

# Drivers of symbiont diversity in freshwater snails: a comparative analysis of resource availability, community heterogeneity, and colonization opportunities

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**Abstract** Decades of community ecology research have highlighted the importance of resource availability, habitat heterogeneity, and colonization opportunities in driving biodiversity. Less clear, however, is whether a similar suite of factors explains the diversity of symbionts. Here, we used a hierarchical dataset involving 12,712 freshwater snail hosts representing five species to test the relative importance of potential factors in driving symbiont richness. Specifically, we used model selection to assess the explanatory power of variables related to host species identity, resource availability (average body size, host density), ecological heterogeneity (richness of hosts and other taxa), and colonization opportunities (wetland size and amount of neighboring wetland area) on symbiont richness in 146 snail host populations in California, USA. We encountered a total of 23 taxa of symbionts, including both obligatory parasites such as digenetic trematodes as well as more commensal, mutualistic, or opportunistic groups such as aquatic insect larvae, annelids, and leeches. After validating richness estimates per host population using species accumulative curves, we detected positive effects on symbiont richness from host body size, total richness of the aquatic community, and colonization opportunities. Neither snail

density nor the richness of snail species accounted for significant variation in symbiont diversity. Host species identity also affected symbiont richness, with higher gamma and average alpha diversity among more common host species with higher local abundances. These findings highlight the importance of multiple, concurrent factors in driving symbiont richness that extend beyond epidemiological measures of host abundance or host diversity alone.

**Keywords** Biodiversity loss · Parasite community · Disease ecology · Metacommunity · Macroecology · Invasive species

## Introduction

Despite the significance of parasites and other symbionts for conservation and health, we still know comparatively little about the factors that drive symbiont diversity across multiple scales of organization and among host species within a community (Poulin and Morand 2000; Dobson et al. 2008). Recent advances suggest that the integration of theoretical frameworks from community ecology and epidemiology may offer insight into the factors likely to structure parasite diversity (Rosenzweig 1995; Poulin and Morand 2004; Poulin 2014). For instance, as an extension of island biogeography theory, the richness of parasites within a given host species could reflect an equilibrium between the probability of exposure to different parasites and the likelihood those infections establish and persist (MacArthur and Wilson 1967; Guégan et al. 1992; Poulin 1995). This ‘hosts as islands’ framework predicts that larger-bodied and longer-lived host species represent larger targets for colonizing parasites and offer a longer time horizon for colonization (Kuris et al. 1980; Zelmer 2014). Most

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By combining field surveys with parasite assessments, Keegan used ecological theory to test alternative drivers of parasite diversity. He spearheaded the data collection, analyses, and writing.

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studies that have examined parasite richness in relation to individual host body size have found positive, albeit weak, correlations (Lindenfors et al. 2007; Kamiya et al. 2014a). Similarly, epidemiological theory suggests that populations with higher densities of suitable hosts should allow for more transmission (Anderson and May 1979; Arneberg 2002), potentially increasing parasite richness by growing population size and limiting the risk of stochastic extinction events. A recent meta-analysis showed that host species' body size, geographical range size (a proxy for colonization opportunities over evolutionary time), and population density were the most consistently identified correlates of parasite richness among host species from 62 studies, encompassing animal, plant, and fungal host taxa (Kamiya et al. 2014a).

However, the biology of host-parasite interactions has several unique elements that challenge efforts to directly apply predictions developed from free-living community ecology. Because animal hosts are alive and vary in characteristics such as mobility, age, diet breadth, size, and defense strategies, they are not perfectly analogous to habitat patches or islands (Vitone et al. 2004; Zelmer and Gross 2009; Zelmer 2014). High levels of infection, for instance, might kill the host and remove it from the patch network (e.g., Seabloom et al. 2015). Similarly, hosts can defend themselves against infection through both behavioral and immunological pathways. Ecoimmunological theory suggests that longer-lived (and generally larger) hosts should invest more resources into immunological defenses relative to short-lived hosts, which frequently have smaller body sizes but tend to reproduce early (Stearns 1992; Schmid-Hempel 2003; Cronin et al. 2010). Thus, while larger or older hosts are likely exposed to more parasites, whether this will affect the richness of parasite species or simply the average infection load is uncertain. Lastly, evolutionary history and adaptation are likely to influence the richness of parasites within a host species, as suggested by the (1) greater similarity of parasite communities between closely related hosts (phylogenetic niche conservatism) (Mouillot et al. 2006), (2) the higher parasite richness in host species with larger geographic ranges (Price and Clancy 1983; Gregory 1990), and (3) the tendency for invasive species to exhibit fewer infections than co-occurring native hosts (Torchin et al. 2003; Cronin et al. 2010; Mitchell et al. 2010; Roche et al. 2010). Such observations underscore the dynamic nature of host–parasite–environment interactions and, in turn, the competing forces that combine to structure parasite species richness over ecological and evolutionary scales.

While identifying the factors driving the heterogeneous distribution of parasite richness has been a central goal of parasite ecology for the last half century (Wisniewski 1958; Dogiel 1964; Esch et al. 1990; Kennedy and Bush

1992; Goater et al. 2014; Poulin 2014), the relative importance of these variables is likely to vary by the level of ecological organization, including among individual hosts (infracommunity), across populations of a single host species (component community), and across communities of hosts (compound community) (Esch et al. 1990; Bush et al. 1997). Thus far, most studies of symbiont diversity either compare the total number of parasite species among different host species, often as a function of particular traits (e.g., body size, geographic range, phylogeny) (Morand and Poulin 1998; Nunn et al. 2003; Lindenfors et al. 2007; Bordes et al. 2009; Cooper et al. 2012), or assess how the number of parasites in a specific host species varies across geographic areas (e.g., latitude, elevation, precipitation, introduced range) (Rhode 1999; Krasnov et al. 2004; Nunn et al. 2005; Marcogliese et al. 2016). While these efforts have yielded important insights (Esch et al. 1990; Poulin 1997; Kennedy 2009; Goater et al. 2014), including emerging syntheses (e.g., Kamiya et al. 2014a, b; Poulin 2014), relatively few studies have investigated the drivers of symbiont richness both among host species and across environmental gradients (but see Ebert et al. 2001; Krasnov et al. 2011), in part because of the paucity of datasets that include well-replicated information not only on hosts and parasites but also on the biotic and abiotic environment. Such information is necessary to rigorously test the relative roles of dispersal opportunities, habitat heterogeneity, and resource availability.

Aquatic snails offer an excellent system in which to investigate patterns of symbiont richness and their underlying drivers (e.g., Torchin et al. 2015). They are the obligate first intermediate hosts for parasitic flatworms (trematodes), some of which affect the health of humans, domestic animals, or wildlife (Crompton 1999; Johnson et al. 1999; King et al. 2005; Gryseels et al. 2006). Trematodes have complex life cycles in which they often sequentially infect multiple aquatic and terrestrial species, alternating between asexual reproduction (within snails or other molluscs) and sexual reproduction (in dispersing definitive hosts, such as birds, mammals, reptiles or fishes) (Gibson 1987). In freshwater systems, pond snails are also colonized by a broad range of other parasitic, commensal, and mutualistic symbionts, including nematodes, oligochaetes, arthropods, and leeches (Sarah 1971; Esch et al. 2001; Prat et al. 2004; Zimmermann et al. 2011). Because pond ecosystems are spatially discrete and well delineated, they facilitate simultaneous comparisons of parasite richness across multiple replicate communities within a landscape as well as between snail host species, which vary in characteristics such as body size, growth rate, seasonality, lifespan, dispersal ability, and habitat preference (Brown and DeVries 1985; Osenberg 1989).

