



HOST TRAITS EXPLAIN MORE VARIATION IN OCCUPANCY OF GENERALISTS THAN SPECIALISTS DUE TO STRONG HOST PREFERENCES AMONG GENERALISTS

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KEY WORDS ABSTRACT

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The range of hosts a parasite can successfully occupy is partially determined by the niche breadth, that is, the set of environmental conditions necessary to maintain a stable population. Niche breadth is often quantified using host specificity, which encompasses the number of host species a parasite can exploit and the parasite's distribution among its hosts. Parasites with a wider niche breadth can potentially occupy more host species and are often more evenly distributed among hosts than parasites with a narrower niche breadth. However, parasites interact with potential hosts within the context of a geographic locality and the set of environmental characteristics associated with it. The extent to which environmental filters associated with host individuals and the geographic context explain variation in occupancy of parasites, and the extent to which variation in occupancy is associated with host range and specificity, is poorly understood. Using data from small mammals and ectoparasites in Vermont, I used a multiscale, multispecies occupancy model (MSOM) to (1) estimate ectoparasite occupancy at 10 geographic sites and on individual hosts within each site, (2) quantify the variation in occupancy explained by the site and host levels of the model using Bayesian R^2 , and (3) evaluate associations between explained variation and host range of ectoparasites. For ectoparasites collected from at least 4 different host species, I calculated structural specificity to determine the distribution of these parasites across the hosts, and β -specificity to evaluate changes in host use across habitats. Host range was significantly associated with host-level Bayesian R^2 : generalist parasites had more variation in occupancy explained by host-level covariates than specialist parasites. This result may be explained by differences in structural specificity: many generalists disproportionately occurred on a single-host species, suggesting that host characteristics act as habitat filters for these parasites. There were no significant associations between site-level Bayesian R^2 and host specificity. However, some generalists demonstrated high β -specificity, suggesting these parasites may “switch” hosts, depending on host availability. These results highlight that the terms *specialist* and *generalist* are context dependent and may not accurately describe the niche breadth of parasite taxa. Understanding variation in host specificity as it pertains to potential habitat filters may be important for predicting which parasites can bypass host filters and “jump” to a novel host, which has implications for the surveillance and management of vector-borne diseases.

The ability of a species to occupy a given locality is determined, in part, by the set of abiotic and biotic variables with which the species interacts, in other words, the operative environment (Spomer, 1973; Dunham, 1993; Agosta and Klemens, 2008). Species are more likely to occupy a locality in which the operative environment meets the minimum conditions for nonnegative population growth and are typically more abundant in operative environments that facilitate higher rates of growth (i.e., the niche, Chase and Leibold, 2003; but see exceptions, such as population sinks, Pulliam, 1988, 2000; Heinrichs et al., 2019). The range of operative environments that meet these minimum conditions, or

the niche breadth, in turn, influences the range of localities a given species may occupy. Thus, abiotic characteristics of a locality can act as filters that limit which species can comprise the local community (Chase and Leibold, 2003; Leibold et al., 2004). Species with a relatively narrow niche breadth, or environmental specialists, are likely to have occupancy that is restricted to a few localities compared with more tolerant generalists due to the reduced ability to bypass a locality's habitat filters (Futuyma and Moreno, 1988; Pulliam, 2000; Devictor et al., 2010).

Associations between niche breadth, characteristics of the operative environment, and occupancy can be difficult to evaluate

because observations of niche breadth can be sensitive to scale (Devictor et al., 2010). Arthropod ectoparasites that infest small mammals are useful for circumventing this problem because, although occupancy and niche breadth are still sensitive to scale, the environment of the individual host is a clearly defined sampling unit with a range of traits that may act as habitat filters. (Cardon et al., 2011). Characteristics of parasite communities can also be measured at broader scales: across host individuals in a geographic locality, a host metapopulation or metacommunity, or across a host species' geographic range (Krasnov et al., 2011a, 2011b, 2015; Euclides et al., 2022), which can be useful for determining whether a parasite species' niche breadth is consistent across geographic space.

For parasites, niche breadth is typically measured using host specificity (Timms and Read, 1999), consisting of the number of habitat types or host taxa a parasite can occupy (i.e., host range) and the distribution of parasites among these habitats (Rohde, 2013). For example, consider 2 parasite species with an identical host range. One parasite may be constrained to several closely related hosts that share ancestral traits (i.e., hosts with similar habitat filters), whereas the other may be able to exploit hosts across different families. Differences in host taxonomic breadth between parasites are known as phylogenetic specificity, a measure of the phylogenetic diversity of operative environments (i.e., hosts) a parasite can exploit (Poulin and Mouillot, 2003). Alternatively, 1 parasite may achieve high abundances on a particular host, while only incidentally exploiting alternative hosts, whereas the other may be evenly distributed among exploited host species. A measurement of the differences in parasite population structure across host species is termed *structural specificity*, which is usually quantified by comparing the relative proportion of a parasite's population that occurs on each host species (Benton and Ceronka, 1960; Krasnov et al., 2004b, 2011a; Poulin et al., 2011). Accounting for abundance distributions of parasites in addition to host range provides a better estimate of niche breadth because it allows for differentiating between hosts that may facilitate population growth and may act as incidental hosts or population sinks (Agosta et al., 2010; Poulin et al., 2011).

Host–parasite interactions do not occur in a vacuum, and habitat filters associated with a geographic locality can influence whether a parasite can successfully infest a host individual (Cardon et al., 2011), which, in turn, can affect measures of occupancy and niche breadth (Berkhout et al., 2020; Bolnick et al., 2020). Previous work suggests that local environmental conditions can structure host communities, influencing which host species are available to parasitize (Krasnov et al., 2008, 2015; van der Mescht et al., 2016). Changing host availability can result in variation in parasite species' β -specificity, or the consistency with which a parasite exploits hosts across the parasite's geographic range (Krasnov et al., 2011a, 2011c; Poulin et al., 2011). Characteristics of the geographic site can also directly act as an environmental filter for parasite species, particularly species that spend a portion of the life cycle off host. Ticks, for example, spend the majority of the life cycle off host and therefore are potentially affected by a variety of environmental conditions (Stafford, 1994; Ostfeld and Brunner, 2015; Burtis et al., 2019), especially conditions that may affect questing behavior, which would influence the tick's ability to colonize a new host (Randolph and Storey, 1999; Randolph, 2004). The occupancy and abundance of nest parasites at a given geographic locality may be influenced by available nesting

material (Moors, 1979; Scott-Baumann and Morgan, 2015; Deeming, 2023); and other conditions such as temperature and humidity can potentially affect parasites of varying life history strategies (Stafford, 1994; Krasnov et al., 2008; van der Mescht et al., 2016). Although filters associated with the geographic site do not necessarily influence host specificity directly, these filters can play an important role in providing the context in which a parasite may encounter and exploit a given host.

