Relative importance of host environment, transmission potential and host phylogeny to the structure of parasite metacommunities

Tad Dallas and Steven J. Presley

T. Dallas (tdallas@uga.edu), Odum School of Ecology, Univ. of Georgia, Athens, GA 30606–4288, USA. – S. J. Presley, Center for Environmental Sciences and Engineering and Dept of Ecology and Evolutionary Biology, Univ. of Connecticut, Storrs, CT 06269–4210, USA.

Identification of mechanisms that shape parasite community and metacommunity structures have important implications to host health, disease transmission, and the understanding of community assembly in general. Using a long-term dataset on parasites from desert rodents, we examined the relative contributions of host traits that represent important aspects of parasite environment, transmission probability between host species, and host phylogeny to the structure of a parasite metacommunity as well as for taxonomically restricted parasite metacommunities (coccidians, ectoparasites and helminths). This was done using a combination of metacommunity analysis and variance partitioning based on canonical correspondence analysis. Coccidian and ectoparasite metacommunities did not exhibit coherent structure. In contrast, helminths and the full parasite metacommunity had Clementsian and quasi-Clementsian structure, respectively, indicating that parasite species distributions for these metacommunities were compartmentalized along a dominant gradient. Variance decomposition indicated that characteristics associated with the host environment consistently explained more variation than did host traits associated with transmission opportunities or host phylogeny, indicating that the host environment is primary in shaping parasite species distributions among host species. Moreover, the importance of different types of host traits in structuring parasite metacommunities was consistent among taxonomic groups (i.e. full metacommunity, coccidians, and helminths) despite manifest differences in emergent structures (i.e. Clementsian, quasi-Clementsian, and random) that arose in response to variation in host environment.

The emergence of "spatial parasitology" (Guégan et al. 2005) has formed increasingly strong mutualisms among ecology, evolutionary biology and biogeography (Thomas et al. 2005). Indeed, the use of parasite populations, communities and metacommunities as model systems has advanced ecological, evolutionary and biogeographical theory, while application of those theories to parasitic systems has enhanced understanding of interactions among parasites as well as between parasites and their hosts and environments. More specifically, parasite systems have been useful in the study of facilitation (Krasnov et al. 2005a), sexual selection (Moore and Wilson 2002), sex allocation (Presley 2012), density compensation (Tello et al. 2008), relative effects of phylogeny and environmental variation on community composition (Krasnov et al. 2004, 2010), geographical variation in the nature of species interactions (Krasnov et al. 2004, 2006), roles of stochastic processes (Poulin 1996) or priority effects (Norton et al. 2004) in structuring communities, and mechanisms associated with nested subsets (Zelmer and Arai 2004, Zelmer et al. 2004, Krasnov et al. 2005b, 2011, Presley 2007), island biogeography (Kuris et al. 1980), and network theory (Lima et al. 2012).

Here, we provide an application of metacommunity theory to parasite communities, with the goal of determining the mechanisms structuring parasite assemblages among host species. Metacommunity theory, specifically the creation of the elements of metacommunity structure framework (hereafter EMS framework; Leibold and Mikkelson 2002), has provided a new way to examine emergent structures that result from structuring mechanisms (Leibold et al. 2004, Holyoak et al. 2005). A metacommunity is a set of ecological communities at different sites (potentially but not necessarily linked by dispersal), whereas a community is a group of species at a given site (Leibold and Mikkelson 2002). The EMS framework evaluates three characteristics of species distributions to distinguish between 14 different metacommunity structures (Presley et al. 2010). Although the EMS framework can determine the best fit structural model for a metacommunity, additional analyses are required to determine the gradient and nature of that gradient (i.e. environmental factors associated with spatial variation,) along which a metacommunity is structured (Presley et al. 2009, López-González et al. 2012) or the likely mechanisms that gave rise to a particular structure (Meynard et al. 2013). We employ variance partitioning based on canonical correspondence analysis to determine the relative contributions of different types of host characteristics to gradients along which parasite metacommunities are structured.

In general, parasite communities are more similar on hosts that are geographically, phylogenetically, ecologically

or developmentally similar (Locke et al. 2013). Similarity of parasite community composition often is associated with characteristics of host populations or species (Krasnov et al. 2010, Poulin 2010), with these characteristics potentially affecting transmission or establishment of parasites. However, which host traits have strong associations with variation in parasite composition often differs, reflecting variation in the autecology of hosts and their parasites. For example, evolutionary distance was a strong predictor of metazoan parasite community similarity among freshwater cyprinids (Seifertová et al. 2008), but was a poor predictor for another freshwater system (Poulin 2010).

In our conceptual framework, a community contains all parasite species found on a host species and communities are connected via transmission of parasites between host species. Some host characteristics (e.g. abundance or density, home range size, dietary breadth) may affect parasite metacommunity structure primarily by influencing transmission opportunities. More specifically, these variables can influence interspecific transmission of parasites via effects related to host quality, for which host abundance is often an effective proxy (Rigaud et al. 2010). Alternatively, host traits such as dietary breadth can affect host contact rates with parasites, with greater diet diversity leading to greater parasite diversity (Locke et al. 2014). In addition, host species differ in characteristics that represent the environment in which parasites live, creating a gradient among host species in the suitability of the host environment for establishment of parasite populations. Host characteristics such as body size, metabolic rate, trophic status, and reproductive characteristics may be analogous to patch quality in the traditional metacommunity framework, as these variables influence successful colonization and propagation of parasite species on hosts (Kuris et al. 1980, Combes 2004, Poulin et al. 2011). Indeed, many of these host traits are often used as proxies for host quality (Rigaud et al. 2010), which may affect parasite population dynamics as well as composition and diversity of communities. Finally, host phylogeny represents variation in unmeasured host traits as well as the co-evolutionary relationship between host and parasite. By using these three types of host traits, we can identify the relative importance of host environment, transmission opportunities afforded by the host, and host phylogeny on molding metacommunity structure of parasites. In addition, the use of phylogeny in the variance partitioning framework allows us to control for any phylogenetic signal present in host traits. Using this approach, we draw on three dimensions of biodiversity (taxonomic, functional and phylogenetic; World Resource Institute 1992) to integrate evolutionary and ecological processes that structure metacommunities. More specifically, we use information on host phylogeny and host functional traits to understand variation in parasite community composition among host species.