Here, we compared the relative influence of hypothesized structuring forces in driving symbiont richness among freshwater snail populations. Specifically, we asked: (1) how does symbiont richness vary among populations of multiple host species and across wetland communities? And (2) what is the relative importance of factors underlying this variation, including host species identity, characteristics related to resource availability (average body size, host density), the richness of the community (including snails and other aquatic taxa), and the spatial position of the habitat (wetland size and nearby sources for dispersal)? To address these questions, we conducted detailed assessments of symbiont richness from 12,712 aquatic snails within 93 ponds in the California Bay Area, USA. We analyzed these data using a model selection approach in which host populations were nested within ponds to compare parasite richness among host species and sites. We broadly considered symbiont diversity to include the richness of parasitic, mutualistic, and commensal taxa, given that these organisms often inhabit the same component community and that their classification may be context dependent; for instance, commensals can become opportunistically parasitic depending on resource conditions (Prat et al. 2004; Zimmermann et al. 2011; Stoll et al. 2013; Skelton et al. 2016). Additionally, the drivers of community richness for commensal and mutualist taxa remain poorly understood, despite potentially important implications for human and animal health (Walter and Ley 2011; Godon et al. 2016). For example, Hopkins et al. (2016) showed that the presence of protective symbionts (*Chaetogaster limnaei limnaei*) can lower trematode transmission to snail intermediate hosts, thus reducing the likelihood of parasitic castration.

## Materials and methods

### Field sampling

From May to August 2013, we collected snails from freshwater ponds Contra Costa, Alameda, and Santa Clara counties (Johnson et al. 2013; Richgels et al. 2013). We selected accessible pond ecosystems across grassland, oak woodland, and chaparral biomes to encompass a broad range in resource availability, community composition, surrounding habitat, and physical and spatial characteristics. Sites occurred on lands managed for a wide range of purposes, including wildlife refuges, recreational parks, private ranching operations, and watershed management districts. Site perimeters, which ranged from 22 to 1853 m (mean  $\pm$  1 SE = 179 m  $\pm$  80.7 m), were measured by walking the water's edge with a handheld GPS. Each pond was sampled twice over the course of the summer to help account for any temporal shifts in parasite community composition

(Sapp and Esch 1994; Fellis and Esch 2004). The first round of sampling occurred from 9 May to 3 July and the second round between 8 July and 15 August, with an average inter-sample period of 60 days.

On each visit, we conducted 1-meter long dipnet sweeps (D-frame net, 1.2 mm mesh size) every ~10 m around the pond perimeter to assess the presence and abundance of each snail species and quantify taxonomic richness of other aquatic organisms (e.g., larval insects, fishes, and larval amphibians). These sweeps were conducted by extending the dipnet approximately 1 m out from shore and rapidly skimming it along the benthos and through the associated vegetation toward the shoreline. The contents of each sweep were transferred to a sorting tray, identified to the lowest possible taxonomic level, and counted. We randomly selected 50 individuals of each snail species for dissection. When necessary, we supplemented the standardized dipnet sweeps with up to three person-hours of additional collections to achieve the desired sample size of 50 snails from each species. To prevent inadvertent transfer of organisms among ponds, all equipment was soaked in 10% bleach after each pond visit.

### Symbiont assessment

Collected snails were kept alive and necropsies were performed between 24 and 72 h (average: 37 h) post-collection. After measuring the shell length of each snail using digital calipers, we gently cracked the shell using a pair of pliers and teased the tissue from the shell with forceps, systematically examining all parts of the snail under an Olympus SZX10 stereomicroscope. We examined the internal and external spire of the shell for insects, the foot and under the hood for oligochaetes, and the internal organs and gonads for trematode rediae, sporocysts, cercariae, and metacercariae. For larval trematodes, we based identifications on the morphology of mature cercariae using keys from Yamaguti (1971) and Schell (1985). Although the majority of organisms found while examining the snail were parasitic, here we use the term “symbiont” inclusively to describe any organism regularly observed living on or within a snail host with a known interaction with freshwater snails. All the symbionts included in this study were regularly detected inhabiting or attached to snails and have previously documented relationships with freshwater snails, whether parasitic, commensal, mutualistic, or predatory. For example, some leeches (*Helobdella* spp.) undergo prolonged feeding on snails that can eventually kill the host (Sarah 1971; Aditya and Raut 2005), while oligochaetes (*Tubifex tubifex*) often feed on snail excrement and dead tissue (Eveland and Haseeb 2011). Larval midges are thought to have a phoretic relationship with snails (i.e., as a means of transportation; Prat et al. 2004). For trematodes,

we treated unique life stages as distinct taxa (e.g., echinostome rediae and metacercariae) because of their different ecologies and the challenges in differentiating species, particularly for larval stages for which morphological distinctions can be hard to identify.

Because sampling effort is always a key consideration when examining patterns of species richness (Walther et al. 1995; Dove and Cribb 2006), we built a series of species accumulation curves to determine whether the number of individuals sampled from a host population was sufficient to capture symbiont richness within that species. Specifically, we used the fossil package (Vavrek 2011) in the statistical software program R (version 3.0.2) to analyze and estimate richness for a subset of 82 host populations across our range of sample sizes (20 sites with sample sizes between 20 and 50, 58 sites between 51 and 100, and four sites with sample sizes greater than 100). We then assessed the difference between observed richness and predicted richness using the Chao2 estimator (Heltshe and Forrester 1983; Chao et al. 2005). Because this study was not explicitly focused on seasonal changes in symbiont communities, we pooled information from the two visits to give a more complete picture of symbiont richness.

## Analysis

To investigate the relative importance of factors associated with symbiont richness, we built a series of generalized linear-mixed effects models using the lme4 package in R (Bates et al. 2015). In each, the response variable was symbiont species richness at the host population-level as a Poisson-distributed variable with a log-link function and wetland identity was included as a random intercept term. We focused on population-level symbiont richness (i.e., the total number of symbionts found in particular snail species-by-pond combination) rather than individual hosts given the small range in richness at the infracommunity level (i.e., many individual hosts have zero or one symbiont only); analyses of symbiont richness at the pond level (compound community) were similarly challenging owing to similar parasite morphotypes detected in different snail host species; in the absence of molecular data, determination of whether these groups were taxonomically distinct was not possible (Leung et al. 2009).