Using terrestrial small mammal communities and the component community of ectoparasites in Chittenden County, Vermont, as a model system, I will use a multiscale, multispecies occupancy model (multiscale MSOM) to (1) estimate ectoparasite occupancy measured at the level of the geographic site (i.e., the locality containing the host community) and the level of the individual host, while correcting for detection error, (2) evaluate effects of site-level and host-level covariates on ectoparasite occupancy, and (3) calculate Bayesian R^2 to quantify the explanatory power of each level of the model. This modeling framework incorporates the scale at which niche breadth is measured and the environmental context in which a parasite interacts with its host environment. I will test for associations between Bayesian R^2 and the number of host species parasitized (i.e., host range) to examine whether the explanatory power of habitat characteristics on occupancy is related to host specificity. I will then quantify the host specificity of parasites with a relatively high host range, specifically structural specificity and β -specificity (Poulin et al., 2011). These additional metrics will quantify host specificity beyond host range and may be useful for explaining potential associations between the explanatory power of each level of the model and host range.

If host traits act as habitat filters, parasites that are strongly constrained by these filters will likely parasitize fewer hosts, and the occupancy will be highly associated with host characteristics. This will result in a significant, negative association between host range and host-level Bayesian R^2 . However, the inverse could be true if generalists with a high host range have high structural specificity (i.e., essentially specialists with incidental occurrences on nonpreferred hosts) or β -specificity (i.e., host preferences that vary across geographic localities). A lack of a significant association is also possible if host-level occupancy is mostly stochastic (Rynkiewicz et al., 2019). Because habitat filters at the scale of the geographic site are unlikely to directly affect host range or specificity, I do not expect significant associations between the number of parasitized hosts and site-level Bayesian R^2 , but some ectoparasite species may exhibit significant responses to site-level covariates, depending on the life history.

MATERIALS AND METHODS

Site-level environmental measurements

I define *site* as the geographic locality in which small mammal or ectoparasite communities were sampled, following the MSOM literature (Dorazio and Royle, 2005; Iknayan et al., 2014; Szcwzyk and McCain, 2019). This definition differs from Bush et al. (1997), which defines site as the anatomic location at which a parasite was collected. The former definition is more useful in the context of this article because (1) it better reflects the point at which occupancy was measured and (2) many ectoparasites, such as fleas and mesostigmatid mites, move freely about the external

anatomy of the host, rendering this definition less useful than in the context of parasites that are sessile or restricted to specific anatomic features.

I sampled 10 geographic sites located throughout Chittenden County, Vermont, from May to August 2020 (Suppl. Data 1, Fig. S1). Four sites were located on active farms, 3 in old fields, and 3 in forested habitats. I sampled each site 3 times over the course of the study: the first sampling period was from 26 May 26 to 14 June; the second from 19 June to 9 July; and the third from 15 July to 3 August. I set a 300-m linear sampling transect at each site. When possible, the transect began at the edge of the habitat patch and extended toward the center. Transects were sampled for a total of 3 consecutive trap days per sampling period for a total of 9 day per transect.

I measured site-level environmental variables on the first day of each trapping session at 30-m intervals along the sampling transect. I measured vegetation cover and vertical structure within a 0.5-m² quadrat because ground cover and structure are associated with host-seeking behavior (Leal et al., 2020) and overwintering survival (Burtis et al., 2019) of ticks and can act as a rough measure of available vegetative nesting material that may affect nest parasite occupancy (Moors, 1979; Deeming, 2023). I quantified vegetation cover by recording the relative proportion of each cover type (e.g., grass, leaf litter) within the quadrat. Vertical structure was quantified using the point-touch method described in Wiens (1969). I measured the canopy cover at each quadrat using a spherical convex densitometer, as canopy cover can affect local temperature and humidity (von Arx et al., 2012). I repeated vegetation data collection once per sampling period and reduced the dimensionality of the data using a principal component analysis (PCA). I ran separate PCAs for vegetation composition variables, vertical structure variables, and all vegetation variables.

Small mammal trapping

To capture small mammal hosts, I placed trap stations every 10 m along the 300-m sampling transect. Each trap station consisted of 2 Sherman live traps ($7.62 \times 8.89 \times 22.86$ cm), baited with sunflower seeds and 5-g dried mealworms, and placed to maximize trapping efficiency (e.g., along fallen logs). I placed batting in each trap when night temperatures fell below 10 °C to reduce cold-related mortality (Do et al., 2013). Traps were set each evening and checked just after dawn the following morning for 3 consecutive trap days per sampling period.

Upon checking traps, captured mammals (excluding bycatch species, described in the following) were transferred to a cloth handling bag. Rodents were marked with a unique ear tag, and shrews were marked by clipping a patch of fur near the rump or shoulders, the location of which was used to identify individuals. Species, sex, mass, and standard external measurements (Hall, 1962) were recorded for each mammalian host. I then searched for ectoparasites for at least 2 min. Collected ectoparasites were stored in 70% ethanol. After handling, mammals were released at the point of capture. Because MSOMs assume a certain degree of ecologic similarity of species in the community, arboreal rodents (e.g., *Glaucomys* spp.) and small carnivores (e.g., *Mustela* spp.) were considered bycatch and were released at the point of capture without handling. Mammals found dead in the trap or euthanized due to poor body condition were prepared as museum specimens and deposited in the Zadock Thompson Natural History

Collections at the University of Vermont (Burlington, Vermont). All handling procedures followed guidelines from the American Society of Mammalogists (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists, 2016) and were approved by the University of Vermont IACUC (protocol PROTO202000114).

Parasite sampling

After collection, all ectoparasites were prepared for identification and permanent storage. Fleas and ticks were cleared of host blood and other soft tissues by making a small incision in the exoskeleton and suspending the parasite in 10% KOH for 12–24 hr. After clearing, fleas and ticks were returned to a 70% ethanol solution for 24 hr. All parasites were dehydrated by soaking for at least 24 hr in increasing concentrations of ethanol: 70, 85, and 95%. After dehydration, parasites were identified to the lowest possible taxonomic level and preserved in either 95% ethanol or slide mounted using synthetic Canada balsam medium. Fleas were identified to species using Benton (1983) and Lewis (2000, 2009); adult and nymph ticks were identified to species using Keirans and Litwak (1989), whereas larval ticks were identified to species using Coley (2015); mites were identified to order and, when possible, family and genus, using Krantz and Walter (2009) and Allred and Beck (1966). All parasites were deposited in the Zadock Thompson Natural History Collections at the University of Vermont (Suppl. Data 2).

Analytical methods

All analyses were completed in R 4.1.2 (R Core Team, 2021) unless otherwise specified. Data and code are available at https://github.com/Beasley015/Beasley2024_Host_traits_explain_occupancy_of_generalists.

To test for spatial autocorrelation between sites, I used multiple matrix regression with randomization (MMRR; Wang, 2013) to test for associations between geographic distance and (1) vegetation composition and (2) Bray–Curtis distances of the host communities.