Small mammals and their parasites represent ideal systems for examining metacommunity structure. Many hosts are abundant, harbor numerous parasite individuals and species, serve as vectors of disease, and are important contributors to terrestrial ecosystem structure (Morand et al. 2006). We applied the EMS framework to data gathered over six years on parasites of Sonoran Desert rodents, collected as part of the Sevilleta Long Term Ecological Research

(LTER) project. These data provide a uniquely detailed examination of the parasite community, including data on ectoparasites, helminths and coccidians. In our analysis of parasite metacommunities on small mammals, host species are equivalent to sites, and host traits represent environmental characteristics, transmission potential among host species, or variation in unmeasured host traits and co-evolutionary relationship between hosts and parasites. The application of metacommunity theory to parasite communities, specifically in combination with null model analyses such as ours (HilleRisLambers et al. 2012), allows for clearer identification of structuring forces in parasite species distributions among sympatric hosts (Mayfield and Levine 2010, Pavoine et al. 2011, Mihaljevic 2012, Richgels et al. 2013).

Based on the ecology of host–parasite systems, we make two predictions about metacommunity structure for parasites of desert rodent hosts. First, we expect parasite metacommunities to be coherent, because many parasitic species exhibit host preferences as a function of shared evolutionary history or shared derived host traits. However, we expect parasites to have independent responses along this gradient. This combination of responses is consistent with Gleasonian structure (Leibold and Mikkelson 2002). Second, we expect host traits that define the environment for parasites as well as host traits that affect transmission potential to each account for significant unique variation in parasite community composition among host species after accounting for variation associated with host phylogeny. In general, parasites are highly adapted to their host environments (Kim 1985, Poulin 2011); therefore, we expect that host traits will explain a significant amount of variation in parasite communities among host species. Because of ecological differences among parasite groups, each group may evince different responses to variation in host environment, transmission, and phylogeny. For this reason, we performed analyses for both primary and secondary ordination axes and for the full parasite metacommunity (herein defined as ectoparasitic arthropods, coccidians and helminths, recognizing that other undetected parasites may exist on these hosts), as well as for subsets based on parasite group (i.e. coccidians, ectoparasites, helminths).

Methods

Study site

Rodent and parasite data (available at <http://sev.lternet. edu/data/sev-13>) were collected as part of the Sevilleta Long-Term Ecological Research (LTER) project, located in central New Mexico. Six small mammal kill webs, each comprised of 145 traps, were sampled in early and late summer. Data are from 1992 to 1997, and represent 2547 parasitized host individuals belonging to 15 host species that were parasitized by 65 parasite species. Endo- and ecto-parasites were examined by necropsy, following the methodology of Duszynski and Wilber (1997), including examination of host coat, stomach, intestines, body cavity and feces. The thorough treatment of each host ensured that these data represent accurate records of parasite infracommunities. To ensure that parasite communities for host species were sufficiently well

characterized, we only analyzed host species captured at least five times during the six year sampling effort.

Metacommunity data

Host-by-parasite presence–absence data were assembled for the full parasite community and for each of three taxonomic subsets: coccidians, ectoparasites and helminths. Taxon-specific parasite metacommunities are likely structured by different factors, as environmental conditions for an endoparasite (such as a coccidian) are different from those of an ectoparasite. For all analyses, unparasitized host species were removed from site-by-species matrices prior to ordination (one and two hosts removed for coccidians and ectoparasites, respectively).

Elements of metacommunity structure

The framework to evaluate metacommunity structure is based on analysis of presence–absence data to quantify three aspects of species distributions: coherence, species turnover, and range boundary clumping (Leibold and Mikkelson 2002, Presley et al. 2010). Analyses are based on ordination via reciprocal averaging (Gauch 1982), which simultaneously maximizes the correspondence of parasite species distributions among hosts and the correspondence of parasite community compositions of host species. Axis scores from this ordination represent a gradient of similarity of parasite community composition among host species. Details regarding the analytical and conceptual approach for identifying metacommunity structures are available elsewhere (Leibold and Mikkelson 2002, Presley et al. 2009, 2010). For a metacommunity to be coherent, two things must be true. First, species occurrences must be a function of environmental characteristics that differ among sites (i.e. host species) and that represent a gradient of environmental variation to which species respond. Second, a majority of species in the metacommunity must respond to the same gradient. Metacommunities that do not exhibit coherence are said to have random structure. Note that random structure does not indicate that species occur at random in the metacommunity, but indicates only that species distributions are independent of one another (i.e. distributions are not determined by the same environmental gradient). Negative coherence is indicative of checkerboards. For a checkerboard structure to manifest for a metacommunity, and not just for pairs of species, the environmental distributions of mutually exclusive species pairs must be independent of other such pairs, resulting in a structure that is reminiscent of, but not identical to, that