We constructed a total of six models for comparison. In the first ('species-only model'), we included snail host species identity as a fixed effect to broadly capture among-species variation stemming from evolutionary history, physiological defenses, and overall body size (Poulin and Morand 2000; Kamiya et al. 2014a, b; Poulin 2014). The 'epidemiological model' included variables related to resource availability, namely in the form of host density (mean count of snails caught per dipnet,  $\log_{10} + 1$  transformed)

and average host size (as a z-score to factor out overall size differences among snail species) (Anderson and May 1979; Arneberg 2002). For the 'heterogeneity model', we incorporated snail richness and the richness of other free-living aquatic taxa as additional fixed effects (measured as a discrete count of the taxa encountered during dipnet surveys, including macroinvertebrates, fishes, and amphibians), with the rationale that for generalist symbionts, these taxa may function as alternative or additional hosts (Hechinger and Lafferty 2005). Fourth, the 'colonization model' included characteristics hypothesized to influence parasite colonization and establishment, such as pond area ( $\log_{10} + 1$  transformed) and the percentage of wetland habitat within a 1 km radial buffer of each pond (derived from the National Land Cover Database using ArcGIS), although we acknowledge that such variables could also have effects on variables such as total host population size (Richgels et al. 2013; Zelmer 2014). Finally, we built both an 'intercept-only' model and a 'global model' containing all the fixed effects after verifying a lack of collinearity among predictors (Richgels et al. 2013). Other individual or host species-level traits were either not measurable (e.g., days alive) or not relevant to this system (e.g., sex, as all snail host species included here are hermaphroditic). Predictor variables were scaled to facilitate comparisons of their coefficients, and we compared among models using Akaike's information criterion (AIC) (see Zuur et al. 2009).

## Results

We examined 12,712 individual snails from 93 wetlands for symbionts, including 5578 *Helisoma trivolvis*, 5249 *Physa* spp., 1030 *Gyraulus* spp. (species *parvus* or *crista*), 500 *Lymnaea columella*, and 355 *Radix auricularia*. Of these, *H. trivolvis* was the most common species, occurring in 82% of wetlands, followed closely by *Physa* spp. (possible mixture of *P. gyrina* and *P. acuta*), which occurred in 75% of sites. *Gyraulus* spp., *L. columella*, and *R. auricularia* were less common, occurring at 28, 19, and 12% of sites, respectively. We collected sufficient data to analyze symbiont richness from 146 different host populations.

## Symbiont richness

Across all host species and sites, we encountered 23 distinct taxa of parasites and symbionts (Table 1). This is likely an underestimate of true species richness given the challenges of identifying many of these groups to the species level based on morphology, particularly for fungi, larval helminths and midge larvae (e.g., Miura et al. 2005; Leung et al. 2009). In addition, some specialist taxa such as larval trematodes can represent different species when found

**Table 1** Symbionts and their snail host species from a survey of 93 ponds in the California Bay Area, USA

Symbiont	Classification	Snail host species	Morphotype
<i>Chaetogaster limnaei limnaei</i>	Oligochaeta	HT, PY, G, LC, RA	
<i>Chaetogaster limnaei vaghini</i>	Oligochaeta	PY, G	
<i>Tubifex Tubifex</i>	Oligochaeta	HT, PY	
Chironomidae larvae	Insecta	HT, PY, G, LC, RA	
<i>Helobdella</i> spp.	Hirudinea	HT, PY	
Unidentified fungal infection	Fungi	HT, PY, G, LC, RA	
<i>Daubaylia potomaca</i>	Nematoda	HT, PY, G, LC	
<i>Echinostoma</i> or <i>Echinoparyphrium</i> spp. (metacercariae)	Trematoda	HT, PY, G, LC, RA	
Tetracotyle (metacercariae)	Trematoda	HT, PY, G,	Tetracotyle
<i>Allassostomoides</i> spp.	Trematoda	HT, PY	Amphistome
<i>Cephalogonimus</i> spp.	Trematoda	HT, PY, G,	Armatae
Schistosomatidae or Spirorchidae spp.	Trematoda	HT, PY, G, LC, RA	Brevifurcate–apharyngeate
<i>Clinostomum</i> spp.	Trematoda	HT	Brevifurcate–pharyngeate
Bucephalidae spp.	Trematoda	G	Bucephaloid
<i>Halipegus occidualis</i>	Trematoda	HT	Cystophorous
<i>Halipegus eccentricus</i>	Trematoda	PY	Cystophorous
<i>Echinostoma</i> or <i>Echinoparyphrium</i> spp. (cercariae)	Trematoda	HT, PY, G, LC, RA	Echinostome
<i>Ribeiroia ondatrae</i>	Trematoda	HT	Gymnocephalous
Strigeidae spp.	Trematoda	HT, PY, G	Longifurcate–pharyngeate
Echinostomatidae or Psilostomidae spp. (cercariae)	Trematoda	HT	Magnacauda
Notocotylidae, Nudacotylidae, or Pronocephalidae spp.	Trematoda	PY, G	Monostome
<i>Haematoloechus</i> spp.	Trematoda	PY, G	Ornate
Allasoniporidae spp.	Trematoda	HT	Virgulate

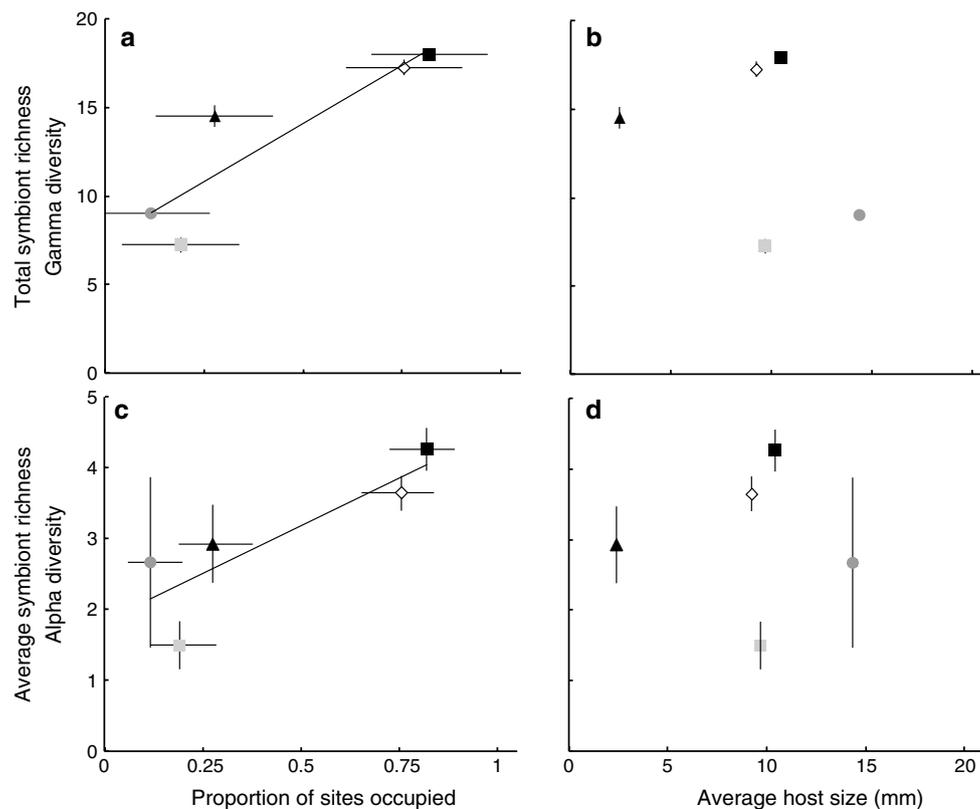
Presented here is the specific symbiont, its taxonomic classification, and the snail host species in which it was recorded. For larval trematodes, the cercariae morphotype from Schell (1985) is listed in the final column

HT, *Helisoma trivolvis*; PY, *Physa* spp.; G, *Gyraulus* spp.; LC, *Lymnaea columella*; RA, *Radix auricularia*

in distinct snail host species. Of all symbionts detected, 17 were larval trematodes and 3 were oligochaetes (*T. tubifex*, *C. l. limnaei*, and *C. l. vaghini*), with 1 taxon from each of the following groups: leech (*Helobdella* spp.), nematode (*Daubaylia potomaca*), midge (Chironomidae) larva, and an unidentified fungal infection.