I estimated ectoparasite occupancy at the site and host level using a multiscale MSOM (Nichols et al., 2008; Szcwzyk and McCain, 2019). Similar to other hierarchical detection models, multiscale MSOMs differentiate between an ecologic metric of interest (e.g., occupancy) and the survey process used to observe the ecologic metric (e.g., small mammal trapping). Using data from repeated sampling events, hierarchical detection models can estimate the detection error in the sampling method and use it to generate more accurate estimates of the ecologic metric (MacKenzie et al., 2002; Dorazio and Royle, 2005; Iknayan et al., 2014). In addition, the community aspect of MSOMs allow rare species to “borrow” data from those that are common (Link and Sauer, 1996), which is of particular importance in ectoparasite assemblages due to the rarity or low detectability of many species (Poulin, 1998).

Multiscale MSOMs differ from other hierarchical detection models by introducing multiple scales at which the ecologic metric can be measured (McMahon and Diez, 2007; Nichols et al., 2008). In the context of this study, ectoparasite taxa may or may not occupy a geographic site. If an ectoparasite taxon occupies the site, it may or may not be present on individual small

mammals inhabiting that site: essentially, each host individual acts as a subsample of the host community inhabiting the geographic site (Szewczyk and McCain, 2019). Similarly to single-scale MSOMs, multiscale MSOMs use data collected from multiple sampling periods to estimate detection probability, which is then used to generate more accurate estimates of occupancy at each scale of the model (Nichols et al., 2008; Szewczyk and McCain, 2019). In the context of ectoparasites inhabiting small mammals, recapturing individual mammalian hosts act as the repeated samples from which detection probability for ectoparasites is estimated.

Environmental covariates can be included at each level of the multiscale MSOM to improve occupancy estimates and evaluate the effects of the covariates on occupancy. For the site-level model, I included vegetation covariates based on the results of the PCA (Eq. 1). The site-level model also included number of captured hosts (as a proxy for host density) and host diversity (Krasnov et al., 2002; Kamiya et al., 2014a, 2014b; Eq. 1). Covariates in the host-level model included host species, adjusted body mass, and host sex, each of which may affect ectoparasite occupancy patterns (Poulin and Mouillot, 2003; Krasnov et al., 2012; Kamiya et al., 2014b; Sponchiado et al., 2017; Eq. 2). Host mass was scaled within each host species to better reflect body size variation of individuals within a species rather than across species. Detection covariates included Julian date, as ectoparasite detection can vary seasonally (Lareschi and Krasnov, 2010; Ostfeld and Brunner, 2015), and capture number to account for the removal of ectoparasites during previous captures of a host individual (Equation 3). All covariates except for body mass were scaled to have a mean of 0 and a SD of 1. I also included an interaction term consisting of host species and the first principal component, as ectoparasites may change the primary host, depending on host availability (Benton and Cerwonka, 1960; Krasnov et al., 2011a).

$$\text{logit}(\Psi_{ij}) = a0_i + a1_i PC1_j + a2_i PC2_j \quad (\text{Eq. 1})$$

$$\text{logit}(\theta_{ijk}) = \beta0_i + \beta1_i \text{Species}_{jk} + \beta2_i \text{Mass}_{jk} + \beta3_i \text{Sex}_{jk} \quad (\text{Eq. 2})$$

$$\text{logit}(p_{ijkl}) = \gamma0_i + \gamma1_i \text{Date}_{jkl} + \gamma2_i \text{Capture}_{jkl} \quad (\text{Eq. 3})$$

I analyzed the model using a Bayesian framework using JAGS 4.3.0 (Plummer, 2017) with the R package R2jags (Su and Yajima, 2015). I used uninformative priors for all model parameters. Markov chain Monte Carlo sampling was completed using 3 chains of length 30,000, including a burn-in period of 15,000, thinned by 20 to reduce autocorrelation. Model convergence was assessed by visually examining the trace plots of the Markov chains and using the R-hat statistic (Gelman and Rubin, 1992); an R-hat less than 1.1 was considered converged. Full-model specifications are available in Suppl. Data 3. Because larvae and nymphs of *Ixodes scapularis* vary in their ecology, particularly in phenology and host preferences (Kocan et al., 2015; Levi et al., 2015), I analyzed the model with *I. scapularis* life stages treated as separate taxa. I also analyzed 3 alternative models with (1) *I. scapularis* aggregated, (2) mesostigmatid mites disaggregated, and (3) rare hosts (fewer than 10 captured individuals) removed (Suppl. Data 4).

Because adding parameters to a model will always increase R^2 , I performed model selection using the Watanabe–Akaike information criterion (WAIC) to identify any covariates that contributed relatively little to a model's predictive power. WAIC is an information criterion that performs better for hierarchical Bayesian models than traditional methods such as AIC (Hooten and Hobbs, 2015). I performed model selection separately for the site and host levels of the model. In other words, when calculating the WAIC for each combination of model covariates for the site-level model, the host-level model remained fixed with all covariates and vice versa. Models with the lowest WAIC value were considered the best; models within 2 WAIC values of each other were considered equivalent. Covariates that did not occur in the best models and for which there were no significant taxon-specific coefficients (based on the 75% CI) were removed to achieve a more parsimonious Bayesian R^2 .

I calculated the variance explained by each level of the model using the Bayesian R^2 value proposed by Gelman et al. (2019). In the context of hierarchical models, Bayesian R^2 differs from classical R^2 definitions in 2 important ways: first, other measures of explained variance for hierarchical models are in comparison to a null model (Gelman and Pardoe, 2006), whereas Bayesian R^2 as defined by Gelman et al. (2019) summarizes the fit of each level within a single model. Second, there are certain instances in a Bayesian framework in which the formula for classical R^2 (essentially, explained variance/total variance) can yield a result greater than 1 (Tjur, 2009). Bayesian R^2 always yields a value between 0 and 1 (Eq. 4).

$$\text{Bayesian } R^2 = \frac{\text{Explained variance}}{\text{Explained variance} + \text{residual variance}} \quad (\text{Eq. 4})$$

I calculated Bayesian R^2 for the site and host levels of the model based on Gelman et al. (2019). Further details of the analysis are available in Suppl. Data 3.

Because some generalist parasites can display a clear host preference, while others do not (Benton and Cerwonka, 1960), I further evaluated occupancy patterns of generalist ectoparasites (i.e., occupying 4 or more host species, Poulin et al., 2006) by calculating (1) structural specificity and (2) geographic host specificity (or β -specificity, Poulin et al., 2011). Structural specificity measures the degree to which a parasite population is concentrated on 1 or a few of the host species it parasitizes and can be calculated using an evenness index such as the Bulla index or a diversity index such as the Shannon index (Poulin et al., 2011). Calculating β -specificity is similarly flexible, requiring the adaptation of a dissimilarity index such as the Sørensen index (Diserud and Ødegaard, 2007; Poulin et al., 2011).

I calculated both specificity metrics after adjusting parasite counts based on relative host abundance—a rough way to account for differences in host availability (Poulin, 2007). I quantified structural specificity using the Bulla index, as this index is independent of the number of parasitized host species (Smith and Wilson, 1996). I used the Bray–Curtis multisite dissimilarity index using the R package betapart (Baselga and Orme, 2012) to calculate the β -specificity of generalist parasites. Due to low sample sizes at some geographic sites, I pooled geographic sites by habitat type (e.g., forest, old field, active farm) and then calculated β -specificity across habitats.

