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ISLAND BIOGEOGRAPHY OF SMALL MAMMALS AND ASSOCIATED

ECTOPARASITES IN THE OZARK GLADES

A Masters Thesis

Presented to

The Graduate College of

Missouri State University

In Partial Fulfillment

Of the Requirements for the Degree

Master of Science, Biology

By

Emily M. Beasley

December 2017

ISLAND BIOGEOGRAPHY OF SMALL MAMMALS AND ASSOCIATED

ECTOPARASITES IN THE OZARK GLADES

Biology

Missouri State University, December 2017

Master of Science

Emily M. Beasley

ABSTRACT

Island Biogeography Theory (IBT) explains and quantifies broad-scale ecological patterns among islands and isolated habitat patches. IBT predicts that the number of species per habitat patch varies as a function of area and isolation as a result of local colonization and extinction. IBT has been extended to habitat islands and hosts as islands for their associated parasites. In the latter system, host body mass acts as a substitute for island area, whereas host population density is used as a measure of isolation. Using the fragmented Ozark glades and the small mammals therein as a model system, I 1) used a multi-species occupancy model to correct for imperfect detection of species and generate species richness estimates, and 2) used the model to evaluate the effects of patch area, isolation, and shape on species richness. I then considered the mammalian hosts of the glades as islands for their associated ectoparasites, and evaluated 1) the effects of host population size on ectoparasite diversity metrics, and 2) tested for associations between mammalian host and ectoparasite communities. I captured a total of 8 mammal species and 7 ectoparasite orders in May–July 2016–2017. Glade area, but not isolation or shape, affected mammalian species richness. Ectoparasite richness and diversity were positively affected by host population size, and strong host-ectoparasite associations were present. IBT explains many of the patterns in small mammal and ectoparasite richness in the glade network, but matrix effects and host specificity may limit its applicability in this system.

KEYWORDS: Island Biogeography Theory, small mammals, ectoparasites, hierarchical occupancy models, Ozark glades

This abstract is approved as to form and content

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Sean P. Maher, PhD
Chairperson, Advisory Committee
Missouri State University

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OVERVIEW

Research on islands and island-like systems has influenced biological theory for over a century. Beginning in the 19th century with the work of Charles Darwin and Alfred Russell Wallace, island research has provided key insights into mechanisms of evolution (Clegg et al. 2002, Darwin 1859, Rowe et al. 2016, Wallace 1880), habitat fragmentation and conservation (Laurance 2009, Pimm 1991), and metacommunity dynamics (Diamond 1975, Gotelli 2000, Hubbell 2001). Islands have several properties that make them ideal for ecological study, including clearly defined boundaries, presence of local (within-island) and regional (across archipelago) processes, and greater simplicity than mainland systems (Santos et al. 2016). One crucial theory that arose from island research is Island Biogeography Theory (IBT). First proposed by Munroe (1948), the theory went largely unnoticed until it was independently formulated by MacArthur and Wilson (1963, 1967; Brown and Lomolino 1989). This theory quickly became a paradigm of spatial ecology and has heavily influenced other areas of ecology in decades since (Lomolino 2000, Santos et al. 2016).

IBT explains and quantifies patterns of large-scale ecology among oceanic or habitat islands (MacArthur and Wilson 1967). IBT hypothesizes that species richness, or the number of species present on an island, depends on island size, isolation from the mainland and other islands, and habitat complexity as a result of varying rates of colonization and extinction (MacArthur and Wilson 1967). Larger islands will host more species than smaller islands due to lower rates of extinction, and isolated islands will host fewer species than less isolated islands due to reduced colonization rates (Figure 1). The
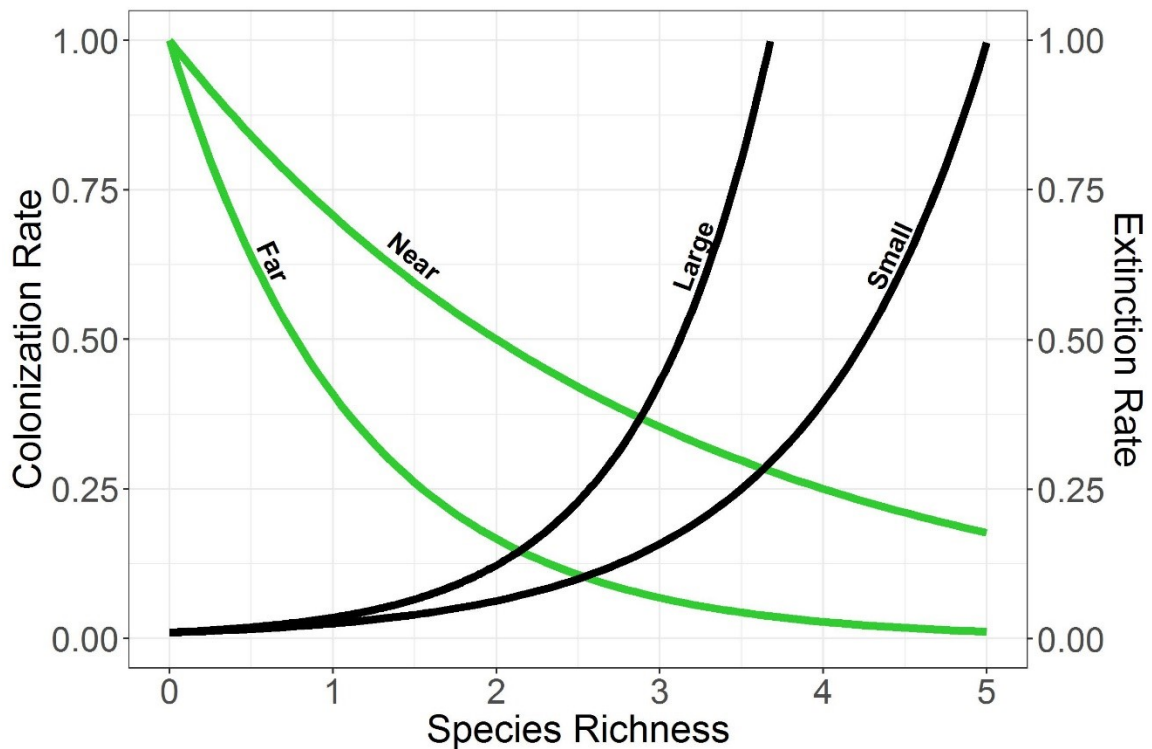
Figure 1. Species richness on islands is determined by colonization and extinction rates, which in turn are affected by island isolation and area. Species richness of an island is predicted by the point at which the colonization and extinction curves intersect. Figure modified from MacArthur and Wilson (1963).

theory also predicts that the species richness on each island will ultimately reach a dynamic equilibrium, where the total species richness will remain constant but species composition will fluctuate due to colonization and extinction of individual species.

The Ozark glades, open and rocky habitats embedded within the surrounding forest, can be considered habitat islands embedded in a forest "sea" (Figure 2). Shallow soils and the absence of a developed tree canopy characterize glades (Heikens 1999, Kucera and Martin 1957, Nelson and Ladd 1983). Typically, glades are arid relative to the surrounding forest but may contain seasonal seeps or pools (Nelson 2010). Glades
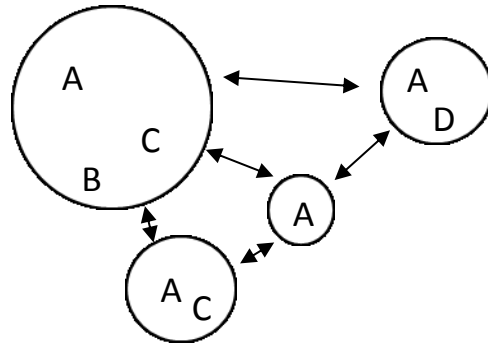
Figure 2. Conceptual diagram of species A–D in a series of habitat islands. Area and isolation determine species richness of habitat islands in a manner similar to oceanic islands. Arrows represent dispersal routes.

vary in size and quality due to the underlying bedrock and fire frequency (Ladd 1991, Nelson and Ladd 1983, Nelson et al. 2013). Glades support a variety of small mammals including habitat generalists such as the white-footed mouse (*Peromyscus leucopus)* and Eastern wood rat (*Neotoma floridana)*, as well as open-canopy specialists such as the Texas mouse (*P. attwateri*) and Fulvous harvest mouse (*Reithrodontomys fulvescens*). The small mammal communities, in turn, host a suite of ectoparasites such as fleas (Order Siphonaptera) and ticks (Order Ixodida). The patchy distribution of the glades and the diversity of small mammal and ectoparasite species they contain makes them a suitable system to examine IBT.

My research tests the predictions of IBT in two hierarchically organized assemblages in the Ozark glades. The first chapter implements a multi-species occupancy model to correct for imperfect detection of small mammals, a common source of sampling error in ecology (MacKenzie et al. 2005). I then used the detection-error corrected community data to evaluate the effects of area, isolation, and other patch characteristics on species occupancy and richness. The second chapter treats the small mammals as a series of habitat patches and evaluates the roles of host characteristics on

ectoparasite community composition. Because ecological processes are often dependent on scale (Wiens 1989), evaluating IBT in the context of the hierarchically organized small mammals and ectoparasites will provide insight on the applicability of broad-scale theories to different levels of community organization.

APPLYING ISLAND BIOGEOGRAPHY TO SMALL MAMMALS IN THE

OZARK GLADES WHILE ACCOUNTING FOR IMPERFECT DETECTION

Introduction

Island biogeography theory (IBT) predicts that species richness on an island increases with area and decreases with isolation due to higher rates of extinction on small islands and lower rates of colonization on distant islands (MacArthur and Wilson 1963, 1967). Shortly after its publication, IBT was applied to small mammals on isolated mountaintops in the Great Basin, in which area but not isolation had a significant effect on species richness (Brown 1971). IBT has been extended to a variety of habitat types in years since, with varying results (Belmaker et al. 2007, Fox and Fox 2000, Lomolino 1984, Watling and Donnelly 2006). Although the species-area relationship predicted by IBT is typically present in terrestrial islands (Fox and Fox 2000, Lomolino 1984, Watling and Donnelly 2006; but see Cook et al. 2002), isolation effects tend to be less consistent for terrestrial habitat patches (Watling and Donnelly 2006, but see Prevedello and Vieira 2010).

The discrepancy in isolation effects between oceanic and habitat islands largely is due to differences between the intervening matrix, the habitat or habitats surrounding the focal patches (Cook et al. 2002, Evans et al. 2017, Ewers and Didham 2006, Ricketts 2001). Matrix types between habitat islands vary considerably in their permeability to dispersing individuals (Evans et al. 2017, Ewers and Didham 2006, Kupfer et al. 2006, Prevedello and Vieira 2010), and many habitat islands are embedded in a heterogeneous matrix consisting of a variety of habitat types (Biswas and Wagner 2012, Deans and

Chalcraft 2016, Kupfer et al. 2006, Ricketts 2001). In addition to variation in matrix permeability, isolation effects can be masked by spill-over of species from the matrix to the habitat patch of interest (Brown and Dinsmore 1988, Cook et al. 2002). Thus, effective isolation between habitat patches is more complex than geographic distance alone.

The Ozark glades, open and rocky habitats embedded within the surrounding forest, can be considered habitat islands embedded in a forest matrix. Shallow soils, the absence of a developed tree canopy, and aridity relative to the surrounding forest characterize glades (Heikens 1999, Kucera and Martin 1957, Nelson 2010, Nelson and Ladd 1983). Glades require periodic fires to maintain ecosystem health (Ladd 1991, Nelson and Ladd 1983, Nelson et al. 2013); isolation therefore has the potential to affect recolonization after each disturbance event. Glades support a variety of small mammals including habitat generalists such as the white-footed mouse (*Peromyscus leucopus*) and Eastern wood rat (*Neotoma floridana*), as well as open-canopy specialists such as the Texas mouse (*P. attwateri*) and Fulvous harvest mouse (*Reithrodontomys fulvescens*). The patchy distribution of the glades and the diversity of small mammal species they contain makes them a suitable system for testing predictions of IBT.