Ten symbiont taxa appeared to be relative generalists, occurring in all or most snail species, most notably *C. l. limnaei*, which lives on or under the mantle of snails and can range from parasitic to mutualistic depending on the environmental conditions and infestation level (Khalil 1961; Gamble and Fried 1976; Stoll et al. 2013). Other apparent generalists included digenetic trematodes in the echinostome complex (species in the genera *Echinostoma* and *Echinoparyphium*), the unidentified fungal infection, and the larval chironomid. Seven symbionts were observed in a single snail species only. For example, parasites specific to *H. trivolvis* included the larval trematodes *Ribeiroia ondatrae*, *Clinostomum* spp., and a Magnacauda-morphotype cercaria (family Echinostomatidae). Likewise, trematodes in the family Bucephalidae were only observed in *Gyraulus* spp.

At the regional scale, total symbiont richness (gamma diversity) correlated with the overall occurrence and average density of the snail host species. Thus, the most common snail species (*H. trivolvis* and *Physa* spp.) also supported the highest symbiont diversity (18 and 17 taxa, respectively), while the considerably less common *Gyraulus* spp. had a total symbiont richness of 14, and the non-native snails *L. columella* and *R. auricularia* had 7 and 6 symbionts, respectively ( $P = 0.03$ , adjusted  $R^2 = 0.77$ ; Fig. 1a). Across all the examined individual hosts, 54% of *H. trivolvis* harbored one or more symbionts compared with 33% of *Physa* spp., 35% of *Gyraulus* spp., 34% of *L. columella*, and 25% of *R. auricularia*. Average host density ( $P = 0.07$ , adjusted  $R^2 = 0.61$ ) also correlated with gamma diversity, whereas average host size did not ( $P = 0.50$ ; Fig. 1b). At the population level, symbiont richness ranged from 0 to 8 with an average of 3.75 symbionts per host population. *Helisoma trivolvis* again supported the highest overall symbiont richness with an average of 4.26 taxa per population, whereas *L. columella* had the fewest with 1.5 symbionts per population. Overall, the frequency of the host taxon across sampled sites correlated most strongly



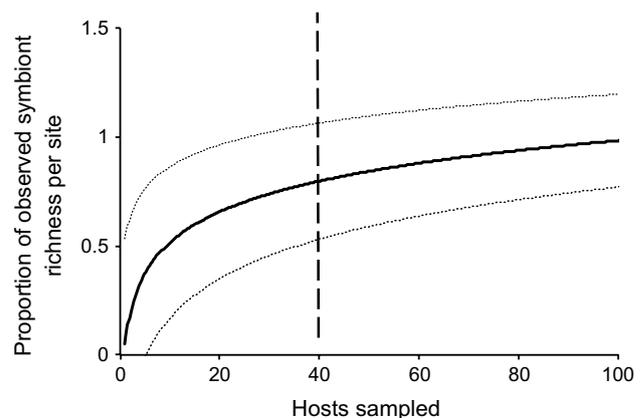
**Fig. 1** Correlates of symbiont richness at the regional (a, c) and local (b, d) scales. The proportion of total sites occupied by a host species ( $\pm 95\%$  CI for a binomial) correlated positively with both gamma symbiont diversity (a) and average symbiont diversity at the population scale (c), whereas average host size exhibited little relationship to either gamma or average alpha diversity (b, d). Error bars repre-

sent  $\pm 95\%$  CI for a binomial (proportion of sites), 95% CI for richness (gamma diversity), and  $\pm 1$  SE (average snail size and average population-level symbiont richness). Sample sizes: *Gyraulus* (solid triangle): 13, *Helisoma* (solid squares): 65, *Lymnaea* (light square): 6, *Physa* (open diamond): 59, and *Radix* (gray circle): 3

with average symbiont richness ( $P = 0.07$ , adjusted  $R^2 = 0.63$ ; Fig. 1c), followed by average host density ( $P = 0.26$ , adjusted  $R^2 = 0.19$ ) but little connection to average host size ( $P = 0.97$ , adjusted  $R^2 = 0.0003$ ; Fig. 1d). The most common symbiont was *C. l. limnaea*, which occurred in nearly 75% of populations, followed by echinostome trematodes (64% occurrence), midge larvae (34% occurrence), and strigeid trematodes (29% occurrence).

### Predictors of symbiont richness among host populations

Species accumulation curves suggested that a sample size of 40 individual hosts was adequate to capture symbiont richness (Fig. 2). With this cutoff, 50% of sites appeared to reach an asymptote (no difference between observed and Chao2 estimated richness), 21% had a discrepancy of 1 or less, and 20% of populations had a discrepancy between one and 3 taxa ( $n = 84$  examined populations with a sample size of 40 or higher). Thus, any populations with fewer than 40 individuals sampled were removed

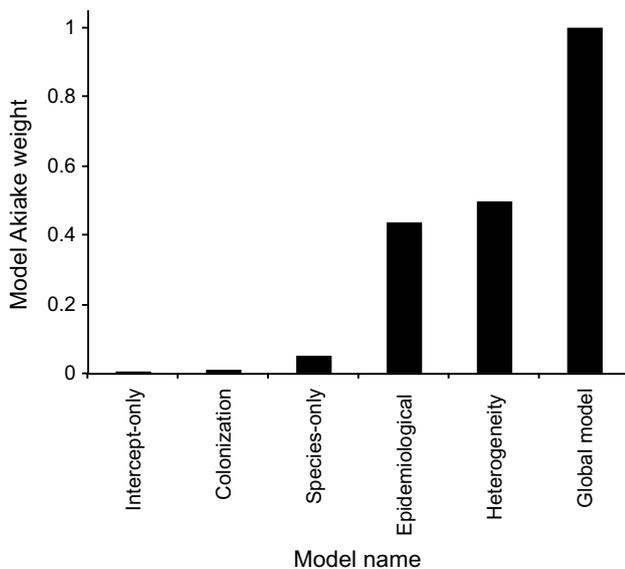


**Fig. 2** Results of species accumulation curves for symbiont richness within a subset of examined snail populations ( $n = 84$ ). The relationship between the number snail hosts examined within a population and the proportion of the estimated species richness captured relative to observed species richness ( $\pm 95\%$  CI) is presented. From these data, we selected a minimum cutoff of 40 hosts sampled for a population to be included in the analysis (vertical dashed line), leaving a total of 146 eligible host populations

