parsimonious models for assessing alpha diversity, and agriculture clumpiness index was identified by the partial distance-based redundancy test as being influential on beta diversity, suggesting that anthropogenic influences affect biodiversity across multiple measurements.

Our hypothesis that forest cover related variables would influence mammalian alpha and beta diversity was partially supported. Forest proximity index represents the mean sum of forest patch size (ha) divided by the squared distance (m) from the focal patch and increases as forest patches are closer and more contiguous (McGarigal et al., 2002). While we interpreted no support for the influence of these variables on alpha diversity, both the partial distance-based redundancy analysis and partial Mantel tests reported the influence of forest cover and forest proximity on beta diversity. The weak, positive correlations between beta diversity and percentage forest cover and forest proximity index demonstrated the reliance on forests by our study species (Harlow, 1984; Lanham, 1998; Joly and Meyers, 2001) and supported our hypothesis that larger forest patches with higher forest cover would be positively correlated with beta diversity. The correlation between beta diversity and these forest related variables was likely due to the reliance of many study species on forested sites for cover and food (Harlow, 1984; Edwards et al., 1998; Taulman, 2006; Anstedt, 2016; Morin et al., 2022). Gray fox use forest stands to escape predation via climbing trees (Lesmeister et al., 2015; Morin et al., 2022), while southern flying squirrels (Rexroad, 2021), fox squirrels (Amspacher et al., 2019), and eastern gray squirrels (Edwards et al., 1998) use forested sites for den-making and food. Even larger species, such as white-tailed deer, use forested areas for food and thermal or escape cover (Harlow, 1984).

5. Conclusion

Our study provides evidence for the influence of habitat heterogeneity, anthropogenic influences, and forest-related variables on mammalian occupancy and alpha and beta diversity, in addition to demonstrating the importance of examining biodiversity at multiple scales and the usefulness of hierarchical modeling approaches to investigate ecological questions. While total forested area in Illinois has remained stable over recent years, changes in land ownership and land use for agriculture has resulted in shifting distributions of forest patches (Crocker et al., 2017). Additionally, southern Illinois contains multiple areas designated as Wildlife-Urban Interfaces, increasing the risk of forest fragmentation (Radeloff et al., 2005; Crocker et al., 2017). Hierarchical modeling provides a novel approach to investigate how such changes influence natural communities and alter biodiversity (Royle and Dorazio, 2009; Zipkin et al., 2009). By allowing researchers to examine difficult ecological questions and test increasingly complex hypotheses about the natural world, hierarchical modelling has proven to be an effective tool in researchers' toolbox. Differing metrics of biodiversity have similarly proven to be effective tools in ecological research (Magurran, 2021). By examining how environmental characteristics influence different metrics of biodiversity, researchers are able to gain a more comprehensive understanding of current ecological processes.

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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.

Data availability

The authors do not have permission to share data.

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Appendix A. Year effect modeling results

See appendix Table A1 and Table A2.

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