To further investigate how parasite occupancy on a given host may change depending on habitat, I examined patterns of ectoparasite occupancy and infrahost abundance (i.e., zero-inclusive counts of collected parasites from a host individual, Bush et al.,

Table I. Number of individual small mammals captured per species, per site in Chittenden County, Vermont, in 2020. Small mammals were captured in various habitats, including farms (Hort2, Hort3, Inter1, Inter2), old fields (Audubon1, StM1, StM2), and forests (Audubon2, Jericho1, Jericho2).

Species	Audubon1	Audubon2	Hort2	Hort3	Inter1
<i>Blarina brevicauda</i>	5	3	1	0	0
<i>Microtus pennsylvanicus</i>	17	0	4	4	6
<i>Peromyscus leucopus</i>	3	39	5	13	25
<i>Zapus hudsonius</i>	30	0	1	0	37
<i>Myodes gapperi</i>	0	4	0	0	0
<i>Napaeozapus insignis</i>	0	4	0	0	0
<i>Peromyscus maniculatus</i>	0	4	0	0	0
<i>Tamias striatus</i>	0	0	4	7	0
Total	55	54	15	24	68
Species	Inter2	Jericho1	Jericho2	StM1	StM2
<i>Blarina brevicauda</i>	3	4	0	0	0
<i>Microtus pennsylvanicus</i>	15	0	0	2	5
<i>Peromyscus leucopus</i>	44	30	30	12	21
<i>Zapus hudsonius</i>	5	0	0	4	1
<i>Myodes gapperi</i>	0	1	0	0	0
<i>Napaeozapus insignis</i>	0	0	0	0	0
<i>Peromyscus maniculatus</i>	0	2	3	1	0
<i>Tamias striatus</i>	2	11	3	2	0
Total	69	48	36	21	27

1997) on host species that occurred in multiple habitat types. For each host from which I collected ectoparasites in multiple habitat types, I used a zero-inflated negative binomial regression with the first component of the PCA described previously as the predictor variable and (1) the presence or absence of ectoparasites on an individual host and (2) number of ectoparasites collected from a host as the response variables. I performed the analysis using the R package *pscl* (Zeileis et al., 2008). Changes in occupancy or the number of collected parasites would suggest that ectoparasite infracomunities change, depending on habitat context.

RESULTS

Data summary

The raw data consisted of 753 capture events representing 11 species. Of these, 2 nontarget species (*Tamiasciurus hudsonicus* and *Mustela* sp.) and 1 species in which the only individual was found dead in the trap (*Sorex cinereus*) were removed from the dataset. An additional 11 individuals that were found dead in the trap before the final day of sampling (2 *Microtus pennsylvanicus*, 9 *Blarina brevicauda*) were also removed from the dataset. The final dataset consisted of 417 unique individuals representing 8 species (Table I), of which 162 individuals were captured more than once. The most common species was the white-footed mouse (*Peromyscus leucopus*) with 219 individuals, followed by the meadow jumping mouse (*Zapus hudsonius*) with 76 individuals. The least abundant species was the woodland jumping mouse *Napaeozapus insignis* with 4 captured individuals.

I collected 410 ectoparasites representing 4 orders and at least 17 species from the captured small mammals (Table II). Prevalence (i.e., the proportion of hosts from which at least 1 ectoparasite was collected: Bush et al., 1997), averaged 0.465 across all host species and ranged from 0.105 to 0.788 among host species (Fig. S2). Parasite intensity (i.e., counts of collected ectoparasites per host individual, excluding zeros; Bush et al. 1997) per capture

Table II. Number of individuals of each ectoparasite species collected from small mammal communities in Chittenden County, Vermont, in 2020.

Species	No. collected
<i>Ctenophthalmus pseudagyrtes</i>	11
<i>Cuterebra fontinella</i>	7
<i>Doratopsylla blarinae</i>	1
<i>Epitedia wenmanni</i>	2
<i>Ixodes scapularis</i> larva	87
<i>Ixodes scapularis</i> nymph	12
<i>Megabothris acerbus</i>	8
<i>Megabothris asio</i>	6
<i>Megabothris quirini</i>	53
<i>Monopsyllus vison</i>	1
<i>Orchopeas howardii</i>	1
<i>Orchopeas leucopus</i>	192
<i>Peromyscopsylla hesperomys</i>	4
<i>Peromyscopsylla scotti</i>	1
Unknown Mesostigmata	21

event was typically 1 ectoparasite, with a range of 1–10 parasites (Fig. S3).

Vegetation composition, vegetation height, and canopy cover were highly correlated ($r = 0.844$), and the PCA with all vegetation data indicated that most of the variation in the data was explained by composition variables (Table S1). Thus, the results of the composition-only PCA were included in the model (Table S2). The PCA yielded a first principal component that explained 92.5% of the variation in the vegetation data and ranged from primarily grass and forb cover to primarily dead vegetation, specifically leaf litter (Fig. S4). The second principal component explained 7.2% of the variation in the data and ranged from primarily grass cover to primarily forb cover. The remaining principal components explained less than 5% of the variation in the data and were not included in the model.

The MMRR yielded no significant associations between geographic distance and PC1 ($F = 0.148$, $P = 0.661$, $R^2 = 0.003$) or between geographic distance and host community composition ($F = 0.067$, $P = 0.783$, $R^2 = 0.002$). Another MMRR with ectoparasite community distance as the response variable and vegetation distance, geographic distance, and host community distance as predictors was not significant overall ($F = 2.451$, $P = 0.174$, $R^2 = 0.152$), but there was a significant association between ectoparasite community distance and vegetation distance ($t = 2.262$, $P = 0.020$).

As reported in previous host–ectoparasite systems, there was a significant, positive association between the number of host species parasitized by an ectoparasite taxon and the log-transformed total abundance (i.e., counts of collected ectoparasites across all host individuals) of an ectoparasite taxon ($F_{1,13} = 30.65$, $P < 0.001$, $R^2 = 0.679$; Fig. 1). There was also a positive, albeit non-significant, relationship between host richness and ectoparasite richness ($F_{1,8} = 5.184$, $P = 0.052$, $R^2 = 0.317$; Fig. S5).

Model results

All models presented in the main text and Suppl. Data 4 converged based on R-hat values less than 1.1 and visual inspection of the trace plots (Fig. S6).