**Table 2** Candidate explanatory models for explaining population-level variation in symbiont richness in snail hosts

Model	$\Delta$ AIC	WAIC	Covariates	Metric type/transformation
Global	0	1	Species identity	Categorical
			Average host body size (z-score)	Continuous (z-score)
			Host density	Continuous ( $\log_{10} + 1$ )
			Snail richness	Count
			Pond area	Continuous ( $\log_{10} + 1$ )
			Wetland habitat within 1 km	Proportion
			Richness of free-living organisms	Discrete count
Heterogeneity	30.43	0.497	Snail richness	Discrete counts
			Richness of free-living organisms	Discrete counts
			Wetland identity	Random intercept
Epidemiological	30.68	0.437	Host density	Continuous ( $\log_{10} + 1$ )
			Average host body size (z-score)	Continuous (z-score)
			Wetland identity	Random intercept
Species-only	34.91	0.053	Species identity	Categorical
			Wetland identity	Random intercept
Colonization	37.89	0.012	Pond area	Continuous ( $\log_{10} + 1$ )
			Wetland habitat within 1 km	Proportion
			Wetland identity	Random intercept
Intercept-only	43.02	0.001	Wetland identity	Random intercept

Listed are the model categories, the covariates included (along with corresponding information about the variable and/or its distribution), the  $\Delta$ AIC of the model as well as its weighted AIC (wAIC)



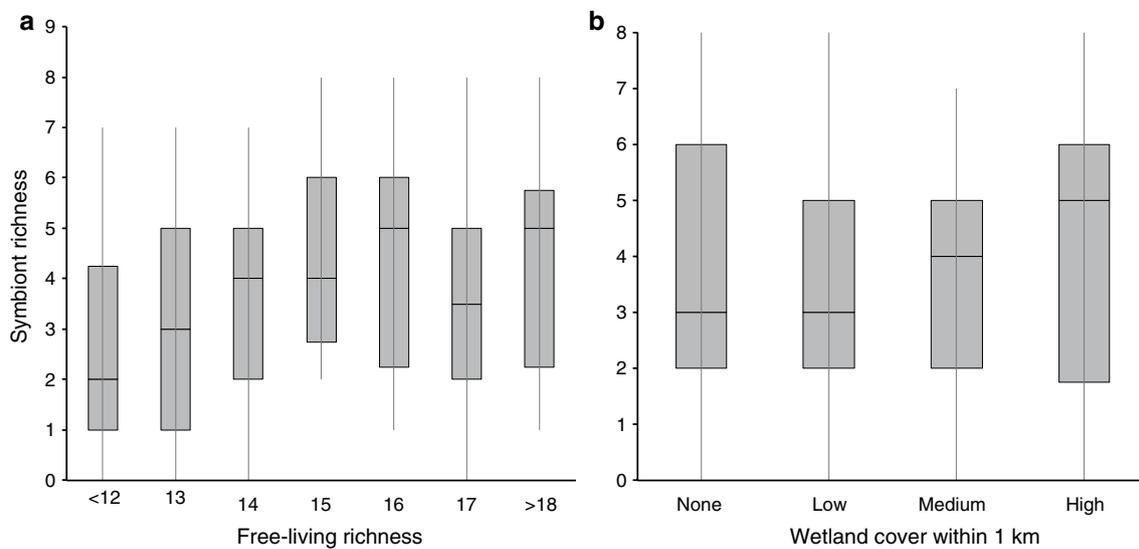
**Fig. 3** Cumulative Akaike weights of the six candidate models used to explain variation in the symbiont richness of freshwater snail populations. See Table 2 for a description of the models and the covariates included. Akaike weights offer a measure of model importance among considered models ranked between 0 (least important) and 1 (most important). All models included a random intercept term for the specific wetland

from the dataset, leaving 146 snail host-by-pond combinations. Across all the tested models, the global model with all seven fixed effects had the lowest overall AIC value and the greatest explanatory power (conditional  $R^2 = 0.40$ ; Table 2; Fig. 3). The next best-fitting model was the heterogeneity model, which included the richness of snails and other aquatic taxa ( $\Delta$ AIC = 30.43), followed closely by the epidemiological model, which included average host size and density ( $\Delta$ AIC = 30.68). No other models were within 34 AIC units of the global model. Host species identity strongly influenced symbiont richness: *H. trivolvis* (coefficient = 0.570,  $z = 3.068$ ,  $P = 0.002$ ) and *Physa* spp. (coefficient = 0.392,  $z = 2.072$ ,  $P = 0.038$ , Fig. 3) both had more symbionts than other snail species. Within the global model (Table 3), positive predictors of symbiont richness included average host body size (z-scored) (scaled coefficient = 0.207,  $z = 4.44$ ,  $P < 0.0001$ ), free-living richness (scaled coefficient = 0.143,  $z = 2.46$ ,  $P = 0.014$ ; Fig. 4a), pond area (scaled coefficient = 0.145,  $z = 2.73$ ,  $P = 0.006$ ) and the amount of nearby wetland area (scaled coefficient = 0.103,  $z = 2.52$ ,  $P = 0.012$ ) (Fig. 4b). For instance, the richness of symbionts in populations of *H. trivolvis* increased by 1 with every 1.6 mm increase in average host body size. In contrast to expectations from the epidemiological hypothesis, we found no effect of host density, snail species richness, or the combined density of all snail species at a site on symbiont richness. Removal of

**Table 3** Results from the global model used to predict population-level symbiont richness in freshwater snails

Factor	Categorical	Scaled coefficient	z-value	P-value
Species identity	HT	0.570	3.068	0.002*
	LC	−0.228	−0.587	0.557
	PY	0.392	2.072	0.038*
	RA	−0.123	−0.301	0.764
Average host body size (z-score)		0.844	4.748	0.000*
Host density		−0.021	−0.432	0.665
Snail richness		0.067	1.356	0.175
Pond area		0.145	2.726	0.006*
Wetland habitat within 1 km		0.103	2.518	0.012*
Richness of free-living organisms		0.143	2.462	0.014*

For each covariate, presented is its scaled coefficient value, z-value, and P-value from a generalized linear mixed model analysis. Asterisks indicate statistical significance. Note that the coefficient values for snail species identity are relative to the fifth snail species, *Gyraulus* spp.

**Fig. 4** The relationship between symbiont richness per host population and either **a** free-living taxonomic richness at a site (including fishes, amphibians, and aquatic macroinvertebrates) or **b** the propor-

tion of neighboring wetland area within a 1 km radius of a pond. Sample sizes for each bin as follows: **a**  $n = 28, 24, 13, 16, 26, 20$  and  $18$ ; **b**  $n = 52, 31, 31, \text{ and } 32$

these predictors tended to improve model fit ( $\Delta\text{AIC} = -3$ ). In a post hoc analysis, neither total dissolved nitrogen, total dissolved phosphorus (mg/L,  $\log_{10}$ -transformed), nor pH explained significant variation in symbiont richness (scaled coefficient =  $-0.022, -0.084, 0.087$ ;  $z = -0.35, -1.39, 1.57$ ;  $P = 0.728, 0.164, 0.117$ ; respectively), regardless of whether we included snail body size or population density in the model.

## Discussion

An extensive body of previous research has highlighted the diversity of parasites distributed among either among

individual hosts within a region or between host species spanning distinct geographic regions (Guégan et al. 1992; Kennedy and Bush 1994; Morand et al. 2000; Guernier et al. 2004; Hechinger and Lafferty 2005; Krasnov et al. 2006; Dunn et al. 2010; Poulin 2014; Johnson et al. 2016). Nonetheless, identifying the drivers of symbiont at intermediate scales remains a major research priority, particularly between the population- and metacommunity scales at which diversity is simultaneously influenced by species interactions, habitat heterogeneity, and especially colonization opportunities (Ricklefs 2004; Cronin and Reeve 2005; Goater et al. 2014). Our results explored the relative importance of conceptual frameworks developed for free-living diversity and to identify specific correlates

associated with symbiont richness across populations of freshwater snails.