first proposed by Diamond (1975). In contrast, each coherent structure requires species distributions to be molded by a common environmental gradient that may represent a combination of biotic and abiotic factors that differ among sites. Structures must be coherent for metrics of species turnover and range boundary clumping to effectively reflect the concepts that they are intended to measure (Leibold and Mikkelson 2002); therefore, turnover and boundary clumping are only analyzed for coherent metacommunities. Twelve coherent structures are defined by unique combinations of species range turnover and range boundary clumping (Presley et al. 2010). Nested structures are characterized by negative turnover, whereas Clementsian, Gleasonian and evenly spaced structures are defined by positive turnover. Boundary clumping can distinguish three types of nested subsets (with clumped species loss, stochastic species loss or hyperdispersed species loss) as well as Clementsian (clumped boundaries), Gleasonian (stochastic distribution of boundaries), and evenly spaced (hyperdispersed boundaries) structures (Table 1). Each of these six structures has an analogous quasi-structure (Presley et al. 2010), which are defined by stochastic range turnover. The EMS framework can be viewed as a three-dimensional space, in which communities represent points in space (Fig. 1), allowing metacommunities to be qualitatively compared to one another. Analyses of metacommunity structure were performed using the *metacom* package ver. 1.3 (Dallas 2013) in R ver. 2.15, relying heavily on the *vegan* package (Oksanen et al. 2013).

A recent evaluation of pattern detection via null model analysis attempted to resolve seemingly incongruent results that may be derived from a diverse suite of metrics that are designed to detect different non-random (e.g. nestedness, coherence, aggregation, segregation) aspects of presence–absence data in site-by-species matrices (Ulrich and Gotelli 2012). That work questioned the ability of the combined analysis of coherence, range turnover and range boundary clumping to detect distinct patterns along particular environmental gradients. Nonetheless, analyses of coherence exhibited good type I error properties when an appropriate null model was used and Morisita's index exhibited good power at detecting compartmentalized structures (Ulrich and Gotelli 2012), validating these metrics in the analytical framework of Leibold and Mikkelson (2002). Unfortunately, Ulrich and Gotelli (2012) did not use a metric that measures range turnover among all species in a metacommunity or evaluate the ability of combinations of coherence, range turnover and range boundary clumping to distinguish among different structures along a particular gradient, negating the studies ability to effectively evaluate the conceptual

Table 1. Summary of the 6 idealized metacommunity structures and their respective results for analyses of coherence, range turnover and boundary clumping.

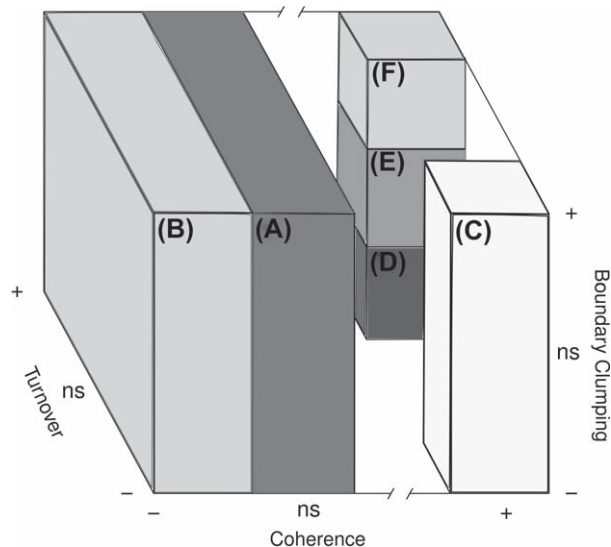| Pattern	Definition	Coherence	Turnover	Boundary clumping
Random	species ranges follow no detectable gradient	ns	+;−; ns	+;−; ns
Checkerboards	species pairs have mutually exclusive distributions	−	+;−; ns	+;−; ns
Nested subsets	species ranges form nested groups	+	−	+;−; ns
Evenly spaced gradients	species ranges distributed evenly across gradient	+	+	−
Gleasonian	species ranges adhere to gradient, but do so individualistically	+	+	ns
Clementsian	species ranges form groups, which replace each other along gradient	+	+	+

Figure 1. Conceptual diagram showing the relationships of six idealized metacommunity structures (Table 1) in three dimensional space characterized by coherence, turnover, and boundary clumping. (A) random, (B) checkerboard, (C) nested subsets, (D) evenly spaced gradients, (E) Gleasonian, (F) Clementsian. The x-axis is broken to better show relationships among patterns (C-F).

and analytical framework. Analyses of metacommunity structure only evaluate structure along specific latent environmental gradients as defined by reciprocal averaging (Leibold and Mikkelson 2002) and the same metacommunity may exhibit different structures along different axes (Presley et al. 2009, 2011). One cannot ignore the axis along which the analysis is being conducted. For example, if an island metacommunity is nested along a gradient of richness, but richness is not associated with island size or island isolation, it would not be surprising to discover that the metacommunity was not nested along gradients of island size or isolation. Similarly, it should not be surprising to discover that analyses conducted with respect to different gradients may exhibit different structures.

Host traits associated with metacommunity structure

For each parasite group, we assessed the relative importance of environment, transmission potential and host phylogeny on variation in community composition. Factors whose primary influence is associated with parasite transmission opportunities among host species include host abundance, diet breadth and home range size (Kuris et al. 1980, Combes 2004, Locke et al. 2013, 2014). Host environmental factors that may explain variation among hosts in parasite community composition include body mass, reproductive potential, longevity and trophic status. Reproductive potential is equal to average litter size multiplied by the total number of reproductive bouts possible within a year (mean litter interval + mean gestation length), resulting in the mean number of offspring a female may produce in one year. Host traits that may affect parasite community composition (Table 2) were obtained from the mammalian supertree (Bininda-Emonds et al. 2007), the PanTHERIA database (Jones et al. 2009) and other sources (Supplementary material Appendix 1 Table A1). Phylogenetic associations among host species

Table 2. Host characteristics that represent aspects of the host environment, transmission potential afforded by the host, and host phylogeny that define gradients of variation that may determine distributions of parasites among host species and along which parasite metacommunities may be structured.