The results of the model with *I. scapularis* disaggregated and the Mesostigmata aggregated are shown in the following. This model was chosen because larval and nymph *I. scapularis* differ in

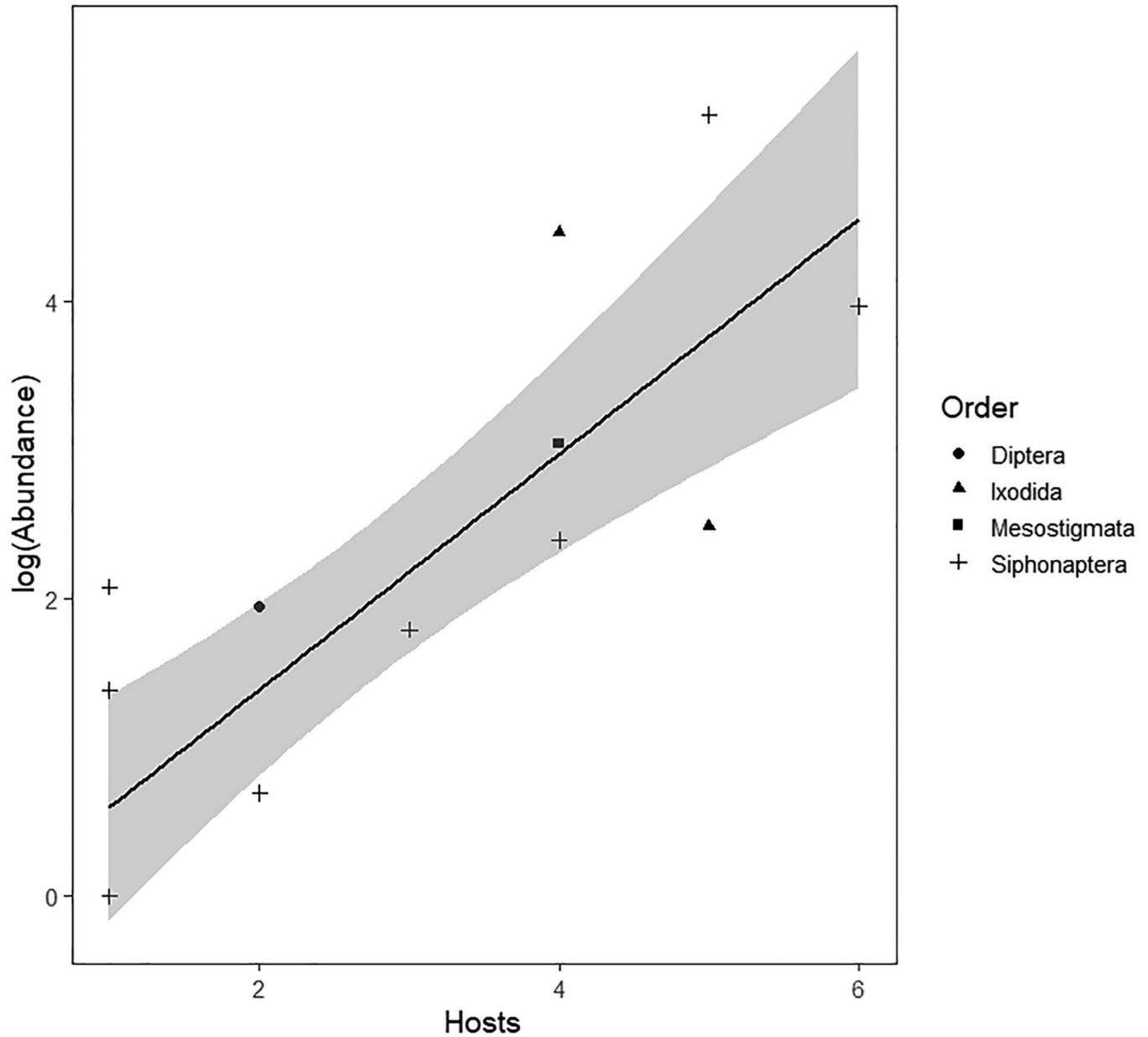


Figure 1. Associations between host range (i.e., number of host species parasitized by an ectoparasite species) and the log total abundance (i.e., counts of collected ectoparasites across all host individuals) of the ectoparasite species in Chittenden County, Vermont. Shapes denote ectoparasite order. There was a significant, positive association between number of hosts and log abundance ($F_{1,13} = 30.65$, $P < 0.001$, $R^2 = 0.679$).

certain covariate responses (e.g., Fig. S7) and structural and β -specificity (Table III), whereas the Mesostigmata typically do not vary in covariate responses (e.g., Fig. S6 in Suppl. Data 4) and identifiable genera of Mesostigmata typically parasitize too few host species for structural and β -specificity to be useful. Results for models with *I. scapularis* aggregated, Mesostigmata disaggregated, and rare hosts removed typically only differed for the parasite taxa that were involved in the change (i.e., aggregating *I. scapularis* only changes the results for *I. scapularis*; S4).

Model selection at the site level did not yield clear results, with 6 models performing equally well (Table S3). However, the covariate for host abundance was only in 2 of the 6 best models, and no ectoparasite taxa had significant responses to this covariate

based on the 75% CI. Therefore, the results in the following are from a model that did not include host abundance. A model including host mass and host sex performed best at the host level (Table S4), but because many ectoparasite taxa had significant responses to host species and the interaction term based on the 75% CI (Tables S5, S6), the following results are from a model that included all 4 host covariates.

Ectoparasites varied in detectability based on the number of times the host was captured (Fig. S8a) and Julian date (Fig. S8b), based on the 75% CI. Larval *I. scapularis*, *Megabothris quirini*, and the Mesostigmata were more likely to be detected in earlier captures, whereas *Orchopeas leucopus* was more likely to be detected after a host was captured multiple times. Larval *I.*

Table III. Structural and β -specificity of generalist ectoparasites collected from small mammals in Chittenden County, Vermont. Structural specificity was measured using the Bulla index; lower values correspond to higher evenness across infested host species. The β -specificity was measured using the Bray–Curtis multisite dissimilarity index.

Parasite	No. host species	Structural specificity	β -specificity
<i>Ctenophthalmus pseudagyrtus</i>	4	0.586	0.866
<i>Ixodes scapularis</i> (larva)	5	0.367	0.775
<i>Ixodes scapularis</i> (nymph)	5	0.721	1.00
<i>Megabothris quirini</i>	6	0.556	0.933
<i>Orchopeas leucopus</i>	5	0.472	0.892
Mesostigmata	4	0.379	0.646

scapularis, *M. quirini*, and *O. leucopus* were more likely to be detected earlier in the year.

Host range, or the number of host species parasitized by an ectoparasite, was not significantly associated with Bayesian R^2 at the site level ($F_{1,13} = 3.309$, $P = 0.092$, $R^2 = 0.142$; Fig. 2a). There was a significant, positive relationship between host range and Bayesian R^2 at the host level ($F_{1,13} = 14.35$, $P = 0.002$, $R^2 = 0.488$; Fig. 2b), suggesting that the host-level model has greater explanatory power for host generalists.

Generalist parasites, or parasites that were collected from 4 or more host species, varied in structural and β -specificity (Table III). *Ixodes scapularis* larvae and mesostigmatid mites had the lowest structural specificity, meaning these parasites were the most concentrated upon a single-host species. Estimates from the host species covariate of the host-level model support these findings (based on the 75% CI): *I. scapularis* larvae were more likely to occupy *P. leucopus* compared with *Tamias striatus*, *Z. hudsonius*, and *M. pennsylvanicus*, whereas the Mesostigmata were positively associated with *M. pennsylvanicus* (Table S5). By contrast,

I. scapularis nymphs were more evenly distributed among parasitized host species and did not have any significant host preferences based on the 75% CI.