Overall, the best-supported model in our analysis included variables associated with host characteristics, epidemiological processes, community diversity, and dispersal opportunities (Fig. 2). Host populations with larger hosts, on average, tended to support more symbionts, consistent with previous research (Guégan et al. 1992; Poulin 1995). Populations with larger-bodied hosts could represent a direct increase in resource availability or reflect a greater fraction of older snails that have had more time for parasite colonization, either of which could promote parasite colonization and reduce local extinctions. Alternatively, parasite-induced changes in snail body size could promote an overall link between infection and average host size (e.g., ‘gigantism’, Mouritsen and Jensen 1994). Host species identity also had a strong influence on observed parasite richness, such that *H. trivolvis* and *Physa* spp. supported roughly 4 more symbiont taxa than *Gyraulus* spp. and 11 more than either *L. columella* or *R. auricularia*. This pattern could reflect local adaptation on the part of the symbionts to infect common hosts (Lively 1989; Lagrue et al. 2016), especially given that *H. trivolvis* and *Physa* spp. were the most frequently encountered and most abundant snails in the region (Fig. 1). Augmenting this trend could be the non-native status of two of the hosts: both *L. columella* and *R. auricularia* are suspected to have been aquarium introductions in California, which could contribute to their reduced suitability for local symbionts (Duggan 2010). Previous work on the ‘enemy escape hypothesis’, for instance, has demonstrated that introduced species support fewer infections, particularly for specialized infections such as larval trematodes (Wolfe 2002; Torchin et al. 2003).

Concurrently, our results identified a strong influence of community diversity in affecting symbiont richness, consistent with the ‘diversity-begets-diversity’ hypothesis (Hechinger and Lafferty 2005; Thieltges et al. 2011; Kamiya et al. 2014b; Johnson et al. 2016). Thus, wetlands with a greater number of free-living species, including vertebrates and invertebrates, supported more symbionts in the resident snail populations, even after accounting for snail species identity and total snail density. Such data are often unavailable in studies of parasite or symbiont diversity. In part, this is likely a consequence of the potential for shared infections between different snail species; however, the stronger effect was for non-snail richness, a variable that included larval amphibians, fishes, larval insects, and other macroinvertebrates. Given that many of the detected infections were trematode parasites that depend on multiple host species, systems with richer free-living communities could either support a wider range of parasite life cycles or attract more definitive hosts that deposit infectious stages (e.g., birds, fishes, and mammals). Similarly, increases in pond

size and the amount of nearby wetland area correlated positively with symbiont richness, consistent with expectations for greater colonization opportunities (Connor and McCoy 2001). In contrast to previous work, however, neither host density nor the total density of snails was important contributors to parasite richness, suggesting that parasite dispersal opportunities (pond characteristics and diversity) and patch quality (snail size or species) were more influential for symbiont diversity relative to the total number of patches.

This study builds upon and extends previous work focused on parasite richness within pond communities. In a study of trematode richness and metacommunity structure within *H. trivolvis*, Richgels et al. (2013) found that the probability of infection in individual hosts associated strongly with snail body size, while trematode richness at the population level correlated negatively with pH and marginally positively with pond size. Our results not only supported the influential roles of host body size and pond area but also highlighted the effects of free-living richness and colonization opportunities. Interestingly, in a post hoc analysis, we found little support for pH or dissolved nitrogen in predicting the richness of symbionts (parasites and non-parasites) across all snail species. More recently, Johnson et al. (2016) used both field surveys and a mesocosm experiment to test how the drivers of symbiont richness in amphibian hosts from the same study region varied with the biological level of organization, ranging from individual hosts (infracommunities) to host metacommunities (compound communities). Despite differences in the host taxa considered (e.g., amphibians versus snails), the results of that study as well as those from the current investigation jointly emphasize the importance of free-living richness in predicting parasite richness, with comparatively weaker effects of host density. Thus, similar to findings from the community ecology of plants, insects, birds, and mammals, symbiont richness associates more tightly with the habitat heterogeneity hypothesis rather than with resource availability per se, lending general support for diversity begetting diversity.

Understanding the structuring forces underlying parasite and symbiont diversity is particularly important, given that such organisms often (1) affect community structure for free-living species, (2) can be key indicators of environmental change, and (3) form complex micro-faunas within hosts that shape human and animal disease (Scott 1988; Marcogliese 2005; Rigaud et al. 2010; Johnson et al. 2015). Using a multi-host, multi-parasite system to examine the drivers of symbiont taxonomic richness across a large number of replicate communities, the current study offered an opportunity to test a suite of potential explanatory factors. Our results link population-level patterns of parasite richness to several factors often used to account for richness

patterns at both larger (e.g., biogeographic and evolutionary) as well as smaller (e.g., individual host) scales. Additionally, these results illustrate how habitat and species-level effects also play formative roles in driving meta-community symbiont richness, helping to connect work on free-living and parasitic diversity. Because the current study was limited to morphological identification of symbionts, we emphasize the importance of future work that additionally incorporates molecular differentiation to better capture cryptic variation among morphologically similar taxa (e.g., Miura et al. 2005; Leung et al. 2009).

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#### Compliance with ethical standards

**Ethical approval** All applicable institutional and/or national guidelines for the care and use of animals were followed.