Based on IBT, I predict that species richness will be a function of patch area; specifically that there will be a positive effect of area due to lower extinction rates on larger islands. While IBT predicts a negative effect of isolation on richness, I predict that the presence of several generalist species and permeability of the matrix will diminish or negate the effect of isolation on richness. Because patch shape, here defined as the amount of edge relative to area, should be correlated with habitat complexity, I predict

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that it will affect species-specific occupancy, but the direction and magnitude of these effects will vary due to variation in life history of the species in the community. Alternatively, if species are essentially neutral in life history, there should be a positive effect of shape on occupancy given IBT. Because IBT predicts that small islands have higher rates of extinction than large islands, I predict that small islands will exhibit a higher rate of temporal turnover between sampling years.

Using a multi-species occupancy model, or MSOM, I 1) estimated occupancy and detection probability for each small mammal species in the glade network, 2) used these probabilities to correct for imperfect detection and generate species richness estimates and occurrence matrices, and 3) evaluated the effects of environmental covariates on individual species and the community as a whole. I then used the species richness estimates and occurrence matrices generated by the model to test for relationships between the environmental covariates and species richness and temporal turnover.

Methods

Data collection. I sampled small mammals from a network of sixteen glades in southwest Missouri, spanning an east-west distance of approximately 125 km within the Ozark Highlands ecological section (Nigh and Schroeder 2002, Figure 3). The glades were located within four state or federal management units: Roaring River State Park (RRSP- 4 glades), Mark Twain National Forest Ava-Cassville District (MTNF- 3 glades), Drury-Mincy Conservation Area (DMCA- 5 glades), and Caney Mountain Conservation Area (CMCA- 4 glades). Glades were selected based distribution among management units and size; glades without sufficient length for a 250 m linear transect were excluded
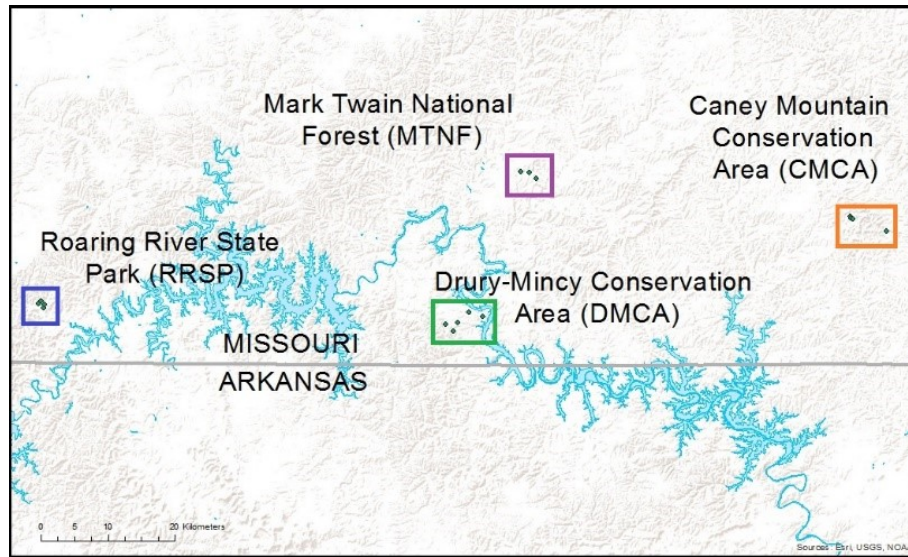
Figure 3. Map of sampling sites. Each point represents a glade.

from sampling. All glades were sampled in May–July 2016 and resampled in May–July 2017.

I used a combination of Sherman live-traps, 7.62×8.89×22.86 cm ("regular") and 10.16×11.43×38.10 cm ("large"), baited with sunflower seeds and/or a peanut-butter oat mixture, to capture small mammals. To standardize trapping effort, each glade was sampled using a ~250 m linear transect, with trap stations set ~10 m apart. Two traps were placed at each station and arranged to maximize capture efficiency (e.g. along runways such as fallen logs or rock ledges). I randomly selected 12 of 25 stations to have one large and one regular Sherman trap; the other 13 stations had two regular Sherman traps. I used GPS receivers to record positions at the beginning, midpoint, and end of each transect. I opened traps each evening and checked them the following morning; each transect was sampled for a period of 4 consecutive trap days.

Upon checking traps, captured mammals were transferred to a cloth bag and handled according to American Society of Mammalogists guidelines (Sikes 2016).

Individuals were identified to species, sexed, and weighed, and standard external measurements (ear length, tail length, and right hind foot length) were taken. Prior approval for this project was obtained from the Missouri State University Institutional Animal Care and Use Committee (IACUC, ID #16-020.0).

Patch area and perimeter were computed by recording the perimeter of each glade with a GPS unit and then converting this output to a polygon shapefile using ArcGIS 10.3.1. Glade area was calculated using the R packages rgdal and rgeos (Bivand et al. 2016, Bivand and Rundel 2017). Isolation between glades was determined by calculating pairwise distances between glade centroids and the shortest pairwise distances between glade edges in R using the rgdal and rgeos packages. Because the longitudinal range of the management units was much greater than the latitudinal range, pairwise distances were only calculated between glades within the same management unit to prevent biased isolation measures of glades near the edges of the longitudinal gradient. Thus, "isolation" as described here is a modified version of the two-or-more nearest neighbors metric (Moilanen and Nieminen 2002). Pairwise distance values were used to calculate standardized distance (Krasnov et al. 2010, Equation 1). Differences in patch shape were quantified using the corrected perimeter-area ratio (Farina 2006, Equation 2).

$$D_{ST} = \frac{D_C}{D_C - D_E}$$

Equation 1. Standardized distance (D_{ST}), where D_C = pairwise distance between centroids and D_E = pairwise distance between edges.

$$CPA = \frac{0.282 \times L}{\sqrt{A}}$$

Equation 2. Corrected perimeter-area ratio (CPA), where L = perimeter length and A = area. Modified from Farina (2006).

Vegetation data were collected to account for habitat heterogeneity between glades. Though IBT assumes habitat islands are homogenous with respect to environmental filters other than area and isolation, variation in insular species composition may be a result of variation in environmental characteristics such as vegetation composition (Lomolino 2000). Vegetation data were collected by placing a 1 m² quadrat at ten randomly selected trap stations; the percent cover for grasses, forbs, shrubs, trees, and total cover was recorded. The dimensionality of the vegetation data was reduced using a principal components analysis (PCA) using the prcomp function in R.

Multi-Species Occupancy Model. Area and isolation effects on species richness can be masked if species are detected imperfectly during sampling (Figure 4). Detection rates of species are variable due to species traits and landscape characteristics (Iknayan et al. 2014), resulting in biased estimates of species occurrence for rare or hard-to-detect species (MacKenzie et al. 2005). Recent advances in statistical methodology and
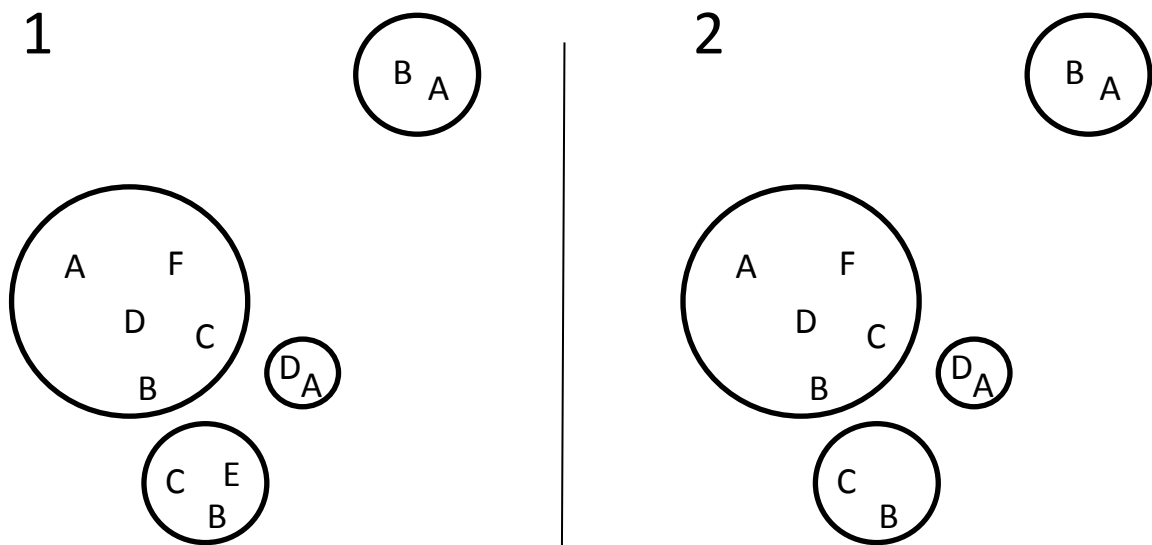
Figure 4. (1) Network of islands inhabited by species A–F. When species are imperfectly detected, such as species E in (2), effects of area and isolation can be masked due to lower observed richness counts.

computing have led to community-level hierarchical models (or multi-species occupancy models, MSOMs) that leverage information from across the community to estimate species-specific occupancy and detection (Dorazio and Royle 2005, Zipkin et al. 2010).

I constructed a single-season hierarchical model in which occurrence of species i at site j, denoted Z_{ij}, is equal to 1 if the species is present at the site and 0 otherwise. Occurrence is assumed to be an outcome of a Bernoulli trial, $Z_{ij} \sim Bern(\Psi_{ij})$, where Ψ_{ij} is the probability that species i is present at site j. The true occupancy state Z_{ij} usually is unknown and imperfectly observed, which leads to confounded estimates of Ψ_{ij}. However, when site j is sampled multiple times over a short period, observation data can be incorporated into a detection model that distinguishes between true species absences and non-detection (MacKenzie et al. 2002).

The detection model is defined as $x_{ijk} \sim Bern(p_{ijk} * Z_{ij})$, where p_{ijk} is the probability of detecting species i at site j during sampling period k, given that species i is present at site j. The dependency of the detection model on the occupancy state ensures that detection probability is zero when the species is not present at a site.

Because MSOMs leverage information from the entire community, rare or poorly detected species which lack sufficient data to model individually can be analyzed by "borrowing" data from the community as a whole (Iknayan et al. 2014). This is done by assuming each species-level parameter is drawn from a common community-level distribution, or "hyper-parameter" (Kéry and Royle 2009, Zipkin et al. 2009). Nondetected species for which there are no data can also be represented by including all-zero encounter histories in a process known as zero augmentation (Kéry and Royle 2009, Royle et al. 2007). Thus, MSOMs generate more accurate estimates compared to single-

species models by accounting for the similarity in the ecology of all members (Link and Sauer 1996, Sauer and Link 2002, MacKenzie et al. 2005).

To account for potential differences in occupancy between sampling years, I used an unpaired-site model (Tingley and Beissinger 2009, Tingley et al. 2012) in which "year" is included as a covariate in a single-season model. This modeling framework is particularly useful for data sets with few sites and/or when there are few changes in occupancy. In addition to year, I incorporated four environmental covariates into the model using the logit-link function (Dorazio and Royle 2005):

$$logit(\Psi_{ij}) = u_i + \alpha 1_i Area_j + \alpha 2_i Isolation_j + \alpha 3_i Shape_j + \alpha 4_i Year_j$$

in which $\alpha 1_i$–$\alpha 3_i$ are the effects of the site-level covariate on the occupancy probability of species i. Detection probability p_{ijk} was modeled in a similar manner:

$$logit(p_{ijk}) = v_i + \beta 1_i Date_{jk}$$

where v_i is the species-specific intercept and $\beta 1_i$ is effect of Julian date on the detection probability of species i. With the exception of year, all covariates were scaled to have a mean zero and a standard deviation of one. Model parameters were estimated using a Bayesian analysis and uninformed priors for the community-level hyperparameters in the program OpenBUGS (Spiegelhalter et al. 2007) based on code modified from Zipkin et al. (2010). Significance of covariates were evaluated using the 95% credible interval (CI); CIs that did not overlap zero were considered significant.