All generalist ectoparasites demonstrated relatively high β -specificity values, indicating that each parasite's distribution among hosts changed to some degree based on habitat (Table III). Mesostigmatid mites had the lowest β -specificity, indicating that the host preference of this taxon changed the least based on habitat (Fig. S9b). The lack of a significant coefficient for the interaction term between host species and vegetation composition supports this finding (Table S6). The β -specificity for *I. scapularis* larvae was also fairly low: this parasite tended to prefer *Peromyscus* spp. across all habitats, but it occasionally occurred on *M. pennsylvanicus* and *Z. hudsonius* in old fields (Fig. 3). *Ixodes scapularis* nymphs and *M. quirini* had the highest β -specificity: the former demonstrated complete turnover of host species between habitat types (Fig. 3). Although *M. quirini* occasionally occurred on *P. leucopus* in all habitat types, it primarily infested *Z. hudsonius* and *M. pennsylvanicus* in farms and old fields and preferred *N. insignis* and *Myodes gapperi* in forests (Fig. 3; Table S6 in Suppl. Data 1).

Hosts that occurred in multiple habitat types tended to have fewer parasites in open habitats compared with wooded habitats (*P. leucopus* coefficient = 0.458, SE = 0.103, $Z = 4.442$, $P < 0.001$; *T. striatus* coefficient = 1.135, SE = 0.3575, $Z = 3.174$, $P = 0.002$; Fig. 4). However, the proportion of hosts from which at least 1 ectoparasite was collected did not vary with habitat (*P. leucopus* coefficient = 5.667, SE = 5.374, $Z = 1.055$, $P = 0.292$; *T. striatus* coefficient = 1.165, SE = 1.568, $Z = 1.052$, $P = 0.293$).

DISCUSSION

Contrary to the hypotheses presented previously, host-level covariates explained more variation in occupancy for generalist parasites than specialist parasites (Fig. 2b). This pattern may be

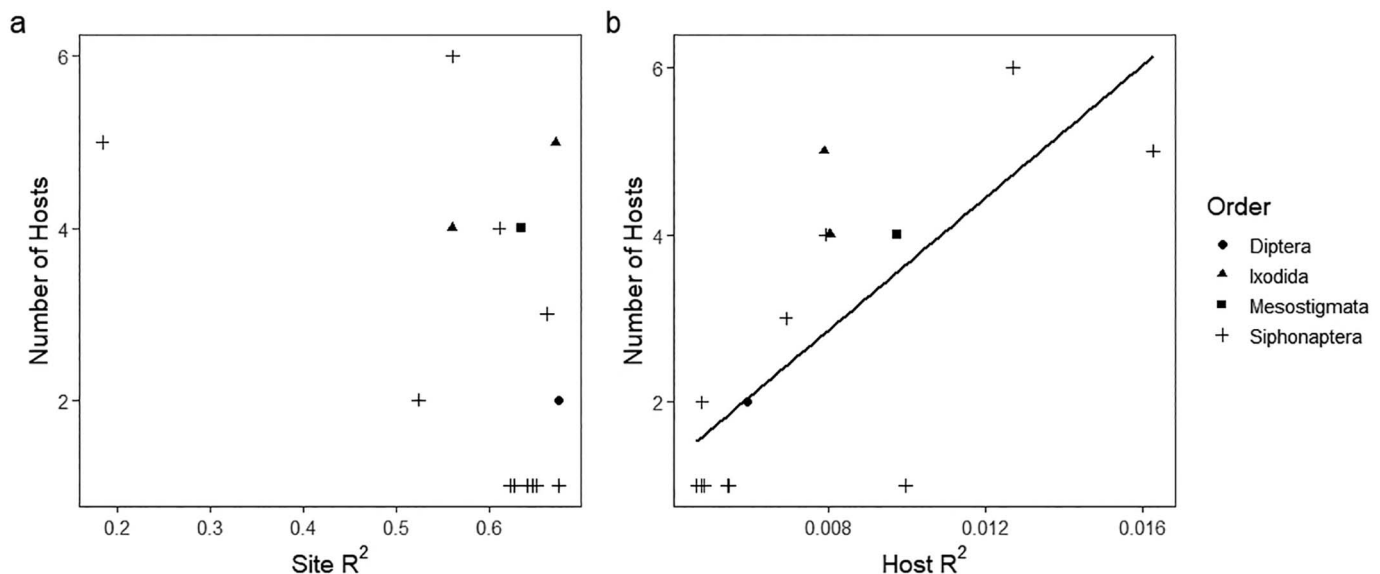


Figure 2. Associations between Bayesian R^2 from the site level (a) and host level (b) of the model and host range of each ectoparasite species. Point shapes denote order. There was a significant, positive relationship between host-level R^2 and host range (b), indicating that host-level covariates tended to explain more variation in occupancy for generalist parasites ($F_{1,13} = 14.35$, $P = 0.002$, $R^2 = 0.488$). There were no significant associations between site-level R^2 and host range ($F_{1,13} = 3.309$, $P = 0.092$, $R^2 = 0.142$); this pattern persisted even when the outlier *Orchopeas leucopus* was removed ($F_{1,12} = 2.058$, $P = 0.177$, $R^2 = 0.075$).

