

# Tracking the assembly of nested parasite communities: Using $\beta$ -diversity to understand variation in parasite richness and composition over time and scale

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## Abstract

1. Community composition is driven by a few key assembly processes: ecological selection, drift and dispersal. Nested parasite communities represent a powerful study system for understanding the relative importance of these processes and their relationship with biological scale. Quantifying  $\beta$ -diversity across scales and over time additionally offers mechanistic insights into the ecological processes shaping the distributions of parasites and therefore infectious disease.
2. To examine factors driving parasite community composition, we quantified the parasite communities of 959 amphibian hosts representing two species (the Pacific chorus frog, *Pseudacris regilla* and the California newt, *Taricha torosa*) sampled over 3 months from 10 ponds in California. Using additive partitioning, we estimated how much of regional parasite richness ( $\gamma$ -diversity) was composed of within-host parasite richness ( $\alpha$ -diversity) and turnover ( $\beta$ -diversity) at three biological scales: across host individuals, across species and across habitat patches (ponds). We also examined how  $\beta$ -diversity varied across time at each biological scale.
3. Differences among ponds comprised the majority (40%) of regional parasite diversity, followed by differences among host species (23%) and among host individuals (12%). Host species supported parasite communities that were less similar than expected by null models, consistent with ecological selection, although these differences lessened through time, likely due to high dispersal rates of infectious stages. Host individuals within the same population supported more similar parasite communities than expected, suggesting that host heterogeneity did not strongly impact parasite community composition and that dispersal was high at the individual host-level. Despite the small population sizes of within-host parasite communities, drift appeared to play a minimal role in structuring community composition.
4. Dispersal and ecological selection appear to jointly drive parasite community assembly, particularly at larger biological scales. The dispersal ability of aquatic parasites with complex life cycles differs strongly across scales, meaning that parasite communities may predictably converge at small scales where dispersal is high, but may be more stochastic and unpredictable at larger scales. Insights into assembly mechanisms within multi-host, multi-parasite systems provide opportunities for understanding how to mitigate the spread of infectious diseases within human and wildlife hosts.

**KEYWORDS**

*β*-diversity, amphibian disease, coinfection, community assembly, disease ecology, infectious disease, multi-scale, trematode

## 1 | INTRODUCTION

Parasites comprise more than one-third of known species on Earth and can be an important driving force in ecosystem dynamics, the maintenance of biodiversity and evolutionary change (Dobson, Lafferty, Kuris, Hechinger, & Jetz, 2008; Hatcher, Dick, & Dunn, 2006; Hudson, Dobson, & Lafferty, 2006; Paterson et al., 2010). Although epidemiology has traditionally focused on one-host, one-parasite interactions, parasites typically interact with rich assemblages of hosts and other symbionts (Rigaud, Perrot-Minnot, & Brown, 2010). Moreover, interactions between host and parasite communities can combine to shape ecological processes across multiple biological scales (Seabloom et al., 2015; Telfer et al., 2010). For instance, co-infecting parasites can dramatically alter disease outcomes for individual hosts (Griffiths, Pedersen, Fenton, & Petchey, 2011; Johnson & Hoverman, 2012) as well as transmission rates within populations (Jolles, Ezenwa, Etienne, Turner, & Olf, 2008; Susi, Barrès, Vale, & Laine, 2015). Scaling up even further, parasite diversity within ecosystems can functionally dictate food web linkages and patterns of energy flow (Lafferty, Dobson, & Kuris, 2006), underscoring the importance of characterizing parasite community composition at multiple scales—from across individual hosts to entire regions (Pedersen & Fenton, 2007).

A key challenge in the ongoing study of parasite community ecology is to understand the ecological processes underlying community structure and how these processes vary with scale (Holmes, 1987; Sousa, 1990). Historically, many studies have employed comparative approaches to quantify compositional differences in parasite communities (e.g. Altman & Byers, 2014; Krasnov et al., 2011; Sousa, 1990; Vidal-Martínez & Poulin, 2003). This work has accumulated valuable information as to how parasite communities are structured at different biological scales: e.g. how parasite communities differ across host individuals (Guégan & Hugueny, 1994), across host populations (Holmes, 1990), across host species (Fecchio et al., 2017; Locke, Mclaughlin, & Marcogliese, 2013) and across environmental or spatial gradients (Poulin, 2003; Thieltses, Dolch, Krakau, & Poulin, 2010). However, fewer studies have integrated multiple scales into the same study (but see Dallas & Presley, 2014; Krasnov et al., 2011), for example, to compare whether host species identity or habitat represent a stronger structuring force. Comparisons of community composition across scales can reveal where and by what mechanisms species distributions are most strongly limited and identify whether assembly is non-random (Crist, Veech, Gering, & Summerville, 2003). Identifying these core structuring processes and their scale-dependence in natural host-parasite systems offers essential opportunities to test hypotheses about the drivers of parasite distributions and better inform strategies for disease

mitigation (Rynkiewicz, Pedersen, & Fenton, 2015). For instance, if parasite communities are strongly structured across environmental gradients, managing habitat features might be an important disease control strategy, whereas high among-individual or among-species variation might require a targeted vaccination program (Paull et al., 2012). More broadly, due to their hierarchically nested structure (Guégan, Morand, & Poulin, 2005), parasite communities offer potential for understanding how assembly processes vary over scale (Mihaljevic, 2012) and therefore represent a powerful study system for addressing one of the major challenges in community ecology (Chase & Myers, 2011; Levin, 1992).