Category	Trait	Description	Units
Host environment	adult mass	Average adult mass	g
	reproductive potential	Mean number of offspring per female possible during one year	no./year
	longevity	Maximum age of adult host	months
	trophic status	Trophic level (1:herbivore, 2:omnivore, 3:carnivore)	–
	abundance	Number of host individuals analyzed for parasites in study area	no.
Transmission potential	diet breadth	Number of categories eaten by host	no.
	home range size	Size of area occupied by average host performing every tasks	km²
Host phylogeny	phylogenetic distance	First two axes from principal coordinates analysis on the phylogenetic distance matrix	–

were estimated by taking the first two axes from principal coordinates analysis (PCoA) on the phylogenetic distance matrix, which was obtained using the R package *ape* (Paradis et al. 2004). The first and second principal coordinate axes represented 86.6% (58.0% and 28.6%, respectively) of the total variation accounted for by the PCoA.

The relative importance of environment, transmission and phylogeny to parasite communitirs

We used variance decomposition based on canonical correspondence analysis (CCA) instead of the traditional approach based on redundancy analysis because host–parasite networks were ordinated based on the gradient identified by CCA. This approach was used to determine: 1) the unique variation among parasite communities that can be attributed to transmission potential, host environment, and host phylogeny while accounting for variation associated with the other two groups of host traits, 2) the amount of shared variation that can be attributed to each possible pair of host trait groups while accounting for variation associated with the third group (e.g. shared variation accounted for by host environment and host phylogeny after accounting for variation associated with transmission potential), and 3) the total amount of variation explained by transmission potential, host environment and host phylogeny.

Variation in the host-by-parasite matrix was partitioned among four traits that represent host environment (body mass, reproductive potential, longevity and trophic status), three host traits that may affect parasite transmission potential among host species (abundance, diet breadth and home range size), and the first two axes of the PCoA on the host phylogenetic distance matrix. Variance decomposition was performed in the R ver. 2.15.1. Significance of partitions was determined through permutation tests on CCA analyses of testable fractions. A significance level (α) of 0.05 was used to assess significance for all analyses.

We evaluated metacommunity structure at two scales: component community scale (i.e. all parasites from a host species) and infracommunity scale (i.e. parasites from each host individual). These represent two larger spatial scales for metacommunity analysis discussed by Mihaljevic (2012). For component communities, parasites from each host species represent a community, each host species represents a site, and metacommunity structure was evaluated among host species. For the infracommunity scale, parasites from each host individual represent a community, each host individual represents a site, and metacommunity structure was evaluated among host individuals of the same species, with analyses conducted separately for each of the 15 host species that were represented by at least 10 individuals. Analyses at the infracommunity scale were conducted to determine the effect of focal scale on parasite metacommunity structure. Variance partitioning could not be conducted at the infracommunity scale as the necessary data on host traits are not available for individual rodents.

Results

Metacommunity structure

For the primary axis, the full parasite metacommunity exhibited positive coherence, non-significant turnover and positive boundary clumping, best associated with quasi-Clementsian metacommunity structure (Table 3). The coccidian metacommunity and the ectoparasite metacommunity were non-coherent, precluding further analysis and indicating that coccidian and ectoparasite communities were not structured along a shared gradient of host traits. The helminth metacommunity was consistent with a Clementsian structure, exhibiting positive coherence, turnover and boundary clumping.

No parasite metacommunity was coherent along the secondary axis (Table 3); therefore, all ensuing results and discussion pertain to the primary axis of correspondence from reciprocal averaging. In addition, none of the parasite infracommunities exhibited coherent structure (Supplementary material Appendix Table A2), indicating that at this scale parasite metacommunities are not structured along a dominant axis of environmental variation. Because coherence did not manifest along the primary axis for the infracommunities of any host species, analyses at this scale were not conducted along secondary axes.

Relative roles of host environment, transmission and phylogeny on parasite community structure

Taken together, host environment, transmission potential, and phylogeny explained a significant component of the variation in parasite community composition for the full metacommunity (74.0% variation explained), coccidians (81.3% variation explained), and helminths (75.4% variation explained). Host environmental variables explained the most variation in community composition (Table 4), while variables relating to transmission potential or host phylogeny never explained a significant portion of the observed variation after accounting for variation shared with other variable groups (i.e. t | [e + p] or p | [e + t]). No partition explained a significant portion of the variation in ectoparasite community structure (Table 4).

Discussion

Metacommunity structute of desert rodent parasites

The full parasite metacommunity and the helminth metacommunity exhibited compartmentalized structures, quasi-Clementsian and Clementsian structures, respectively (Table 3). These structures manifest because a majority of parasite species exhibit host specificity associated with either heteromyid or cricetid rodents (Fig. 2). Over one third (22 of 65) of all recorded parasite species occurred on only one species or genus of host, indicating the importance of co-evolutionary relationships or co-adaptation between hosts and their parasites (Kim 1985, Poulin 2011). In general, parasites exhibited one of three types of distribution: 27 species occurred only on cricetids or on cricetids and sciurids,

Table 3. Results of the analysis of coherence, range turnover, and boundary clumping for the full parasite metacommunity and separately for each of three taxonomic subsets: coccidians, ectoparasites, helminths. Analyses were conducted separately for the primary and secondary axes of correspondence extracted via reciprocal averaging.