I used three chains of length 16000 including a burn-in of 8500 and posterior chains were thinned by 35 to reduce autocorrelation. I evaluated convergence using the R-hat statistic (Gelman and Rubin 1992); convergence is reached when R-hat is near 1.

Statistical Analysis. Species richness, including unobserved species, was

calculated for each glade by summing the estimated species in the occurrence matrix

(Zipkin et al. 2010). Because this modeling framework did not explicitly include

relationships between site-level richness and covariates, effects of covariates on species

richness were evaluated using a general linear model (GLM) using patch area, isolation,

and shape as predictor variables. Year was included in each GLM to account for temporal

variation in richness. Detection error-corrected species richness estimates derived from

the model were used as the response variable.

IBT predicts that small islands have higher rates of extinction than larger islands;

thus, small islands should also exhibit a higher rate of temporal turnover. To test this

prediction, I first used the occupancy and detection probabilities estimated by the model

to generate 22,500 occurrence matrices for each year. I calculated the Jaccard index to

compare the two years using the R package betapart (Baselga and Orme 2012); a large

value of the Jaccard index indicates greater similarity than a smaller value (Jaccard

1901). I tested for associations between patch area and Jaccard values using Spearman's

correlation coefficient. I also used Spearman's correlation coefficient to test for

associations between Jaccard index values and patch isolation and shape. Confidence

intervals were calculated using a general additive model (GAM).

To determine whether differences between years were due to species replacement

or species gain/loss, I used the package betapart to determine the amount of turnover (i.e.

replacement) and nestedness (i.e. gain or loss) between years. To test whether species

nestedness was greater than expected by chance, I treated the contributions of the two

variables as the outcome of a Bernoulli trial in which a success occurred when nestedness

was greater than turnover. The probability of success was set at 0.5. All analyses were carried out in R version 3.3.1 (R Core Team 2016) unless otherwise noted.

Results

I captured a total of 344 individuals representing eight species in the glade network (Table 1). The most frequently detected species was *Neotoma floridana,* which was detected on 11 glades in 2016 and 8 glades in 2017; the least frequently detected species was *Tamias striatus* which was detected on 3 glades in 2016. Overall, detections in 2017 were less than in 2016 across all mammal species.

Glades ranged in size from approximately 3,500–92,000 m^2. The PCA of the vegetation data yielded two principal components with an eigenvalue greater than 1, which together explained 70.8% of the variation in the vegetation data (Figure 5). PC1 and PC2 were correlated with patch area and shape, respectively, so vegetation data were not included in the model.

The MSOM yielded an estimate of 8.67 species across the region. Year was the only significant occupancy covariate; all species had lower occupancy in year 2 (Figure 6). There was strong evidence for a community-wide effect of area on occupancy (Estimate, 75% CI), although there were no significant species-specific effects of area. *Peromyscus attwateri* and *P. leucopus* demonstrated negative responses to patch shape

(i.e. occupancy probability was higher in glades with less edge), whereas *Sigmodon hispidus* demonstrated a positive response to shape (Figure 7).
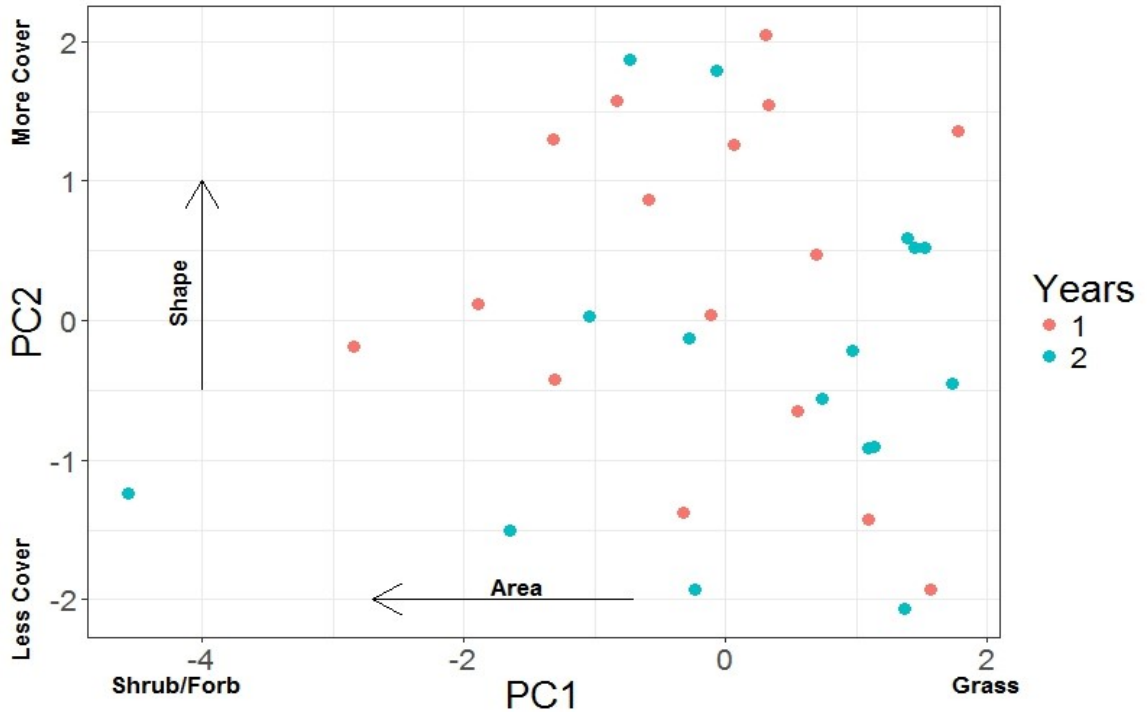
Figure 5. Results of the PCA for vegetation data. PC1 and PC2 explained a cumulative 70.8% of the variation in the data. Each point represents a glade; colors denote years. PC1 was negatively correlated with area; PC2 was positively correlated with shape.

The general linear model was significant (F = 12.99; df = 4, 27; $P < 0.001$) and explained 60.7% of the variation in species richness. Coefficients for area ($\beta = 1.898$, t = 2.469, df = 27, $P = 0.020$) and year ($\beta = -2.277$, t = -6.305, df = 27, $P < 0.001$) were significant (Figure 8), but coefficients for isolation and patch shape were not different from zero ($\beta = -0.038$, t = -0.244, df = 27, $P = 0.876$; $\beta = 0.014$, t = 0.028, df = 27, $P = 0.977$, respectively).

Table 1. Occupancy of mammal species at each site. Presences denoted by an "X".

	Site	*Peromyscus attwateri*	*Reithrodontomys fulvescens*	*Peromyscus leucopus*	*Sigmodon hispidus*	*Peromyscus maniculatus*	*Neotoma floridana*	*Tamias striatus*	*Sylvilagus floridanus*	Observed Richness	Estimated Richness
Year 1	0			X	X		X			3	3.54
	1	X		X	X	X	X		X	6	6.16
	2	X		X	X	X	X		X	6	6.15
	3	X			X		X		X	4	4.14
	4	X		X		X	X	X		5	5.39
	5			X	X	X	X	X		5	5.43
	6		X	X	X	X	X			5	5.28
	7	X		X	X	X				4	4.81
	8	X			X		X			3	3.51
	9	X					X			2	2.85
	10	X								1	1.96
	11			X		X				2	2.63
	12		X	X	X	X				4	4.51
	13		X	X	X	X				4	4.62
	14	X	X	X	X	X	X	X		7	7.33
	15	X		X	X	X	X			5	5.33
Year 2	0			X	X	X				3	3.50
	1				X		X			2	2.18
	2	X			X		X			3	2.79
	3	X			X					2	2.67
	4			X		X				2	2.41
	5			X		X				2	2.30
	6			X		X	X			3	3.09
	7									0	1.28
	8						X			1	1.19
	9	X					X		X	3	3.03
	10	X								1	1.39
	11	X					X			2	2.12
	12									0	1.33
	13			X						1	1.38
	14		X		X		X			3	3.40
	15		X		X		X			3	3.14
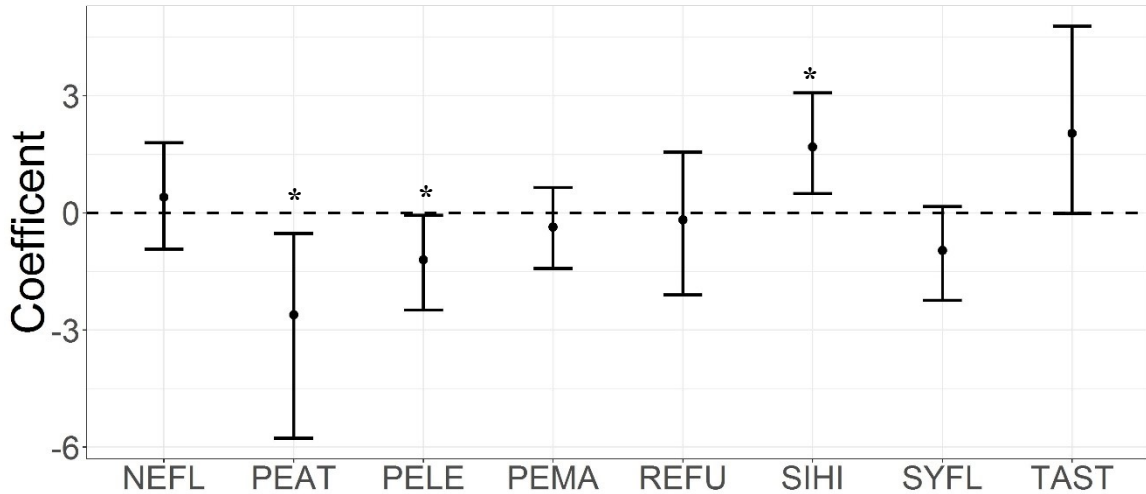
Figure 6. Species-level responses to year. Error bars represent the 95% credible interval; error bars which do not overlap zero (dashed line) are considered significant. Species abbreviations are as follows: NEFL *N. floridana*, PEAT *P. attwateri*, PELE *P. leucopus*, PEMA *P. maniculatus*, REFU *Reithrodontomys fulvescens*, SIHI *Sigmodon hispidus*, SYFL *S. floridanus*, TAST *Tamias striatus*.
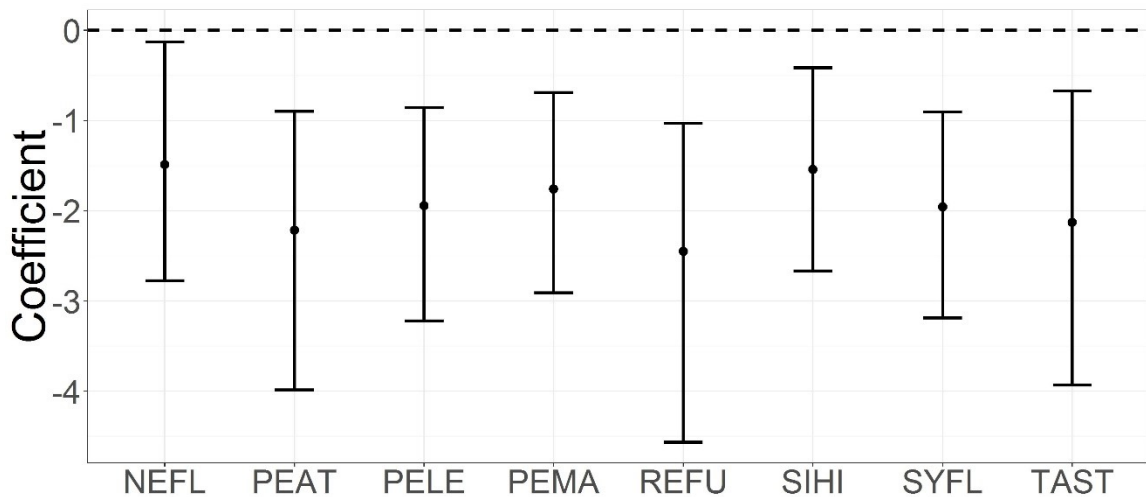
Figure 7. Species-level responses to patch shape. Negative values for shape correspond to a low perimeter/area ratio (less edge), positive values a high ratio (more edge). Error bars represent the 95% credible interval; error bars which do not overlap zero (dashed line) are considered significant. Significant responses are denoted by an asterisk (*). Species abbreviations are as follows: NEFL *N. floridana*, PEAT *P. attwateri*, PELE *P. leucopus*, PEMA *P. maniculatus*, REFU *R. fulvescens*, SIHI *S. hispidus*, SYFL *S. floridanus*, TAST *T. striatus*.
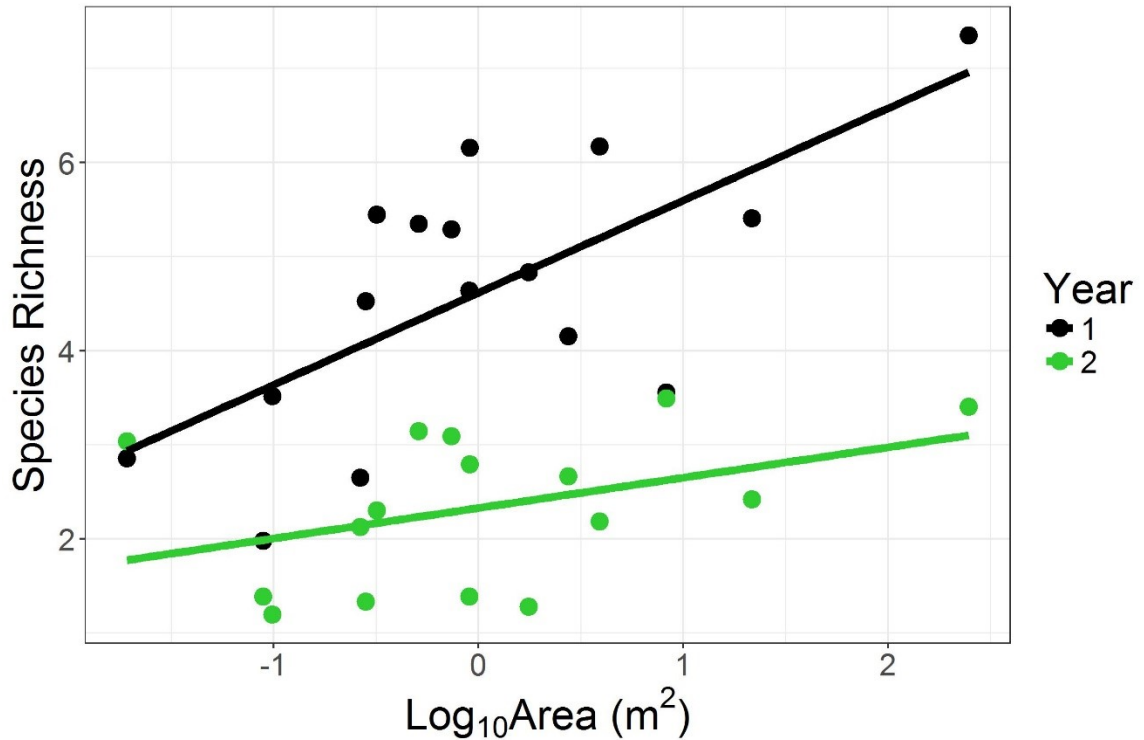
Figure 8. Site-level species richness plotted against log-transformed area. Species richness increased with patch area for both years ($\beta = 1.898$, t = 2.469, $P = 0.020$). Year 2 also had significantly lower richness than year 1 ($\beta = -2.277$, t = -6.305, $P < 0.001$).