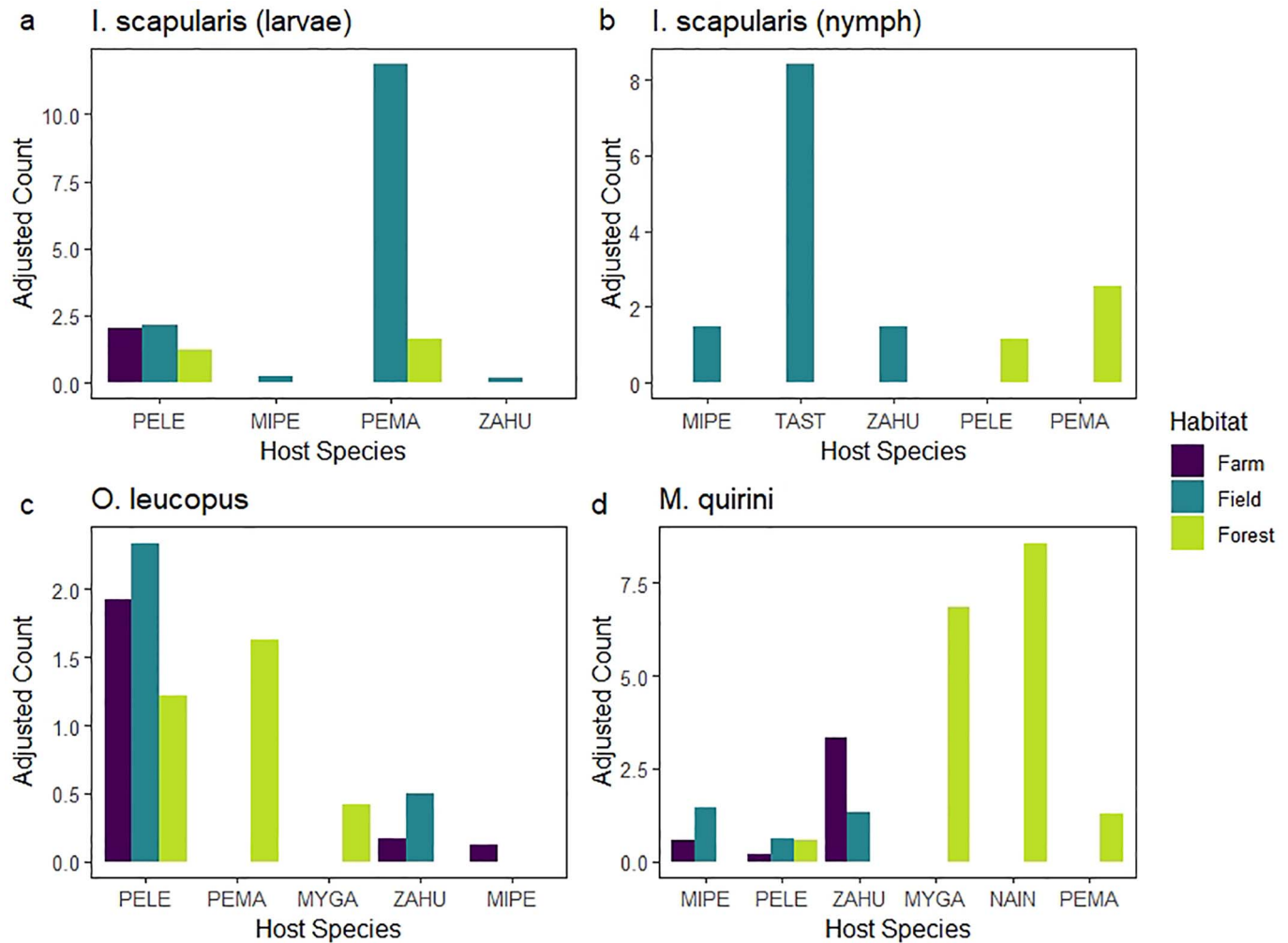


Figure 3. Counts of collected *Ixodes scapularis* larvae (a), *I. scapularis* nymphs (b), *Orchopeas leucopus* (c), and *Megabothris quirini* (d) on various host species adjusted for relative host abundance. Larval *I. scapularis* (a) and *O. leucopus* (c) are more likely to occupy *Peromyscus* spp. regardless of habitat and rarely occur on other hosts. By contrast, host preferences of *I. scapularis* nymphs (b) and *M. quirini* (d) are habitat dependent. Host abbreviations are as follows: PELE = *P. leucopus*; MIPE = *Microtus pennsylvanicus*; PEMA = *P. maniculatus*; ZAHU = *Zapus hudsonius*; TAST = *Tamias striatus*; MYGA = *Myodes gapperi*; and NAIN = *Napaeozapus insignis*. Color version available online.

due to the high structural specificity of some generalist parasites, such as *I. scapularis* larvae or mesostigmatid mites: these parasites display a strong preference for 1 or a few hosts (Tables S5, S6), effectively acting as host specialists, while incidentally occurring on other host species. Furthermore, structural generalists such as *I. scapularis* nymphs or *M. quirini* display high β -specificity, in which the probability of these ectoparasites occupying a given host species depends on the habitat context (Fig. 3; Table III). These results suggest that host characteristics and the environmental context in which the host is encountered are important for all parasites, regardless of host specialization.

Although there is no clear relationship between the explanatory power of site-level characteristics and host range (Fig. 2a), characteristics of the external habitat still influence ectoparasite occupancy. The relatively high Bayesian R^2 values indicate site-level covariates explain a large portion of the variation in site-level occupancy; even though these covariates are not associated with host range (Fig. 2a). In addition, both generalists (*I. scapularis*, *Ctenophthalmus pseudagrytes*) and specialists (*M. acerbus*,

Peromyscopsylla hesperomys) demonstrate significant responses to site-level covariates based on the 75% CI (Fig. S10). Furthermore, hosts that occurred in multiple habitats (*P. leucopus* and *T. striatus*) typically had reduced parasite abundance in open habitats compared with the preferred forested habitats (Fig. 4). An examination of counts of parasites collected from *P. leucopus* demonstrates that the decrease in parasite abundance applies to many parasite taxa: generalist parasites, such as *I. scapularis* and *O. leucopus*, are less abundant in open habitats and specialists, such as *P. hesperomys*, were not detected (Table S7). This pattern cannot be fully explained by decreased host abundance in open habitats: *P. leucopus* tends to be less abundant in fields but not farms (99 and 87 captured in forests and farms, respectively, vs. 36 in fields), as does *T. striatus* (14 individuals in forests, 13 in farms, 2 in fields). The decrease in intensity may be due to the biology of the parasites themselves: parasites that can survive off the host may be leaving the host to seek a more favorable environment, parasites may be unable to complete the life cycle in the unfavorable environment, or both. For example, the survival of