Axis	Community	Coherence				Range turnover				Boundary clumbing		Metacommunity structure
		Abs	p	Mean	SD	Rep	p	Mean	SD	I	p	
Primary	Entire	300	0.036	371.58	34.19	8338	0.653	8011.30	726.84	1.89	<0.0001	quasi-Clementsian
	Coccidians	53	0.185	75.75	17.17	–	–	–	–	–	–	Random
	Ectoparasites	59	0.422	78.70	24.51	–	–	–	–	–	–	Random
	Helminths	65	0.020	92.25	11.70	949	0.001	550.11	125.49	3.04	<0.0001	Clementsian
Secondary	Entire	380	0.269	416.85	33.34	–	–	–	–	–	–	Random
	Coccidians	70	0.523	79.40	14.73	–	–	–	–	–	–	Random
	Ectoparasites	57	0.825	59.82	12.74	–	–	–	–	–	–	Random
	Helminths	95	0.599	101.26	11.92	–	–	–	–	–	–	Random

Table 4. Results from variance partitioning analyses based on canonical correspondence analysis to determine the unique variation explained by host environment (env), transmission potential (trans), and host phylogeny (phylo) while controlling for variation explained by the other two partitions and any shared effects, combined variation explained by of each possible pair of partitions (i.e. sum of unique variation for the two partitions plus the shared variation associated with them) while controlling for variation explained by the remaining partition, and total variation explained by all three groups of host characteristics. Significant results (p ≤ 0.05) are in bold.

Community	Partition	DF	Variation explained	F	p-value
full	env	4	0.3118	1.5009	**0.0320**
metacommunity	trans	3	0.2174	1.3956	0.0956
	phylo	2	0.1414	1.3611	0.1365
	env + trans	7	0.5346	1.4706	**0.0092**
	env + phylo	6	0.4976	1.5968	**0.0056**
	trans + phylo	5	0.3670	1.4133	**0.0411**
	total	9	0.7403	1.5839	**0.0016**
coccidia	env	4	0.3433	1.8402	**0.0493**
	trans	3	0.2485	1.7757	0.1169
	phylo	2	0.1323	1.4181	0.2371
	env + trans	7	0.5963	1.8264	**0.0283**
	env + phylo	6	0.5200	1.8581	**0.0181**
	trans + phylo	5	0.3827	1.6407	0.0676
	total	9	0.8134	1.9376	**0.0085**
ectoparasites	env	4	0.3174	0.9848	0.4640
	trans	3	0.2353	0.9737	0.4764
	phylo	2	0.2124	1.318	0.2728
	env + trans	7	0.5097	0.9037	0.5837
	env + phylo	6	0.5721	1.1834	0.2514
	trans + phylo	5	0.3918	0.9725	0.4613
	total	9	0.7583	1.0457	0.4584
helminths	env	4	0.3351	1.7031	**0.0293**
	trans	3	0.1916	1.298	0.1970
	phylo	2	0.1081	1.0988	0.3696
	env + trans	7	0.5401	1.5684	**0.0325**
	env + phylo	6	0.4974	1.685	**0.0178**
	trans + phylo	5	0.3058	1.2429	0.2048
	total	9	0.7540	1.7029	**0.0351**

20 species occurred only on heteromyids or on heteromyids and *Spermophilus spilosoma*, and 16 species were broadly distributed among cricetids, heteromyids and sciurids (Fig. 2). In addition, multiple species (n ≥ 4) from each group of parasites exhibited each type of distribution among hosts, indicating that these distributional patterns arose among distinct evolutionary lineages of parasites. Importantly, even for metacommunities with random structure (i.e. ectoparasites and coccidians), hosts that were ordered based on parasite community composition generally formed familial groups (Fig. 2). This indicates that evolutionary constraints may determine which family of host a species of parasite can successfully infest, but that within those constraints a single gradient of host traits does not determine the distribution of a preponderance of parasite species. In other words, despite the fact that most ectoparasites or coccidians are constrained to infest a single family of rodent at Sevilleta, their distributions among hosts occur along multiple independent gradients that may be associated with different aspects of host phylogeny, ecology or morphology.

A lack of coherence for analyses at infracommunity scale is consistent with previous observations that structure in parasite composition is difficult to detect at that scale (Poulin 1997 and sources therein). In general, infracommunity composition does not differ from a random assembly of species from the component community (Poulin 1997). This may primarily be a result of small sample sizes that parasites from individual hosts represent. For example, one may use 5-m² plots to sample trees in a forest or trap stations to sample mammals in that forest. Despite the fact that each sample location has the ability to detect any species of tree or mammal that occurs in the forest, it is unlikely that one such sample can effectively characterize the community composition of trees or mammals in the entire forest. Similarly, infracommunities may represent samples that are poor at characterizing communities of parasites from particular host species, resulting in a great number of embedded absences and non-coherent structures.

Relative importance of host environment, transmission potential and phylogeny on parasite metacommunity structure

Despite parasite metacommunities evincing three different emergent structures (i.e. quasi-Clementsian, Clementsian and random), the host environment (as defined by host mass, reproductive rate, longevity and trophic status) was the only pure effect that explained significant variation in community composition associated with these metacommunity structures (Table 4). In general, these host environment traits define the sizes and distributions of parasite habitats (i.e. hosts) in time and space. As island size and distance to source populations affect biodiversity on islands (MacArthur and Wilson 1967), host size and social structure are commonly related to parasite species richness and community composition (Lindenfors et al. 2007, Patterson et al. 2007, Seifertová et al. 2008, Krasnov et al. 2010, Poulin 2010, Presley 2012). Our analyses indicate that host characteristics that define parasite habitat size and distribution can also mold distributions of parasites among hosts, leading to coherent parasite metacommunities. Importantly, although the same suite of host traits may be associated with parasite metacommunity structure, the particular form of that structure may differ among parasite taxa on the same host species.