The mean Jaccard similarity index for each site ranged from little turnover ($J = 0.096$) to nearly complete turnover ($J = 0.961$). There were no significant associations between Jaccard values and patch area ($\rho = 0.038$, $P = 0.891$) or patch shape ($\rho = -0.45$, $P = 0.082$). There was a significant positive relationship between the Jaccard values and isolation ($\rho = 0.532$, $P = 0.036$, Figure 9). There was significantly greater nestedness than turnover than predicted by chance ($P = 0.038$).
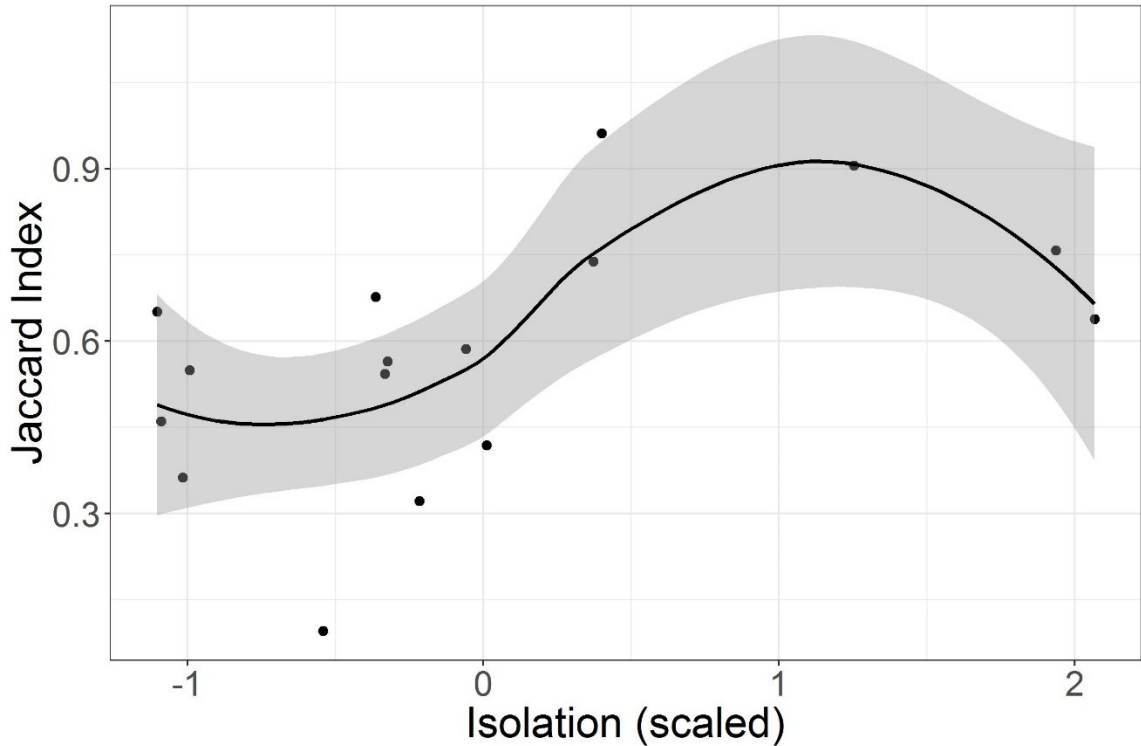
Figure 9. Jaccard index values plotted as a function of isolation. Shading represents the 95% confidence interval as determined by a GAM.

Discussion

Consistent with predictions of IBT, patch area had a significant effect on species richness and there was evidence for an effect on community-wide occupancy. However, area did not significantly influence the occupancy probability of individual species. Although this finding seems counterintuitive, it is consistent with the neutrality assumption of IBT. Neutrality in the context of IBT means that all species are assumed to be ecologically equivalent (Bell 2001, Hubbell 2001, MacArthur and Wilson 1967), and stochastic processes rather than environmental filters determine community structure (Cottenie 2005, Hubbell 2001, Leibold et al. 2004). The lack of significant signal for the

species-specific area covariate suggests the patterns in species richness likely are the result of varying rates of stochastic extinction.

Isolation effects on occupancy and species richness were not significant, a common finding in studies of habitat islands (Brown 1971, Cook et al. 2002, Watling and Donnelly 2006). In the glade network, isolation effects were probably masked by colonization of generalists such as *N. floridana* and *P. leucopus* from the matrix. Additionally, nearest-neighbor isolation metrics such as the one used here frequently are inferior to other types of metrics due to oversimplification of the landscape, especially when the matrix is heterogeneous (Biswas and Wagner 2012, Kindlmann and Burel 2008, Moilanen and Nieminen 2002, Ricketts 2001). Isolation metrics which account for heterogeneity in the matrix, such as landscape friction (McRae et al. 2008),could provide a more accurate picture of isolation effects, but also require assumptions of metrics of conductance and resistance.

The lack of significant associations between patch area and turnover is not consistent with the predictions of IBT. The significant relationship between the Jaccard index and patch isolation indicates that more isolated glades were more similar, and therefore experienced less turnover, between years. Lower colonization rates on more isolated islands as predicted by IBT could explain this pattern. Additionally, differences between years were due more to species nestedness than turnover. Based on this result and the lower occupancy in 2017 derived from the model (Figure 7), differences between years were primarily due to species loss.

Patch shape, usually in the form of edge effects, also can influence species richness and turnover. Species richness can increase with increasing edge due to co-

occurrence of focal habitat and matrix species (Bátary et al. 2014, Guirado et al. 2006, Ingham and Samways 1996, Magura 2002) or decrease due to behaviors such as edge avoidance by certain species (Besnard et al. 2016, Bieringer and Zulka 2003, Orrock and Danielson 2005). Additionally, increasing edge increases the probability that the patch will be encountered by a dispersing individual (Collinge and Palmer 2002) and reduces population persistence (Bevers and Flather 1999, Van Kirk and Lewis 1999), thereby increasing the amount of turnover in a habitat patch. However, individual species responses to patch shape often differ (Figure 7), and the inconsistency of shape effects in the literature reflects this variation (Ewers and Didham 2006).

It should be noted that there are many criticisms of previous attempts to study turnover. Artificially inflated turnover rates, termed pseudoturnover (Nilsson and Nilsson 1983), are usually the result of sampling error. This error can be a result of poor study design, such as when sampling methods are inconsistent (Abbott 1983, Gilbert 1980, Nilsson and Nilsson 1982) or because of variation in detectability between species (Nilsson and Nilsson 1983). Using MSOMs to generate presence-absence matrices that have been corrected for detection error reduces the amount of pseudoturnover in the data, allowing for more accurate estimates of turnover.

Multi-species occupancy models can be a powerful tool for conservation. By assuming that occupancy and detection probabilities of each individual species are drawn from a common distribution, rare species for which data are sparse can be modeled with reasonable accuracy by deriving information from the entire community (Iknayan et al. 2014, Zipkin et al. 2009, 2010). The ability to evaluate rare species in the context of the community, as well as the use of occupancy rather than abundance data, allows for more

efficient use of data than single-species models and can reduce the time and cost necessary for effective biological monitoring (Manley et al. 2005, Rich et al. 2017, Zipkin et al. 2009).

The hierarchical framework used in MSOMs is highly flexible and can be readily applied to a variety of situations (Dorazio and Royle 2005). MSOMs have been extended to quantifying range shifts in response to climate change (Tingley et al. 2012), accounting for open communities by allowing for periods of immigration and emigration (Kéry et al. 2009), predicting species occurrences at unsampled sites (Zipkin et al. 2012), evaluating the effects of land use changes on occupancy (Goijman et al. 2015), and integrating occupancy data from multiple spatial scales (Rich et al. 2017). The efficiency and adaptability of MSOMs provides a solid framework for investigating patterns in species occupancy and informing management decisions.