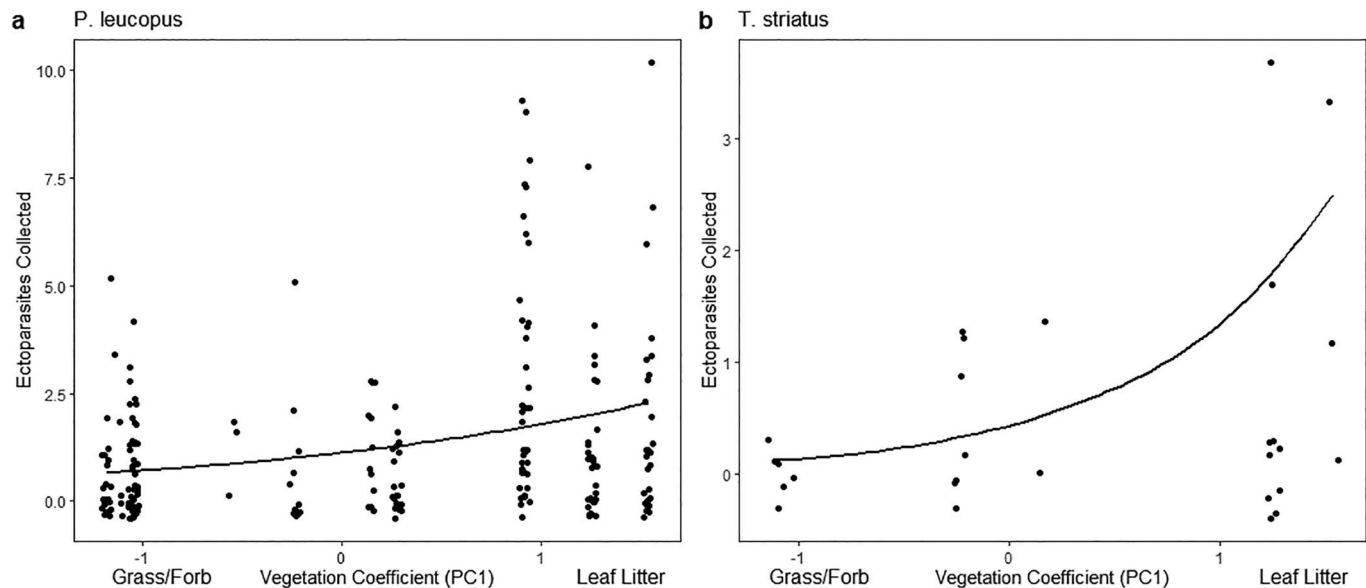


Figure 4. Results of the count model from a zero-inflated negative binomial regression for *Peromyscus leucopus* (a) and *Tamias striatus* (b). There were significant, positive associations between ectoparasite abundance (i.e., zero-inclusive counts of ectoparasites collected from each host individual) and site-level dead vegetation cover for both species (*P. leucopus* coefficient = 0.458, SE = 0.103, $Z = 4.442$, $P < 0.001$; *T. striatus* coefficient = 1.135, SE = 0.3575, $Z = 3.174$, $P = 0.002$). There were no significant associations between ectoparasite occupancy per host and dead vegetation cover (*P. leucopus* coefficient = 5.667, SE = 5.374, $Z = 1.055$, $P = 0.292$; *T. striatus* coefficient = 1.165, SE = 1.568, $Z = 1.052$, $P = 0.293$).

overwintering *I. scapularis* nymphs is higher in sites with greater soil organic matter such as leaf litter (Burtis et al., 2019), so nymphs that detach from the host in open habitats may be less likely to overwinter successfully. Further work is needed to disentangle the effects of the external habitat on ectoparasite occupancy from effects due to host availability.

Conspicuously absent from the data are lice (Order Psocoda) and other species of ticks, which may be affecting the findings discussed previously. The ticks *Ixodes cookei* and *Ixodes angustus* have been previously recovered from small mammals in Vermont (Zadock Thompson Zoological Collections, unpubl. data); however, these species were unlikely to be collected in large numbers due to a preference for larger hosts (*I. cookei*; Scuridae and Carnivora, Durden and Keirans, 1996) and for higher elevations (*I. angustus*; Coley, 2015). Lice are known to parasitize several of the host species captured during the sampling period (e.g., Whitaker and French, 1982; Zadock Thompson Zoological Collections, unpubl. data) but are very difficult to collect from living nonseated hosts, hence, the lack of lice in this dataset. Future work integrating samples from museum specimens and samples from living mammals could be an important step in filling this data gap.

Despite a clear relationship between host range and host-level Bayesian R^2 , the explanatory power of the host model was very low (Fig. 2b). Although this may seem counterintuitive given that many ectoparasites yielded significant responses to model covariates based on the 75% CI, the finding makes sense in the context of the structure of the multiscale MSOM. Because there is more variability in occupancy between host individuals than between host populations (i.e., more variability at the host than site levels), it is more difficult to predict ectoparasite occupancy on an individual host. Previous work has shown similar findings, in which parasite infracommunities (i.e., communities on an individual host) appear to be stochastically structured despite parasite

communities displaying nonrandom structure at the host population level (Rynkiewicz et al., 2019). A null model analysis would be useful in determining whether infracommunities are structured stochastically (Gotelli, 2001; Ulrich and Gotelli, 2013; Canard et al., 2014), but such an analysis is beyond the scope of this article.

These results highlight that the terms generalist and specialist are highly context dependent (Devictor et al., 2010). As discussed previously, the methods used to define and quantify these terms influence which parasite species are labeled generalists or specialists. Within this study, some parasites labeled generalists, when the term is defined using host range, behave more like specialists, when the term is defined in relation to how individuals are distributed among parasitized hosts (Fig. 3; Table III; Krasnov et al., 2004b; Poulin et al., 2011). Different populations of a given parasite can also vary in the degree of host specialization, depending on host availability and local environmental conditions (Poulin et al., 2006); thus, the geographic, host taxonomic, and temporal extent of a given study can affect the observed host specialization (Devictor et al., 2010; Rivera-García et al., 2017). Some generalists within this study occupy different assemblages of host species in different habitats (Fig. 3; β -specificity, Table III; Krasnov et al., 2011a; Poulin et al., 2011), and limiting this study to 1 habitat type would result in these species appearing more specialized than they are. Observed host specificity is also highly dependent on the number of hosts sampled (Poulin, 2011, 2019), and parasites that can occupy less abundant host species may be missing from this dataset. Despite these constraints, host specificity can still be considered a species trait (i.e., repeatable among different populations of the same species; Krasnov et al., 2004a) and can be a useful tool for quantifying parasite niche breadth, provided definitions are consistent and clearly defined (Poulin and Mouillot, 2003; Poulin et al., 2011).

These results demonstrate that generalist parasites vary in host specificity and occupancy patterns, with some generalist parasites acting as specialists and only incidentally occurring on other host species. One possible evolutionary explanation for these results is ecologic fitting (Agosta and Klemens, 2008; Agosta et al., 2010; Araujo et al., 2015): essentially, ectoparasites vary in the ancestral operative environment (e.g., characteristics of the ancestral host under which a parasite achieves high realized fitness) and *sloppy fitness space* (e.g., the range of conditions outside of the operative environment that a parasite can still exploit). Under this hypothesis, there are 2 potential paths to generalism: ectoparasites with a wide operative environment that encompasses several hosts and ectoparasites with a narrow operative environment but wide sloppy fitness space that allows them to incidentally exploit other hosts that they may encounter (Agosta et al., 2010). The latter case may be particularly applicable in the case of structural specialists such as *I. scapularis* larvae, which in this dataset may be exploiting “novel” hosts such as *Z. hudsonius* and *M. pennsylvanicus*, as a result of populations of the primary host *P. leucopus* moving into nonpreferred habitats (Brooks and Boeger, 2019). Although ecologic fitting is a plausible explanation for the variation in host specificity among generalist parasites, the hypothesis cannot be directly tested using the data presented here. Future work may involve evaluating the fitness of generalist ectoparasites on a variety of possible hosts, which can then be used to determine whether these parasites vary in the preferred operative environment and sloppy fitness space (e.g., Khokhlova et al., 2022).

Determining which taxa can be found where is a key component of community ecology, and evaluating characteristics of a species’ niche can provide important information on the range of habitats a species potentially occupies or may colonize in the future (Swihart et al., 2006; Rocha et al., 2018). The latter scenario is particularly important in the context of emerging infectious diseases, as accelerating climate change provides new opportunities for the colonization of new hosts due to shifts in host ranges (Brooks and Boeger, 2019; Wells and Clark, 2019; Singer and Parmesan, 2021; Brooks et al., 2022; Feronato et al., 2022). As this study and others indicate, estimating which parasite species may colonize a new host is more complex than quantifying specialization via host range. Rather, quantifying specialization using more informative metrics than host range and using hierarchical methods to account for the environmental dependency of specialization (Fecchio et al., 2019) can provide more accurate predictions of which parasite species may be able to occupy and persist on a novel host and increase the transmission risk of emerging infectious diseases.

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