Host body size can influence the number of viable populations of parasites the host may safely harbor (Ezenwa et al. 2006), as larger parasite loads may lead to death or lack of reproduction, which are undesirable outcomes for both hosts and parasites. Interspecific interactions or priority effects may influence parasite community composition (Norton et al. 2004), as priority effects may inhibit formation of new associations with hosts. In addition, hosts are temporary habitats for parasites. Although the average lifespan of most hosts is many times longer than that of their parasites, host mortality necessitates frequent transfer to conspecific host individuals to ensure persistence of populations. For parasites that require bodily contact for successful transfer, more frequent breeding creates transfer opportunities between adult males and females as well as to the resulting offspring (Krasnov et al. 2005c, 2006, Patterson et al. 2007). Consequently, litter size and frequency with which they are produced should
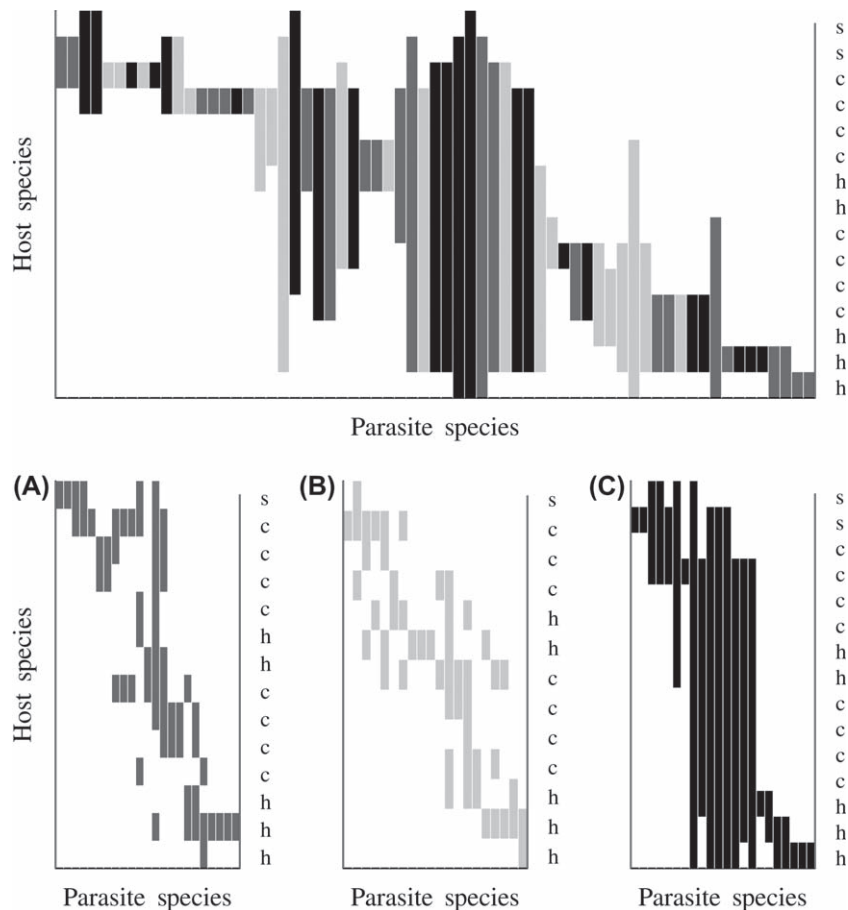
Figure 2. Ordinated matrices for the full parasite metacommunity (top), and separately for (A) coccidians, (B) ectoparasites, and (C) helminths. The right axis for each matrix denotes the family affiliation for each host species (s = Sciuridae, c = Cricetidae, h = Heteromyidae).

be important components of the host environment to ensure persistence of parasite populations. Nonetheless, tradeoffs exist. Larger hosts tend to be longer lived, providing a temporally more stable habitat than smaller hosts, which can affect parasite communities (Morand and Harvey 2000, Ezenwa et al. 2006, Tschirren and Richner 2006). Greater longevity may reduce the frequency of parasite transfer required to ensure persistence; however, larger hosts may reproduce less frequently or have smaller litters. Differences in parasite life history or competitive ability may result in taxon-specific optimal host characteristics, with some parasites being associated with longer lived and slower reproducing species and others associated with shorter lived and faster reproducing species, which may explain the relatively strong association of these host environmental traits with the gradient along which metacommunities were structured.

For a parasite to become integrated into a community and represented in samples from particular host individuals, the parasite must have an opportunity to infest the host and the ability to survive in the host habitat. The variance partition associated with transmission opportunities afforded by the host, as defined by host abundance, dietary breadth, and home range size, did not explain a significant amount of variation for any metacommunity (Table 4). Two factors may contribute to this fact. First, environmental filtering associated with the host environment may result in unsuccessful transmission events, with parasites failing to survive

on particular host species regardless of the opportunities to infest the host. For example, arthropod ectoparasites are highly host specific and many species would not be able to take advantage of transmission opportunities, as such opportunities typically would fail to result in successful transmission to most host species. Second, parasite species may have their own mechanisms for transmission among host species that obviate the need to rely on host characteristics. For example, sporulated oocysts of coccidians can survive in the environment for years (King and Monis 2007); therefore, coccidians may be sufficiently pervasive in the environment to effect their own transmission through time and space among suitable host species, with host environment primarily determining the composition of coccidian communities in host species.

Compared to other parasites groups, ectoparasites tend to form co-evolutionary relationships that often lead to strong host specificity (Poulin 2011, Poulin et al. 2011). Host specificity, especially for taxa that are restricted to a single host species or genus, can de-couple variation in host traits, including host phylogeny, from variation in parasite community composition. For example, a monoxenous parasite (i.e. one that infests only one host species) has the same probability (0.00%) of successfully infesting a sister species of its host as it does a distantly related taxon. As a result, variation in any type of host trait would not be associated with the distribution of highly host specific parasites. Sixty percent

(12 of 20) of ectoparasites occurred on only one or two host species. This dominance of host specific ectoparasites likely explains both the random metacommunity structure and lack of significantly associated host traits with variation in ectoparasite community composition.