A natural extension of MSOMs is the construction of multi-species abundance models, or MSAMs (Iknayan et al. 2014). This modeling framework, which is a multi-species version of the N-mixture model (Royle 2004), estimates (1) the abundance of a species in each site and across the entire metacommunity, and (2) the probability of detecting an individual of that species (Dénes et al. 2015, Guillera-Arroita 2017, Iknayan et al. 2014). The use of MSAMs to reduce detection error in abundance data allows for more accurate tests of abundance-based frameworks such as Hubbell's neutral theory of biodiversity and biogeography (here "neutral theory", Hubbell 2001) and the metacommunity concept (Leibold et al. 2004). Neutral theory, which arose from IBT, predicts that patterns of species abundance in a series of habitat patches arise as a result of stochastic colonization and extinction (Bell 2001, Hubbell 2001). Like IBT, neutral

theory assumes ecological equivalence among members of the network of habitat

patches, but unlike IBT neutral theory assumes equivalence among individuals rather

than species (Hubbell 2001). The metacommunity concept goes a step further, integrating

dispersal-based processes such as neutral theory and niche-based processes such as

environmental filtering to describe patterns of community structure in a landscape

(Cottenie 2005, Holyoak et al. 2005, Leibold et al. 2004). The flexibility of hierarchical

models such as MSOMs and MSAMs allows them to be readily incorporated into

frameworks such as the metacommunity concept, leading to novel methods for

disentangling the processes responsible for patterns of community structure.

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APPLYING ISLAND BIOGEOGRAPHY THEORY TO ECTOPARASITE

ASSEMBLAGES ON MAMMALIAN HOSTS

Introduction

Determining the mechanisms underlying parasite community structure is of great importance in parasitology. Poulin (2004) proposed two main theoretical frameworks to describe the ecological mechanisms underlying parasite diversity: island biogeography theory (IBT) and epidemiological models. Traditional IBT, upon which the first framework is based, predicts that species richness on an island or habitat patch increases with increasing area and decreases with increasing isolation (MacArthur and Wilson 1963, 1967). In host-parasite systems, host population density is frequently substituted for isolation because larger host populations are expected to have greater contact rates between individuals, increasing colonization opportunities (Dearing et al. 2015, Kuris et al. 1980, Stanko et al. 2002). On macroecological scales, host analogues for area include body size, lifespan, and geographic range, which may affect ectoparasite extinction rates (Bossard 2014, Guégan et al. 2005, Kuris et al. 1980, Lindenfors et al. 2007, Morand and Poulin 1998). This concept can be extended to include frameworks such as Hubbell's neutral theory (Hubbell 2001) or the metacommunity concept (Leibold et al. 2004), which still treat hosts as habitat islands but use parasite abundance rather than richness data. I will refer to the use of community-based frameworks to describe parasite diversity as the community assembly perspective.

Poulin's second framework, epidemiological modeling, uses transmission functions to relate host traits to parasite diversity (Anderson and May 1985, Dobson

1989, Poulin and Morand 2000). Transmission functions describe the manner and rate at which parasitic infections spread through the host population (Begon et al. 2002). The transmission rate for density-dependent transmission functions, for example, increases with host population density (Kermack and McKendrick 1927). By contrast, transmission rates for frequency-dependent functions are independent of population density and are instead affected by contact rates between infected and susceptible individuals (de Jong 1995, McCallum et al. 2001). The effects of specific host traits on parasite diversity will vary according to the transmission function used, but in general hosts with traits that facilitate parasite transmission should harbor a higher diversity of parasites than hosts with traits that inhibit transmission (Poulin 2004, 2014).

There is considerable overlap in the predictions derived from community assembly and epidemiological models (Poulin 2004). Community assembly models and density-dependent epidemiological models predict that increasing host population density, for example, will lead to higher parasite diversity due to increased colonization rates (Arneberg et al. 1998; Arneberg 2002; Poulin 2004, 2014). Despite the similarities between the two frameworks, their applicability to specific host-parasite systems varies. Community assembly models such as IBT, which frequently use host density as a proxy for isolation, implicitly assume transmission is density-dependent; an assumption that may be violated in some host-parasite assemblages. However, the transmission function of epidemiological models also is chosen based on biological assumptions of the system at hand (Wonham et al. 2006). Transmission functions which do not accurately model the host-parasite system can lead to erroneous estimates of parasite transmission rates (McCallum et al. 2001, Wonham et al. 2006). Epidemiological models also tend to focus

on one host/one parasite dynamics (Anderson and May 1991, Johnson et al. 2015; but see Holt et al. 2003) and do not explicitly link transmission rates to parasite community structure.

The Ozark glades, open and rocky habitats embedded within the surrounding forest (Heikens 2007, Kucera and Martin 1957, Nelson 2010, Nelson and Ladd 1983), contain a diverse array of small mammal species including habitat generalists such as the Eastern wood rat (*Neotoma floridana*) as well as open-canopy specialists such as the Texas mouse (*Peromyscus attwateri*). These species support a suite of ectoparasites, including fleas (Siphonaptera), ticks (Ixodida), and lice (Phthiraptera). If ectoparasite transmission is density-dependent, then mammalian hosts can be conceptualized as habitat islands for their ectoparasites, and community assembly models such as IBT can be applied.

Using small mammals and ectoparasites of the Ozark glades as a model system, I 1) evaluated the effects of host density on ectoparasite richness, evenness, and diversity per host population, and 2) determined whether host density *per se* or host community composition drives ectoparasite community structure. Based on IBT and the hosts-as-islands extension, I predict that increases in host population density will correspond to increases in ectoparasite richness and diversity due to higher rates of ectoparasite transmission. Additionally, because many ectoparasites specialize on one or a few hosts (Dick 2007, Giorgi et al. 2004, Guerra et al. 2016, Krasnov et al. 2004a, Marshall 1976, Poulin 2011), mammalian community structure will be a significant predictor of ectoparasite community structure.

Methods

  Data collection. I sampled small mammals from a network of sixteen glades in southwest Missouri, spanning an east-west distance of approximately 125 kilometers within the Ozark Highlands ecological section (Nigh and Schroeder 2002). Glades are located within four state or federal management units: Roaring River State Park, Mark Twain National Forest Ava-Cassville District, Drury-Mincy Conservation Area, and Caney Mountain Conservation Area. Glades were selected based on size and distribution among management units. All glades were sampled in May–July 2016 and 2017.

  I used a combination of Sherman live-traps, 7.62×8.89×22.86 cm and 10.16×11.43×38.10 cm, baited with sunflower seeds and/or a peanut-butter oat mixture, to capture small mammals. To standardize sampling effort, each glade was sampled using a ~250 m linear transect, with trap stations set ~10 m apart. At each station, two traps were placed to maximize capture efficiency (e.g. along runways). I used GPS receivers to record positions at the beginning, midpoint, and end of each transect. I opened traps each evening and checked them the following morning; each transect was sampled for a period of 4 consecutive trap days.

  Upon checking traps, captured mammals were transferred to a cloth bag and handled according to American Society of Mammalogists guidelines (Sikes 2016). Individuals were identified to species, sexed, weighed, and standard external measurements (ear length, tail length, and right hind foot length) were collected. To collect ectoparasites, each individual's fur was thoroughly brushed using a denture brush while the animal was held over a plastic 5-gallon bucket. Parasites were collected from the mammal, bucket, and handling bag, and stored in 95% ethanol. Each individual was

marked by snipping off a patch of fur near the rump or by attaching a unique ear tag. Mammals were released from the trap station immediately after processing.

Fleas were identified to species using Benton (1983); the genus *Orchopeas* was identified to species using Lewis (2000). Ticks were identified to species using Keirans and Litwak (1989) and Goddard and Layton (2006). All other ectoparasites were identified to order using Krantz and Walter (2009) and then morphotyped. All collected ectoparasites were deposited at Missouri State University. Prior approval for this project was obtained from the Missouri State University IACUC (IACUC ID #16-020.0).

Statistical Analysis. Because ectoparasites were not detected on all mammalian host species, only host species for which ectoparasites were collected were used in analyses. I fit an *N*-mixture model (Royle 2004) using the R package unmarked (Fiske and Chandler 2011) to estimate the abundance of each host species per transect per year. The latent abundance distribution was set as a negative binomial random variable and the upper index of integration was set at 50. Because each transect was standardized for sampling area, estimating abundance per transect allows abundance estimates to be used as a stand-in for host population density. To test this assumption, I constructed a linear model with glade area as the predictor and host abundance as the response. A significant, positive relationship between area and host abundance would indicate that large abundance estimates are an artifact of large glade size rather than large densities within a sampling area.

The mode of transmission of ectoparasites can be determined by evaluating the relationship between host and ectoparasite abundance (Figure 11). To test the assumption
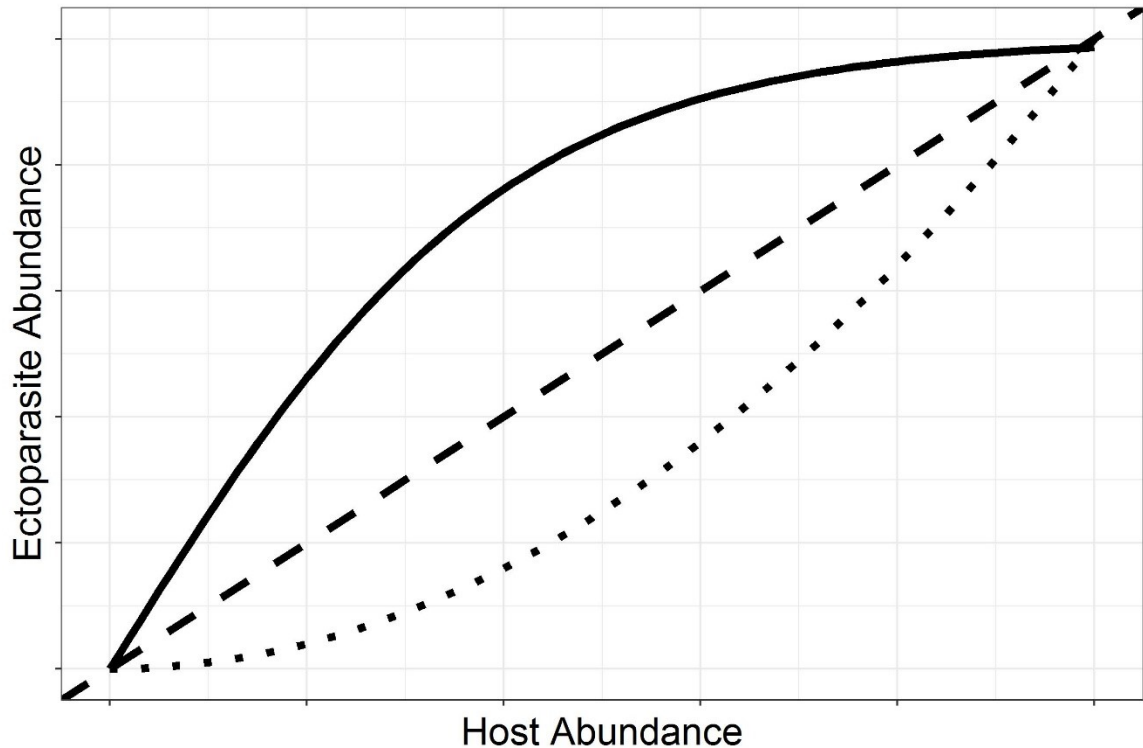
Figure 10. Predicted relationships between host abundance and ectoparasite abundance at the scale of the host population. Negative density-dependence occurs when the rate of ectoparasite accumulation decreases at high host abundances (solid line). In frequency-dependent systems, the rate of ectoparasite accumulation is unaffected by host abundance (dashed line). In positive density-dependent systems, the rate of ectoparasite accumulation increases with increasing host abundance (dotted line).