## References

- Aditya G, Raut SK (2005) Feeding of the leech *Glossiphonia weberi* on the introduced snail *Pomacea bridgesii* in India. *Aquat Ecol* 39:465–471
- Anderson RM, May RM (1979) Population biology of infectious diseases: part I. *Nature* 280:361–367
- Arneberg P (2002) Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematodes of mammals. *Ecography* 25:88–94
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48
- Bordes F, Morand S, Kelt DA, Van Vuren DH (2009) Home range and parasite diversity in mammals. *Am Nat* 173:467–474
- Brown KM, DeVries DR (1985) Predation and the distribution and abundance of a pulmonate pond snail. *Oecologia* 66:93–99
- Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. *J Parasitol* 83:575–583
- Chao A, Chazdon RL, Shen TJ (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecol Lett* 8:148–159
- Connor EF, McCoy ED (2001) Species–area relationships. *Encycl Biodivers* 5:397–411
- Cooper N, Kamilar JM, Nunn CL (2012) Host longevity and parasite species richness in mammals. *PLoS ONE* 7:e42190
- Crompton DWT (1999) How much human helminthiasis is there in the world? *J Parasitol* 85:397–403
- Cronin JT, Reeve JD (2005) Host-parasitoid spatial ecology: a plea for a landscape-level synthesis. *Proc R Soc B Biol Sci* 272:2225–2235
- Cronin JP, Welsh ME, Dekkers MG, Abercrombie ST, Mitchell CE (2010) Host physiological phenotype explains pathogen reservoir potential. *Ecol Lett* 13:1221–1232
- Dobson A, Lafferty KD, Kuris AM, Hechinger RF, Jetz W (2008) Homage to Linnaeus: how many parasites? How many hosts? *Proc Natl Acad Sci USA* 105:11482–11489
- Dogiel VA (1964) General parasitology. Oliver and Boyd, Edinburgh
- Dove ADM, Cribb TH (2006) Species accumulation curves and their applications in parasite ecology. *Trends Parasitol* 22:568–574
- Duggan IC (2010) The freshwater aquarium trade as a vector for incidental invertebrate fauna. *Biol Invasions* 12:3757–3770
- Dunn RR, Davies TJ, Harris NC, Gavin MC (2010) Global drivers of human pathogen richness and prevalence. *Proc R Soc B Biol Sci* 277:2587–2595
- Ebert D, Hottinger JW, Pajunen VI (2001) Temporal and spatial dynamics of parasite richness in a *Daphnia* metapopulation. *Ecology* 82:3417–3434
- Esch GW, Shostak AW, Marcogliese DJ, Goater TM (1990) Patterns and processes in helminth parasite communities: an overview. In: Esch GW, Bush AO, Aho JM (eds) *Parasite communities patterns and processes*. Chapman and Hall, London, pp 1–19
- Esch GW, Curtis LA, Barger MA (2001) A perspective on the ecology of trematode communities in snails. *Parasitology* 123:57–75
- Eveland LK, Haseeb MA (2011) Laboratory rearing of *Biomphalaria glabrata* snails and maintenance of larval schistosomes in vivo and in vitro. In: Toledo R, Fried B (eds) *Biomphalaria* snails and larval trematodes. Springer, Berlin, pp 33–55
- Fellis KJ, Esch GW (2004) Community structure and seasonal dynamics of helminth parasites in *Lepomis cyanellus* and *L. macrochirus* from Charlie's Pond, North Carolina: host size and species as determinants of community structure. *J Parasitol* 90:41–49
- Gamble HR, Fried B (1976) Experimental evidence for parasitism in the relationship between *Chaetogaster limnaei limnaei* (Oligochaeta) and *Physa acuta* (Gastropoda). *Veliger* 18:393–395
- Gibson DI (1987) Questions in digenean systematics and evolution. *Parasitology* 95:429–460
- Goater TM, Goater CP, Esch G (2014) Parasite community ecology. Parasitism: the diversity and ecology of animal parasites. Cambridge University Press, Cambridge, pp 356–358
- Godon J-J, Arulazhagan P, Steyer JP, Hamelin J (2016) Vertebrate bacterial gut diversity: size also matters. *BMC Ecol* 16:1–9
- Gregory R (1990) Parasites and host geographic range as illustrated by waterfowl. *Funct Ecol* 4:645–654
- Gryseels B, Polman K, Clerinx J, Kestens L (2006) Human schistosomiasis. *Lancet* 368:1106–1118
- Guégan JF, Lambert A, Lévêque C, Combs S, Euzet L (1992) Can host body size explain the parasite species richness in tropical freshwater fishes? *Oecologia* 90:197–204
- Guernier V, Hochberg ME, Guégan JF (2004) Ecology drives the worldwide distribution of human diseases. *PLoS Biol* 2:740–746
- Hechinger RF, Lafferty KD (2005) Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts. *Proc R Soc B Biol Sci* 272:1059–1066
- Heltshel JF, Forrester NE (1983) Estimating species richness using the jackknife procedure. *Biometrics* 39:1–11

- Hopkins SR, Ocampo JM, Wojdak JM, Belden LK (2016) Host community composition and defensive symbionts determine trematode parasite abundance in host communities. *Ecosphere* 7:1–10
- Johnson PTJ, Lunde KB, Ritchie EG, Launer AE (1999) The effect of trematode infection on amphibian limb development and survivorship. *Science* 284:802–804
- Johnson PTJ, Preston DL, Hoverman JT, Richgels KLD (2013) Biodiversity decreases disease through predictable changes in host community competence. *Nature* 494:230–233
- Johnson PTJ, de Roode JC, Fenton A (2015) Why infectious disease research needs community ecology. *Science* 349:1259504
- Johnson PTJ, Wood CL, Joseph MB, Preston DL, Haas SE, Springer YP (2016) Habitat heterogeneity drives the host diversity–begets-parasite diversity relationship: evidence from experimental and field studies. *Ecol Lett*. doi:10.1111/ele.12609
- Kamiya T, O’Dwyer K, Nakagawa S, Poulin R (2014a) What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biol Rev* 89:123–134
- Kamiya T, O’Dwyer K, Nakagawa S, Poulin R (2014b) Host diversity drives parasite diversity: meta-analytical insights into patterns and causal mechanisms. *Ecography* 37:689–697
- Kennedy CR (2009) The ecology of parasites of freshwater fishes: the search for patterns. *Parasitology* 136:1653–1662
- Kennedy CR, Bush AO (1992) Species richness in helminth communities: the importance of multiple congeners. *Parasitology* 104:189–197
- Kennedy CR, Bush AO (1994) The relationship between pattern and scale in parasite communities: a stranger in a strange land. *Parasitology* 109:187–196
- Khalil LF (1961) On the capture and destruction of miracidia by *Chaetogaster limmaei* (Oligochaeta). *J Helminthol* 35:269–274
- King CH, Dickman K, Tisch DJ (2005) Reassessment of the cost of chronic helminth infection: a meta-analysis of disability-related outcomes in endemic schistosomiasis. *Lancet* 365:1561–1569
- Krasnov BR, Shenbrot GI, Khokhlova IS, Degen AA (2004) Flea species richness and parameters of host body, host geography and host “milieu”. *J Anim Ecol* 73:1121–1128
- Krasnov BR, Stanko M, Khokhlova IS, Miklisova D, Morand S, Shenbrot GI, Poulin R (2006) Relationships between local and regional species richness in flea communities of small mammalian hosts: saturation and spatial scale. *Parasitol Res* 98:403–413
- Krasnov BR, Stanko M, Khokhlova IS, Shenbrot GI, Morand S, Korralo-Vinarskaya NP, Vinarski MV (2011) Nestedness and B-diversity in ectoparasite assemblages of small mammalian hosts: effects of parasite affinity, host biology and scale. *Oikos* 120:630–639
- Kuris AM, Blaustein AR, Alio JJ (1980) Hosts as islands. *Am Nat* 116:570–586
- Laguerre C, Joannes A, Poulin R, Blasco-Costa I (2016) Genetic structure and host-parasite co-divergence: evidence for trait-specific local adaptation. *Biol J Linn Soc* 118:344–358
- Leung TLF, Keeney DB, Poulin R (2009) Cryptic species complexes in manipulative echinostomatid trematodes: when two become six. *Parasitology* 136:241–252
- Lindenfors P, Nunn CL, Jones KE, Cunningham AA, Sechrest W, Gittleman JL (2007) Parasite species richness in carnivores: effects of host body mass, latitude, geographical range and population density. *Glob Ecol Biogeogr* 16:496–509
- Lively CM (1989) Adaptation by a parasitic trematode to local populations of its snail host. *Evolution* 43:1663–1671
- MacArthur RH, Wilson EO (1967) *The theory of island biogeography*. Princeton University Press, Princeton
- Marcogliese DJ (2005) Parasites of the superorganism: are they indicators of ecosystem health? *Int J Parasitol* 35:705–716
- Marcogliese DJ, Locke SA, Gelinas M, Gendron A (2016) Variation in parasite communities in spottail shiners (*Notropis hudsonius*) linked with precipitation. *J Parasitol* 102:12–31
- Mitchell CE, Blumenthal D, Jarošík V, Puckett EE, Pyšek P (2010) Controls on pathogen species richness in plants’ introduced and native ranges: roles of residence time, range size and host traits. *Ecol Lett* 13:1525–1535
- Miura O, Kuris AM, Torchin ME, Hechinger RF, Dunham EJ, Chiba S (2005) Molecular-genetic analyses reveal cryptic species of trematodes in the intertidal gastropod, *Batillaria cumingi* (Crosse). *Int J Parasitol* 35:793–801
- Morand S, Poulin R (1998) Density, body mass and parasite species richness of terrestrial mammals. *Evol Ecol* 12:717–727
- Morand S, Cribb TH, Kulbicki M, Rigby MC, Chauvet C, Dufore V, Faliex E, Galzin R, Lo-Yat A, Pichelin S, Sasal P (2000) Endoparasite species richness of New Caledonian butterfly fishes: host density and diet matter. *Parasitology* 121:65–73
- Mouillot D, Krasnov BR, Shenbrot GI, Gaston KJ, Poulin R (2006) Conservatism of host specificity in parasites. *Ecography* 29:596–602
- Mouritsen KN, Jensen KT (1994) The enigma of gigantism: effect of larval trematodes on growth, fecundity, egestion and locomotion in *Hydrobia ulvae* (Pennant) (Gastropoda: Prosobranchia). *J Exp Mar Biol Ecol* 181:53–66
- Nunn CL, Altizer S, Jones KE, Sechrest W (2003) Comparative tests of parasite species richness in primates. *Am Nat* 162:597–614
- Nunn CL, Altizer S, Sechrest W, Cunningham A (2005) Latitudinal gradients of parasite species richness in primates. *Divers Distrib* 11:249–256
- Osenberg CW (1989) Resource limitation, competition and the influence of life history in a freshwater snail community. *Oecologia* 79:512–519
- Poulin R (1995) Phylogeny, ecology, and the richness of parasite communities in vertebrates. *Ecol Monogr* 65:283–302
- Poulin R (1997) Species richness of parasite assemblages: evolution and patterns. *Annu Rev Ecol Syst* 28:341–358
- Poulin R (2014) Parasite biodiversity revisited: frontiers and constraints. *Int J Parasitol* 44:581–589
- Poulin R, Morand S (2000) The diversity of parasites. *Q Rev Biol* 75:277–293
- Poulin R, Morand S (2004) *Parasite biodiversity*. Smithsonian Institution Press, Washington DC
- Prat N, Añón-Suárez D, Rieradevall M (2004) First record of podonominae larvae living phoretically on the shells of the water snail *Chilina dombeyana* (Diptera: Chironomidae/Gastropoda: Lymnaeidae). *Aquat Insects* 26:147–152
- Price PW, Clancy KM (1983) Patterns in number of helminth species in freshwater fishes. *J Parasitol* 69:449–454
- Rhode K (1999) Latitudinal gradients in species diversity and Rapoport’s rule revised: a review of recent work and what can parasites teach us about the causes of the gradients? *Ecography* 22:593–613
- Richgels KLD, Hoverman JT, Johnson PTJ (2013) Evaluating the role of regional and local processes in structuring a larval trematode metacommunity of *Helisoma trivolvis*. *Ecography* 36:854–863
- Ricklefs RE (2004) A comprehensive framework for global patterns in biodiversity. *Ecol Lett* 7:1–15
- Rigaud T, Perrot-Minnot MJ, Brown MJF (2010) Parasite and host assemblages: embracing the reality will improve our knowledge of parasite transmission and virulence. *Proc R Soc B Biol Sci* 277:3693–3702
- Roche DG, Leung B, Mendoza Franco EF, Torchin ME (2010) Higher parasite richness, abundance and impact in native versus introduced cichlid fishes. *Int J Parasitol* 40:1525–1530
- Rosenzweig M (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge

- Sapp KK, Esch GW (1994) The effects of spatial and temporal heterogeneity as structuring forces for parasite communities in *Helisoma anceps* and *Physa gyrina*. *Am Midl Nat* 132:91–103
- Sarah HH (1971) Leeches found on two species of *Helisoma* from Fleming's Creek, Michigan. *Ohio J Sci* 71:15–20
- Schell SC (1985) Handbook of trematodes of North America north of Mexico. University Press of Idaho, Moscow, ID
- Schmid-Hempel P (2003) Variation in immune defense as a question of evolutionary ecology. *Proc R Soc B Biol Sci* 270:357–366
- Scott ME (1988) The impact of infection and disease on animal populations: implications for conservation biology. *Conserv Biol* 2:40–56
- Seabloom EW, Borer ET, Gross K, Kendig AE, Lacroix C, Mitchell CE, Mordecai EA, Power AG (2015) The community ecology of pathogens: coinfection, coexistence and community composition. *Ecol Lett* 18:401–415
- Skelton J, Doak S, Leonard M, Creed RP, Brown BL (2016) The rules for symbiont community assembly change along a mutualism-parasitism continuum. *J Anim Ecol* 85:843–853
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- Stoll S, Früh D, Westerwald B, Hormel N, Haase P (2013) Density-dependent relationship between *Chaetogaster limnaei limnaei* (Oligochaeta) and the freshwater snail *Physa acuta* (Pulmonata). *Freshw Sci* 32:642–649
- Thieltges DW, Hof C, Dehling DM, Brändle M, Brandl R, Poulin R (2011) Host diversity and latitude drive trematode diversity patterns in the European freshwater fauna. *Glob Ecol Biogeogr* 20:675–682
- Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. *Nature* 421:628–630
- Torchin ME, Miura O, Hechinger RF (2015) Parasite species richness and intensity of interspecific interactions increase with latitude in two wide-ranging hosts. *Ecology* 96:3033–3042
- Vavrek MJ (2011) fossil: palaeoecological and palaeogeographical analysis tools. *Palaeontol Electron* 14:1T
- Vitone ND, Altizer S, Nunn CL (2004) Body size, diet and sociality influence the species richness of parasitic worms in anthropoid primates. *Evol Ecol Res* 6:183–199
- Walter J, Ley R (2011) The human gut microbiome: ecology and recent evolutionary changes. *Annu Rev Microbiol* 65:411–429
- Walther BA, Cotgreave P, Price RD, Gregory RD, Clayton DH (1995) Sampling effort and parasite species richness. *Parasitol Today* 11:306–310
- Wisniewski WL (1958) Characterization of parasite fauna of a eutrophic lake. *Acta Parasitol* 6:1–64
- Wolfe LM (2002) Why alien invaders succeed: support for the escape-from-enemy hypothesis. *Am Nat* 160:705–711
- Yamaguti S (1971) Synopsis of digenetic trematodes of vertebrates. Keigaku Publishing, Tokyo
- Zelmer DA (2014) Size, time, and asynchrony matter: the species-area relationship for parasites of freshwater fishes. *J Parasitol* 100:561–568
- Zelmer DA, Gross CM (2009) “Active” passive sampling in two species of *Lepomis* from Par Pond, South Carolina, United States: a case study of infracommunity nestedness. *J Parasitol* 95:1054–1061
- Zimmermann MR, Luth KE, Esch GW (2011) Complex interactions among a nematode parasite (*Daubaylia potomaca*), a commensalistic annelid (*Chaetogaster limnaei limnaei*), and trematode parasites in a snail host (*Helisoma anceps*). *J Parasitol* 97:788–791
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York