Synthesis and conclusions

The application of the EMS framework and determination of variables associated with metacommunity structure is new to host–parasite systems and is particularly important for understanding relationships between hosts, which may be reservoirs for emerging diseases, and their parasites, which may be vectors that transmit disease to humans or agriculturally important domestic animals (Daszak et al. 2000, Cunningham et al. 2012). Only host traits associated with the environment were significantly associated with variation in species composition, indicating that responses to the same type of environmental variation can be associated with multiple types of metacommunity structure. Contrary to the suggestion of Meynard et al. (2013), no general a priori relationships between processes and emergent metacommunity structures exist. This is because it is the particular responses of species that give rise to the emergent structures, and not just the identity of the factors to which they respond. For example, strong responses to spatial environmental variation may lead to nested distributions, idiosyncratic distributions (Gleasonian structure), groups of mutually exclusive distributions (Clementsian structure), or species distributions that are associated with multiple environmental gradients (random structure sensu Leibold and Mikkelson 2002).

This suite of distinct responses of parasites from the same host metacommunity highlight the complex and diverse nature of host–parasite systems with respect to how parasites move through the environment, variation in life histories, and level of host specialization they exhibit. Indeed, the suite of mechanisms that contribute to parasite metacommunity structure may be highly complex, as host metacommunities can exhibit complex responses to local and spatial processes (Stevens and Tello 2012), with responses of hosts to large-scale environmental variation and responses of parasites to variation in host characteristics all contributing to parasite metacommunity dynamics.

References

Bininda-Emonds, O. et al. 2007. The delayed rise of present-day mammals – Nature 446: 507–512.

Combes, C. 2004. Parasitism: the ecology and evolution of intimate interactions. – Univ. of Chicago Press.

Cunningham, A. et al. 2012. Disease invasion: impacts on biodiversity and human health. – Phil. Trans. R. Soc. B 367: 2804–2806.

Dallas, T. 2013. metacom: analysis of the 'elements of metacommunity structure'. – R package ver. 1.0. < http://CRAN.R-project.org/package = metacom>

Daszak, P. et al. 2000. Emerging infectious diseases of wildlife – threats to biodiversity and human health – Science 287: 443–449.

Diamond, J. 1975. Assembly of species communities. – In: Cody, M. and Diamond, J. (eds), Ecology and evolution of communities. Harvard Univ. Press, pp. 342–444.

Duszynski, D. and Wilber, P. 1997. A guideline for the preparation of species descriptions in the Eimeriidae. – J. Parasitol. 83: 333–336.

Ezenwa, V. et al. 2006. Host traits and parasite species richness in even and odd-toed hoofed mammals, Artiodactyla and Perissodactyla. – Oikos 115: 526–536.

Gauch, H. 1982. Multivariate analysis in community ecology, vol. 1. – Cambridge Univ. Press.

Guégan, J. et al. 2005. Are there general laws in parasite community ecology? The emergence of spatial parasitology and epidemiology. – In: Thomas, F. et al. (eds), Parasitism and ecosystems. Oxford Univ. Press, pp. 22–42.

HilleRisLambers, J. et al. 2012. Rethinking community assembly through the lens of coexistence theory. – Annu. Rev. Ecol. Evol. Syst. 43: 227–248.

Holyoak, M. et al. 2005. Metacommunities: spatial dynamics and ecological communities. – Univ. Chicago Press.

Jones, K. et al. 2009. PanTHERIA: a species-level database of life history, ecology and geography of extant and recently extinct mammals. – Ecology 90: 2648–2648.

Kim, K. 1985. Coevolution of parasitic arthropods and mammals. – Wiley.

King, B. J. and Monis, P. T. 2007. Critical processes affecting *Cryptosporidium* oocyst survival in the environment. – Parasitology 134: 309–323.

Krasnov, B. et al. 2004. Geographical variation in host specificity of fleas (Siphonaptera) parasitic on small mammals: the influence of phylogeny and local environmental conditions. – Ecography 27: 787–797.

Krasnov, B. et al. 2005a. Covariance in species diversity and facilitation among non-interactive parasite taxa: all against the host. – Parasitology 131: 557–568.

Krasnov, B. et al. 2005b. Nested pattern in flea assemblages across the host's geographic range. – Ecography 28: 475–484.

Krasnov, B. R. et al. 2005c. Sex-biased parasitism, seasonality and sexual size dimorphism in desert rodents. – Oecologia 146: 209–217.

Krasnov, B. et al. 2006. Aggregation and species coexistence in fleas parasitic on small mammals. – Ecography 29: 159–168.

Krasnov, B. et al. 2010. Similarity in ectoparasite faunas of Palaearctic rodents as a function of host phylogenetic, geographic or environmental distances: which matters the most? – Int. J. Parasitol. 40: 807–817.

Krasnov, B. et al. 2011. Nestedness and β-diversity in ectoparasite assemblages of small mammalian hosts: effects of parasite affinity, host biology and scale. – Oikos 120: 630–639.

Kuris, A. et al. 1980. Hosts as islands. – Am. Nat. 116: 570–586.

Leibold, M. and Mikkelson, G. 2002. Coherence, species turnover, and boundary clumping: elements of meta-community structure. – Oikos 97: 237–250.

Leibold, M. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. – Ecol. Lett. 7: 601–613.

Lima Jr, D. et al. 2012. Patterns of interactions of a large fish–parasite network in a tropical floodplain. – J. Anim. Ecol. 81: 905–913.

Lindenfors, P. et al. 2007. Parasite species richness in carnivores: effects of host body mass, latitude, geographical range and population density. – Global Ecol. Biogeogr. 16: 496–509.