that ectoparasite exhibit positive density-dependence, I first log-transformed the total ectoparasite abundance for each host population and the host abundance estimates derived from the *N*-mixture model. I then constructed a linear model with log-transformed host abundance as the predictor and log-transformed ectoparasite abundance as the response. If a significant linear relationship is present, a slope less than 1 would indicate negative density-dependence, a slope greater than 1 would indicate positive density-dependence, and a slope of 1 would indicate frequency-dependence (Figure 12).
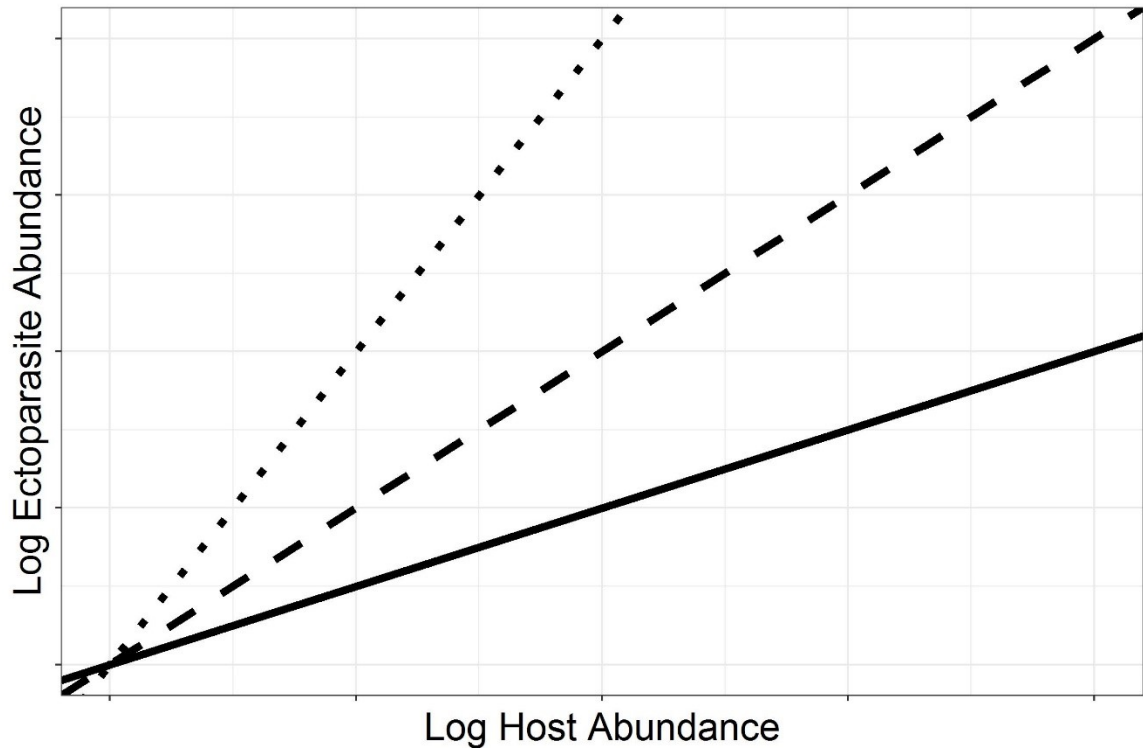
Figure 11. Positive density-dependence (dotted line), frequency-dependence (dashed line), and negative density-dependence (solid line) plotted in log-log space.

To evaluate the effects of host abundance on ectoparasite species richness, I constructed a general linear model (GLM) with ectoparasite richness as the response variable and host abundance and host species as predictor variables. An interaction term between host abundance and host species was also included. Host species with low abundance were excluded from the analysis.

To evaluate the effects of host abundance on ectoparasite diversity and evenness, I quantified ectoparasite diversity with the Shannon diversity index (Shannon 1948) using the R package vegan (Dixon 2003). I constructed a linear model with host abundance as the predictor and the Shannon index as the response. I then quantified ectoparasite evenness using Pielou's evenness metric (Pielou 1975) and included it as the response variable in a linear model with host abundance as the predictor.

To test for associations between host communities and ectoparasite communities, I first characterized site-level differences between small mammal communities using the Bray-Curtis distance index (Bray and Curtis 1957); I repeated the procedure for ectoparasite communities. I used multiple matrix regression with randomization (MMRR, Wang 2013) to test for associations between mammal and ectoparasite communities. Significant, positive coefficients would indicate that host communities that differ have ectoparasite communities that differ. Significant, negative coefficients would indicate that different host communities have similar parasite communities, whereas non-significant coefficients would suggest independence. Euclidian pairwise distances between glades were included in the MMRR to control for effects of geographic isolation by distance. Bray-Curtis and Euclidean distance metrics were scaled to have a mean of zero. All analyses were performed in R version 3.3.1 (R Core Team 2016).

Results

I collected 268 ectoparasites representing seven orders on six host species (Figure 13). Host species varied in abundance, with *Sigmodon hispidus* having the highest abundances and *Reithrodontomys fulvescens* the lowest (Table 2). *Reithrodontomys fulvescens* was removed from subsequent analysis due to low abundances and few ectoparasite samples. The *N*-mixture model yielded site-level abundance estimates between 0 and 42 individuals across all hosts with considerable variability within hosts. Abundances generally were greater in 2016 (Table 3) than in 2017 (Table 4).

The most abundant ectoparasite orders were Trombidiformes with 97 individuals and Siphonaptera with 87 individuals (Table 5, Figure 13). The most species-rich orders

were Siphonaptera with five species and Mesostigmata with four species. All other orders were represented by two or fewer species.

Table 2. Raw abundance counts of small mammal host species by site.

Site	Neotoma floridana	Peromyscus attwateri	P. leucopus	P. maniculatus	Reithrodontomys fulvescens	Sigmodon hispidus
0	3	0	6	1	0	33
1	2	1	2	1	0	20
2	2	11	8	1	0	13
3	1	8	0	0	0	11
4	1	1	8	6	0	0
5	3	0	9	6	0	1
6	3	0	3	6	1	6
7	0	2	3	1	0	9
8	2	2	0	0	0	1
9	3	17	0	0	0	0
10	0	8	0	0	0	0
11	2	1	6	1	0	0
12	0	0	3	1	1	4
13	0	0	14	6	3	1
14	3	5	14	3	7	7
15	4	6	2	4	1	14

The linear model yielded no significant relationship between area and host abundance (F = 1.184; df = 1, 158; $\beta < 0.001$; $P = 0.278$), therefore the assumption that host abundance can be used as a proxy for density was not violated. Additionally, there was no significant relationship between host and ectoparasite abundance (F = 3.602; df = 1, 29; $\beta = 0.328$; $P = 0.068$; Figure 14), which does not violate the assumption that ectoparasite transmission is density-dependent.

Table 3. Results of the *N*-mixture model for 2016. The parameter α is a measure of dispersion; lower values of α indicate higher variance.

Site	*N. floridana*	*P. attwateri*	*P. leucopus*	*P. maniculatus*	*S. hispidus*	Total
1	5.97	0.38	3.05	0.06	41.67	51.13
2	3.57	2.86	3.62	1.09	33.90	45.04
3	2.17	19.52	11.15	1.09	5.95	39.88
4	2.17	8.97	0.32	0.06	11.94	23.46
5	2.85	3.87	9.51	5.96	0.31	22.5
6	5.97	0.38	10.04	3.53	1.91	21.83
7	2.85	0.38	2.30	1.34	10.52	17.39
8	0.90	6.49	8.57	1.34	13.90	31.2
9	2.17	6.03	0.32	0.06	1.91	10.49
10	2.85	13.90	0.32	0.06	0.31	17.44
11	0.90	12.49	0.32	0.06	0.31	14.08
12	0.90	0.38	15.10	1.34	0.31	18.03
13	0.90	0.38	7.76	1.58	6.17	16.79
14	0.90	0.38	23.68	3.58	2.68	31.22
15	2.17	14.67	20.62	3.93	1.91	43.3
16	4.70	15.86	17.97	3.74	2.68	44.95
Total	41.94	106.94	134.65	28.82	136.38	448.73
α	1.22	-0.54	-0.22	0.54	-0.66	

Table 4. Results of the *N*-mixture model for 2017. The parameter α is a measure of dispersion; lower values of α indicate higher variance.

Site	*N. floridana*	*P. attwateri*	*P. leucopus*	*P. maniculatus*	*S. hispidus*	Total
1	1.77	0.15	3.41	1.02	13.90	20.26
2	2.77	0.15	0.00	0.01	8.26	11.19
3	2.77	4.91	0.00	0.01	16.44	24.13
4	1.77	15.78	0.00	0.01	3.43	20.98
5	1.77	0.15	2.10	1.04	0.08	5.14
6	1.77	0.15	4.38	1.01	0.08	7.39
7	2.77	0.15	2.26	2.20	0.08	7.46
8	1.77	0.15	0.00	0.01	0.08	2.01
9	2.77	0.15	0.00	0.01	0.08	3.01
10	2.77	29.64	0.00	0.01	0.08	32.50
11	1.77	25.18	0.00	0.01	0.08	27.04
12	4.00	3.44	0.00	0.01	0.08	7.53
13	1.77	0.15	0.00	0.01	0.08	2.01
14	1.77	0.15	1.01	0.01	0.08	3.02
15	3.41	0.15	0.00	0.01	6.19	9.76
16	2.77	0.15	0.00	0.01	20.40	23.33
Total	38.18	80.60	13.19	5.35	69.43	206.74
α	6.64	-1.99	-1.16	0.26	-1.69	

Table 5. Abundances of ectoparasite species per host species per site.

Host	Site	Amblyomma americanum	Amblyomma maculatum	Ctenophthalmus pseudagyrtes	Cuterebra americana	Cuterebra fontinella	Epitedia wenmanni	Mesostigmata I	Mesostigmata II	Mesostigmata III	Mesostigmata IV	Orchopeas howardi	Orchopeas illinoiensis	Orchopeas leucopus	Phthiraptera I	Sarcoptiformes I	Sarcoptiformes II	Trombidiformes I
S. hispidus	0	2	0	0	0	0	0	6	1	0	0	0	0	0	2	6	0	28
	1	0	1	0	0	0	0	5	4	0	0	1	0	0	6	5	0	11
	2	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	15
	3	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1
	6	1	0	0	0	0	0	9	0	1	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
	13	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	14	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	1	7
	15	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	0	35
	Total	**3**	**2**	**0**	**0**	**0**	**0**	**28**	**5**	**1**	**0**	**1**	**0**	**1**	**10**	**16**	**1**	**97**
N. floridana	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
	1	0	0	0	1	0	0	0	0	0	0	0	6	0	0	0	0	0
	2	0	0	0	1	0	0	0	0	0	0	0	22	0	0	0	0	0
	3	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
	5	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
	8	0	0	0	1	0	0	1	0	0	0	0	3	0	0	0	0	0
	9	0	0	0	0	0	0	0	0	0	0	1	7	0	0	0	0	0
	11	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0
	14	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
	15	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
	Total	**0**	**0**	**0**	**3**	**0**	**0**	**1**	**0**	**0**	**0**	**1**	**59**	**0**	**0**	**0**	**0**	**0**

Table 5 Continued. Abundances of ectoparasite species per host species per site.