Locke, S. A. et al. 2013. Predicting the similarity of parasite communities in freshwater fishes using the phylogeny, ecology and proximity of hosts. – Oikos 122: 73–83.

Locke, S. A. et al. 2014. Vulnerability and diet breadth predict larval and adult parasite diversity in fish of the Bothnian Bay. – Oecologia 174: 253–262.

López-González, C. et al. 2012. Metacommunity analysis of Mexican bats: environmentally mediated structure in an area of high geographic and environmental complexity. – J. Biogeogr. 39: 177–192.

MacArthur, R. and Wilson, E. 1967. The theory of island biogeography, vol. 1. – Princeton Univ. Press.

Mayfield, M. M. and Levine, J. M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. – Ecol. Lett. 13: 1085–1093.

Meynard, C. N. et al. 2013. Disentangling the drivers of metacommunity structure across spatial scales. – J. Biogeogr. 40: 1560–1571.

Mihaljevic, J. 2012. Linking metacommunity theory and symbiont evolutionary ecology. – Trends Ecol. Evol. 27: 323–329.

Moore, S. and Wilson, K. 2002. Parasites as a viability cost of sexual selection in natural populations of mammals. – Science 297: 2015–2018.

Morand, S. and Harvey, P. H. 2000. Mammalian metabolism, longevity and parasite species richness. – Proc. R. Soc. B 267: 1999–2003.

Morand, S. et al. 2006. Micromammals and macroparasites: from evolutionary ecology to management. – Springer.

Norton, J. et al. 2004. Temporal and spatial patterns of nestedness in eel macroparasite communities. – Parasitology 129: 203–211.

Oksanen, J. et al. 2013. vegan: community ecology package. R package ver. 2.0-6. < http://CRAN.R-project. org/package = vegan>.

Paradis, E. et al. 2004. Ape: analysis of phylogenetics and evolution in R language. – Bioinformatics 20: 289–290.

Patterson B. D. et al. 2007. Roosting habits of bats affect their parasitism by bat flies (Diptera: Streblidae). – J. Trop. Ecol. 23: 177–189.

Pavoine, S. et al. 2011. Linking patterns in phylogeny, traits, abiotic variables and space: a novel approach to linking environmental filtering and plant community assembly. – J. Ecol. 99: 165–175.

Poulin, R. 1996. Richness, nestedness, and randomness in parasite infracommunity structure. – Oecologia 105: 545–551.

Poulin, R. 1997. Species richness of parasite assemblages: evolution and patterns. – Annu. Rev. Ecol. Syst. 28: 341–358.

Poulin, R. 2010. Decay of similarity with host phylogenetic distance in parasite faunas. – Parasitology 130: 109–115.

Poulin, R. 2011. Evolutionary ecology of parasites, 2nd ed. – Princeton Univ. Press.

Poulin, R. et al. 2011. Host specificity in phylogenetic and geographic space. – Trends Parasitol. 27: 355–361.

Presley, S. 2007. Streblid bat fly assemblage structure on Paraguayan *Noctilio leporinus* (Chiroptera: Noctilionidae): nestedness and species co-occurrence. – J. Trop. Ecol. 23: 409–417.

Presley, S. 2012. Sex-based population structure of ectoparasites from Neotropical bats. – Biol. J. Linn. Soc. 107: 55–66.

Presley, S. J. et al. 2009. Elements of metacommunity structure of Paraguayan bats: multiple gradients require analysis of multiple axes of variation. – Oecologia 160: 781–793.

Presley, S. et al. 2010. A comprehensive framework for the evaluation of metacommunity structure. – Oikos 119: 908–917.

Presley, S. J. et al. 2011. A complex metacommunity structure for gastropods along an elevational gradient. – Biotropica 43: 480–488.

Richgels, K. et al. 2013. Evaluating the role of regional and local processes in structuring a larval trematode metacommunity of *Helisoma trivolvis*. – Ecography 36:854–863.

Rigaud, T. et al. 2010. Parasite and host assemblages: embracing the reality will improve our knowledge of parasite transmission and virulence. – Proc. R. Soc. B 277: 3693–3702.

Seifertová, M. et al. 2008. Metazoan parasites of freshwater cyprinid fish (*Leuciscus cephalus*): testing biogeographical hypotheses of species diversity. – Parasitology 135: 1417–1435.

Stevens, R. and Tello, S. 2012. Do desert rodents form metacommunities? – J. Mammal. 93: 1029–1041.

Tello, J. et al. 2008. Patterns of species co-occurrence and density compensation: a test for interspecific competition in bat ectoparasite infracommunities. – Oikos 117: 693–702.

Thomas, F. et al. 2005. Parasitism and ecosystems. – Oxford Univ. Press.

Tschirren, B. and Richner, H. 2006. Parasites shape the optimal investment in immunity. – Proc. R. Soc. B 273: 1773–1777.

Ulrich, W. and Gotelli, N. J. 2012. Pattern detection in null model analysis. – Oikos 122: 2–18.

World Resources Institute 1992. Global biodiversity strategy: guidelines for action to save, study and use earth's biotic wealth sustainability and equitably. – World Resour. Inst.

Zelmer, D. and Arai, H. 2004. Development of nestedness: host biology as a community process in parasite infracommunities of yellow perch (*Perca flavescens* (Mitchill)) from Garner Lake, Alberta. – J. Parasitol. 90: 435–436.

Zelmer, D. et al. 2004. Nestedness in colonization-dominated systems: helminth infracommunities of *Rana vaillanti* Brocchi (Anura: Ranidae) in Los Tuxtlas, Veracruz, Mexico. – J. Parasitol. 90: 705–710.

Supplementary material (available as Appendix oik-00707 at (www.oikosjournal.org/readers/appendix). Appendix 1