Host	Site	*Amblyomma americanum*	*Amblyomma maculatum*	*Ctenophthalmus pseudagyrtes*	*Cuterebra americana*	*Cuterebra fontinella*	*Epitedia wenmanni*	Mesostigmata I	Mesostigmata II	Mesostigmata III	Mesostigmata IV	*Orchopeas howardi*	*Orchopeas illinoiensis*	*Orchopeas leucopus*	Phthiraptera I	Sarcoptiformes I	Sarcoptiformes II	Trombidiformes I
P. leucopus	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
	4	3	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0
	12	0	0	0	0	0	0	1	0	0	0	0	0	3	0	0	0	0
	13	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	14	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	15	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0
	Total	**6**	**0**	**0**	**0**	**3**	**0**	**4**	**0**	**0**	**0**	**0**	**0**	**11**	**0**	**0**	**0**	**0**
P. maniculatus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	5	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	15	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	Total	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**3**	**0**	**0**	**0**	**0**

Table 5 Continued. Abundances of ectoparasite species per host species per site.

| Host	Site	Amblyomma americanum	Amblyomma maculatum	Ctenophthalmus pseudagyrtes	Cuterebra americana	Cuterebra fontinella	Epitedia wenmanni	Mesostigmata I	Mesostigmata II	Mesostigmata III	Mesostigmata IV	Orchopeas howardi	Orchopeas illinoiensis	Orchopeas leucopus	Phthiraptera I	Sarcoptiformes I	Sarcoptiformes II	Trombidiformes I
P. attwateri	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	1	0	0	0	3	0	0	0	0
	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	9	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	10	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	14	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0
	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Total	**1**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**1**	**0**	**0**	**8**	**0**	**0**	**0**	**0**
R. fulvescens	13	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	14	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	Total	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**
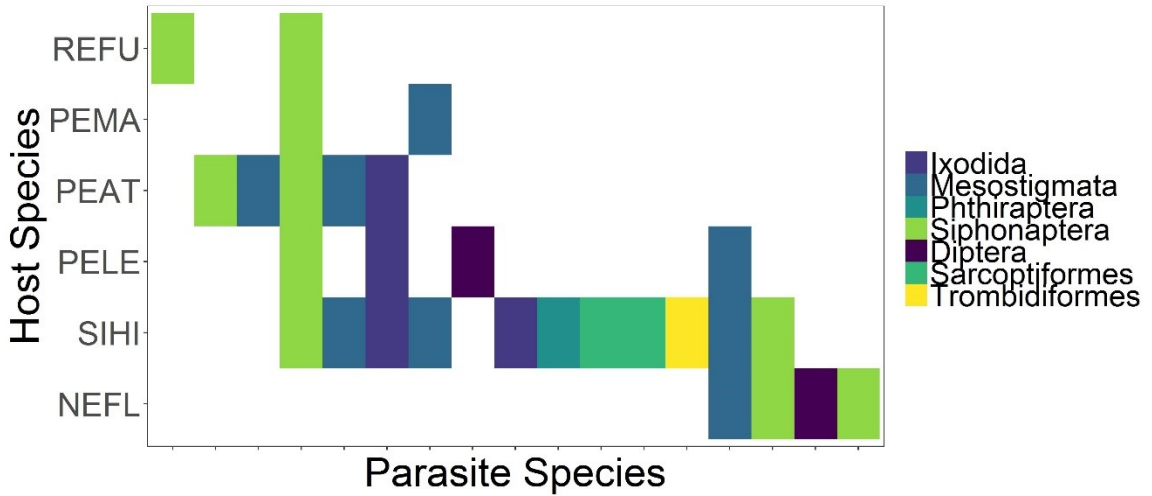
Figure 12. Species-by-site plot of ectoparasite species on host species. Shaded boxes indicate that a parasite species was found on a particular host. Colors denote ectoparasite orders. Host abbreviations are as follows: REFU *R. fulvescens*, PEMA *P. maniculatus*, PEAT *P. attwateri*, PELE *P. leucopus*, SIHI *Sigmodon hispidus*, NEFL *Neotoma floridana*.
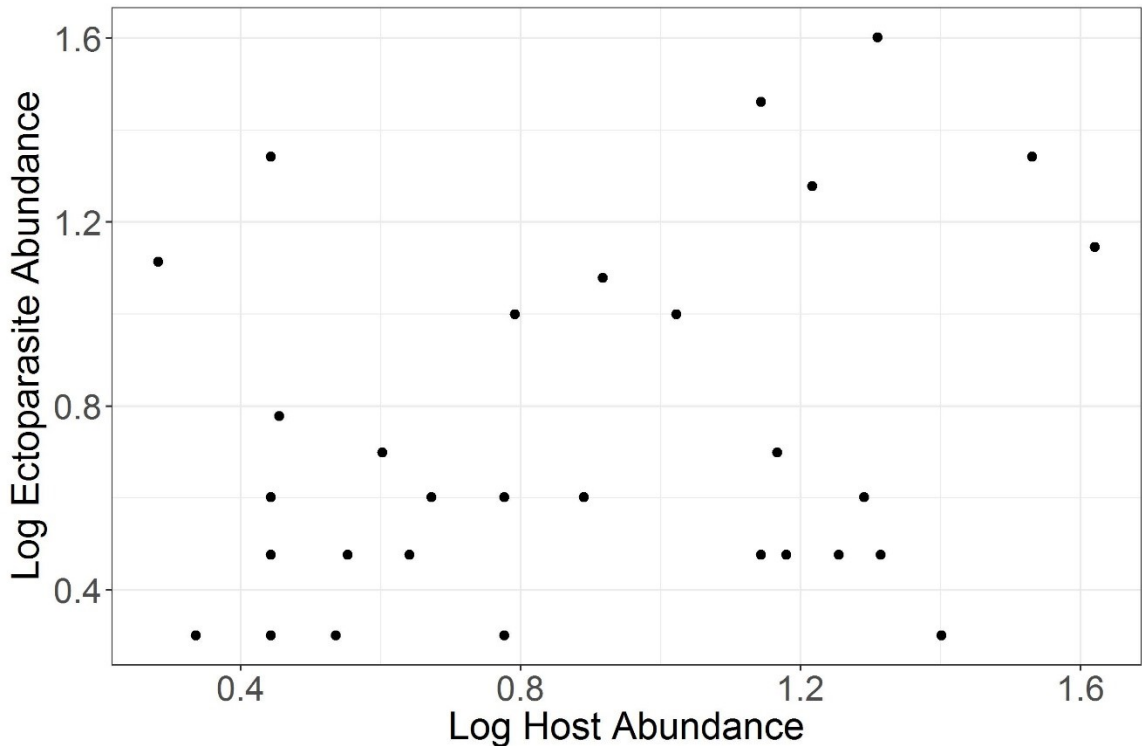

Figure 13. Log ectoparasite abundance plotted as a function of log host abundance. Each variable was log-transformed prior to analysis. The lack of significant relationships between the two variables does not conclusively demonstrate frequency-dependent or density-dependent transmission.

The GLM for host abundance and ectoparasite richness was significant (F =

33.04; df = 10, 149; $P < 0.001$; Figure 15) and explained 67% of the variation in the data.

The coefficient for host population size was significant (df = 129, β = 0.265, t = 3.542, P

< 0.001). *Peromyscus attwateri* and *Peromyscus leucopus* were significantly different

than the other species (Table 4). There were no significant differences between years (df

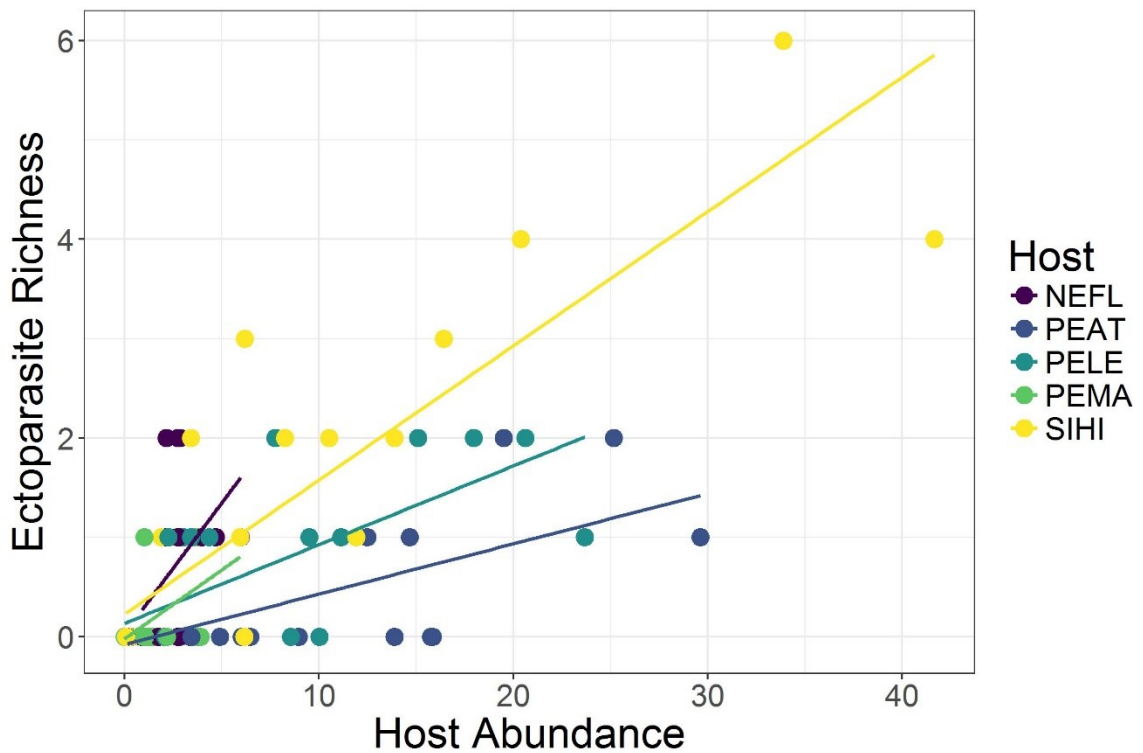= 129, β = 0.061, t = 0.670, P = 0.504).

Figure 14. Ectoparasite species richness plotted as a function of host abundance. Richness was significantly positively correlated with host abundance (β = 0.265, t = 3.542, $P <$ 0.001). Colors denote host species. Host abbreviations are as follows: REFU *R. fulvescens*, PEMA *P. maniculatus*, PEAT *P. attwateri*, PELE *P. leucopus*, SIHI *Sigmodon hispidus*, NEFL *Neotoma floridana*.

Table 6. Coefficients derived from the linear model. Species that are significantly different than *N. floridana* are shown in bold.

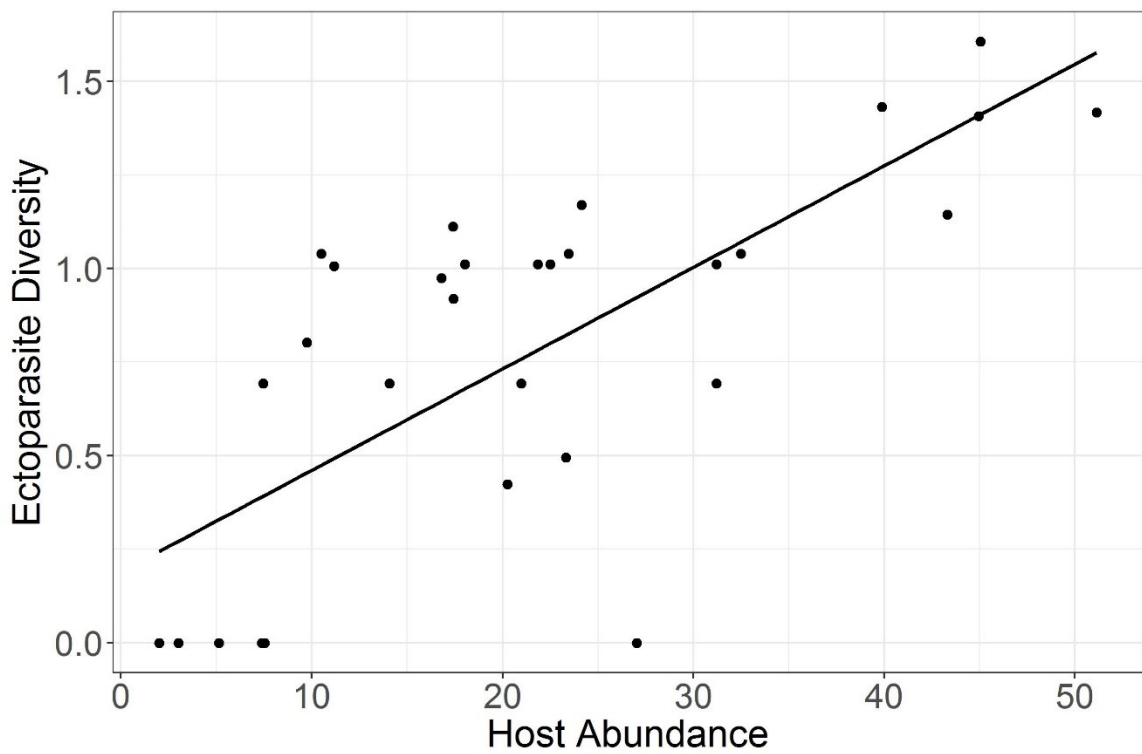| Host Species	Coefficient	t Value	*P*-Value
Abundance *N. floridana*	0.265	3.542	< 0.001
Abundance*S. hispidus	0.136	-1.713	0.089
Abundance*P. maniculatus	0.149	-1.181	0.239
Abundance*P. leucopus	0.082	-2.404	**0.017**
Abundance*P. attwateri	0.051	-2.826	**0.005**

Figure 15. Shannon diversity index values of ectoparasites plotted as a function of host abundance pooled across host species.

A significant, positive relationship was present between host abundance and ectoparasite diversity as measured by the Shannon diversity index (F = 36.73; df = 1, 30; β = 0.027; P < 0.001; R^2 = 0.535; Figure 16). There was no significant relationship between ectoparasite evenness and host abundance (F = 0.63; df = 1, 22; β = -0.069; P = 0.690).

For each year of data, the MMRR results were significant (2016: F = 7.299, P = 0.005, R^2 = 0.111; 2017: F = 22.18, P = 0.001, R^2 = 0.286; Figure 16). Models for both years yielded significant, positive relationships between host and ectoparasite Bray-Curtis distances (β = 0.308, t = 3.76, P = 0.002; β = 0.430, t = 5.874, P = 0.001, respectively;
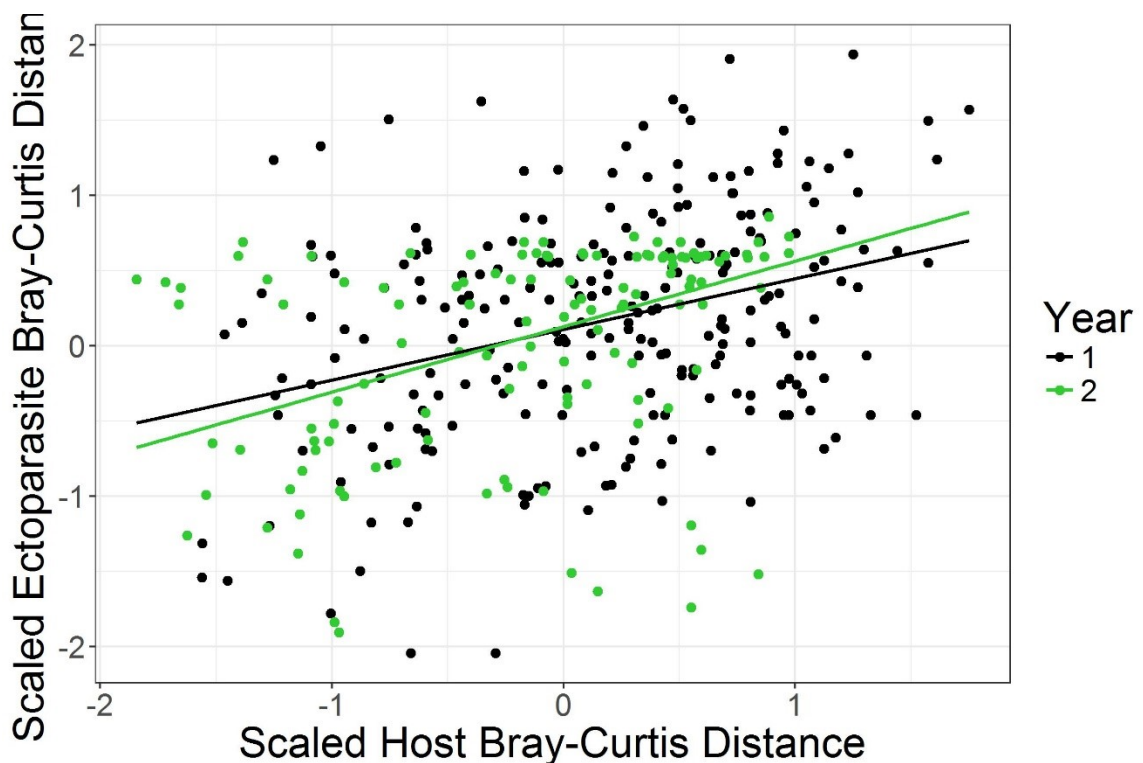

Figure 16. Ectoparasite Bray-Curtis distance plotted as a function of host Bray-Curtis distance. Significant, positive correlations were present for host and parasite Bray-Curtis distances in both years (β = 0.308, t = 3.76, P = 0.002; β = 0.430, t = 5.874, P = 0.001, respectively). Distance metrics were scaled to have mean 0. Colors denote years.

Figure 16). Euclidean geographic distances did not have significant results in either year (2016: β = -0.095, t = -1.291, P = 0.255; 2017: β = 0.027, t = 0.445, P = 0.668).

Discussion

Consistent with the predictions of IBT, ectoparasite species richness increased with host abundance. Ectoparasite diversity also demonstrated a significant, positive relationship with host abundance. Because richness, but not evenness, increased with host population sizes, the positive relationship between parasite diversity and host abundance was likely due to an increased number of rare species in larger host populations.

The significant, positive relationships between host and ectoparasite Bray-Curtis distances suggest that strong associations are present between the host and ectoparasite communities. Specifically, when host communities at two sites differ, the ectoparasite communities at those sites are likely to differ. This result suggests that ectoparasites are responding to host community composition, rather than host abundance *per se*.

Many tests of IBT in host-parasite systems have failed to detect significant effects of "area" metrics such as host body size (Bossard 2014, Krasnov et al. 2004b, Morand and Poulin 1998, Nunn et al. 2003, Poulin and Rohde 1997, Stanko et al. 2002), or host population density (Bossard 2006, 2014). The general inconsistency in results could be due to methodological problems such as variation in sampling effort (Gregory 1990, Guégan and Kennedy 1996, Walther et al. 1995) or as a result of different processes operating at different spatial scales (Kamiya et al. 2014, Poulin 2014) or hierarchical levels of study (Kamiya et al. 2014, Kuris et al. 1980, Poulin 2014). However,

inconsistencies in tests of the hosts-as-islands concept may be due to the use of metrics that are inappropriate substitutes for area and isolation. Many flea species, for example, spend a portion of their life cycle in the host burrow or nest (Vatschenok 1988), and thus nest density may be a better measure of isolation than host density (Krasnov et al. 2002). Additionally, host density is not an adequate proxy for isolation in frequency-dependent systems in which density does not affect transmission rate (de Jong et al. 1995, McCallum et al. 2001). Although there are some host characteristics, such as host body size and population density, which seem to be universal predictors of ectoparasite richness (Kamiya et al. 2014), the choice of substitutes for area and isolation must be tailored to the system at hand.

Community dynamics of hosts and ectoparasites are often complex. Factors contributing to ectoparasite community structure, such as individual host traits (Dallas and Presley 2014, Perkins et al. 2003, Streicker et al. 2013, Stutz et al. 2014), host environment (Ekholm et al. 2017, Krasnov et al. 1997, Krasnov et al. 2004b, Maher & Timm 2014, Poulin and Rohde 1997), interactions between parasites (Krasnov et al. 2010, Heeb et al. 2000, Sebastián Tello et al. 2008, Tripet et al. 2002), and interactions between host and parasite (Heeb et al. 2000, Poisot et al. 2017, Vázquez et al. 2005), often show considerable variability across spatial and hierarchical scales (Kamiya et al. 2014, Poisot et al. 2017, Stutz et al. 2014). IBT is a relatively simple framework, and though it can successfully predict drivers of ectoparasite richness and diversity in some systems (Kamiya et al. 2014, Lindenfors et al. 2007), community assembly models such as the metacommunity concept or network theory may be more suitable for describing

variation in host and ectoparasite communities across organizational and spatial scales (Diuk-Wasser et al. 2016, Johnson et al. 2015).

Due to the recent increase in emerging zoonotic diseases (Jones et al. 2008, Lloyd-Smith et al. 2009), a call has been made for the integration of community assembly and epidemiological models (Johnson et al. 2015). Such an approach would allow for multilevel evaluation of disease dynamics, from the level of the individual host to the entire host/pathogen assemblage. Merging community assembly models such as IBT and epidemiological theory will not only provide new insights into the ecological processes driving parasite diversity, but may also lead to more efficient methods for managing zoonotic disease (Diuk-Wasser et al. 2016, Johnson et al. 2015, Lloyd-Smith et al. 2009, Webster et al. 2016).

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SUMMARY

My results demonstrate the variability in responses of species richness to patch area and isolation among different levels of community organization. Results of the first chapter suggest that patterns of species richness in small mammals of the Ozark glades do align with the predictions of IBT, though it is likely that the lack of matrix homogeny and resistance to movement masked isolation effects. Ectoparasite communities on the small mammal "islands" showed the opposite trend: host size did not have consistent effects on ectoparasite richness, but an "isolation" effect was detected in the form of a positive relationship between host population size and richness. My results suggest that small mammal and ectoparasite communities are structured by mechanisms more complex than those accounted for in traditional IBT. Differences in small mammal and ectoparasite responses to patch area and isolation suggest that different assemblages can be structured by different mechanisms, even when occupying the same geographic space.

The simplicity of IBT is one of the features that allows the theory to be applicable to a broad spectrum of real and conceptual islands. However, the generality of IBT has often been called into question (Gilbert 1980, Lomolino 2000, Santos et al. 2016). A subject of frequent debate is the applicability of IBT to habitat islands. Species-area relationships of oceanic islands tend to have shallower slopes than those of habitat islands (Matthews et al. 2016), and the presence of a heterogeneous, permeable matrix can mask or confound isolation effects (Prevedello and Vieira 2010, Ricketts 2001). Additionally, many communities are structured by mechanisms other than the neutral processes of colonization and extinction assumed by IBT. In non-neutral systems, more complex

models such as the metacommunity concept (Cottenie 2005, Leibold et al. 2004) and epidemiology theory (Anderson and May 1985, Dobson 1989, Poulin 2004) may be more appropriate for determining mechanisms of community assembly.

Despite these criticisms, IBT is still relevant to many areas of ecology and evolution. IBT and the related unified neutral theory of biodiversity and biogeography still influence research in community assembly (Burns et al. 2016, Lowe and McPeek 2014, Tucker et al. 2016). New theories such as the General Dynamic Model extend classical IBT to geological and evolutionary time scales (Borregaard et al. 2016, 2017; Whittaker et al. 2008). Islands also act as natural laboratories for conservation issues such as climate change and invasive species due to their clear boundaries, and because the relative dates of human arrival are usually known (Sax et al. 2002, Sax and Gaines 2008). Research on islands and island systems is still active, and will continue providing insights into biological processes in the years to come.

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