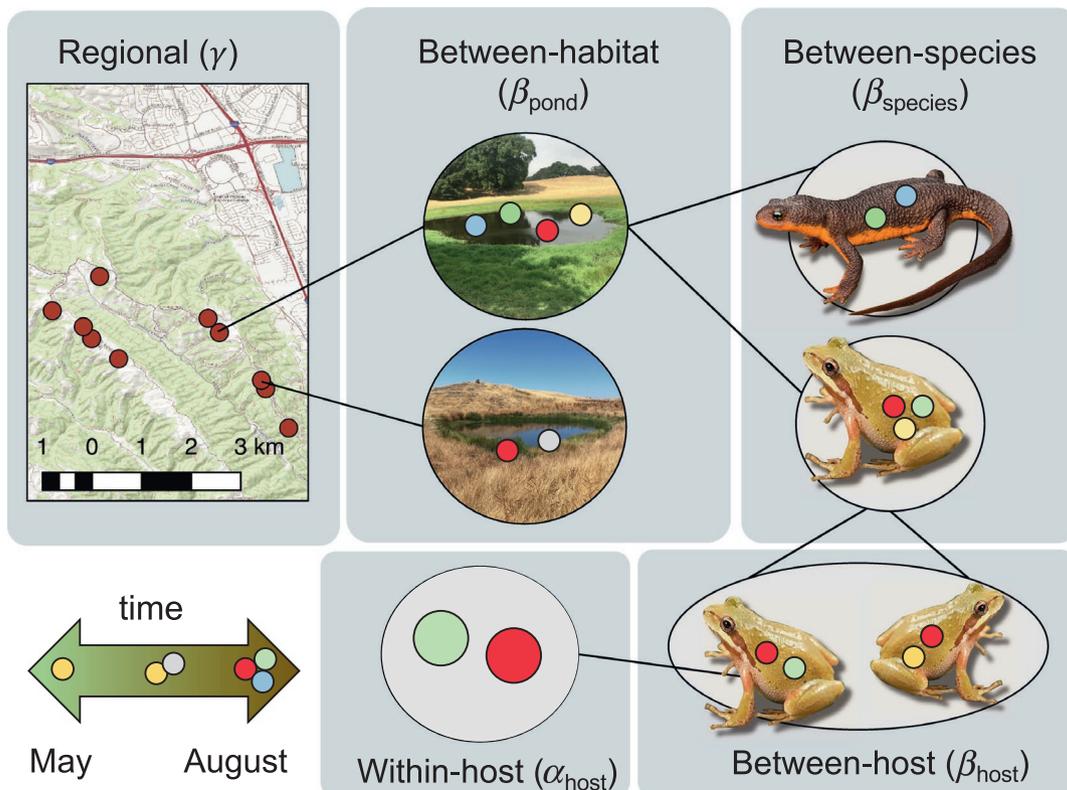
Community ecology theory advances that variation among ecological communities is driven by four key processes: dispersal, ecological selection, drift and speciation (Vellend, 2010). Dispersal is the process by which parasites colonize a site from a given species pool, and this process operates at multiple biological scales; for instance, dispersal structures which parasites arrive to a particular habitat patch from the regional species pool, as well as the parasites reaching a given host within that habitat patch (Guégan et al., 2005). Ecological selection is a niche-based process, whereby abiotic or biotic conditions filter which parasites can persist following dispersal. Selection acts at the habitat-level (if habitat features influence the species able to persist), at the host species-level (if species vary in their susceptibility to different parasites) and at the individual host-level (if hosts differ in susceptibility or if parasite interactions occur). Finally, drift is the change in community composition resulting from stochastic fluctuations; this can occur across all biological scales but is expected to occur most strongly for small communities (Chase & Myers, 2011), such as those at the within-host level.

To better understand how the relative importance of these mechanisms varies with scale, metrics of community dissimilarity (*β*-diversity) can be compared through approaches such as additive partitioning (Johnson et al., 2016; Veech, Summerville, Crist, Gering, & Crist, 2002). For instance, if *β*-diversity is higher across host species than across habitats, ecological selection at the host species-level could be more important than dispersal among habitats or selection due to environmental variables. Moreover, because assembly processes are often temporally dynamic (Fitzgerald, Winemiller, Sabaj Pérez, & Sousa, 2017; Penczykowski, Laine, & Koskella, 2016), quantifying *β*-diversity across a temporal window can further inform how composition shifts with host development or environmental change (Cohen, Einav, & Hawlena, 2015), offering further insight into process. Decreasing *β*-diversity over time indicates convergence among communities, due to high dispersal rates or similar selection regimes (Leibold et al., 2004), whereas increasing *β*-diversity between similar sampling units often indicates an important role of drift (Chase, 2007). Studies examining *β*-diversity over time and scale have

revealed that assembly processes and community compositions are temporally and spatially dynamic (McIntire & Fajardo, 2009; Soininen, McDonald, & Hillebrand, 2007) and have reinforced the idea that temporal studies yield a more process-based understanding of community assembly. For example, by partitioning variance in community composition across scale and over time, Costello et al. (2009) showed that temporal variation in gut microbiomes within the same individual was smaller than among-individual variation, even on the same day, suggesting that different hosts selected particular microbial communities that remained distinct from other hosts' microbiota over time. Temporal analyses of parasite community composition are still relatively rare (but see Budischak, Hoberg, Abrams, Jolles, & Ezenwa, 2016; Cohen et al., 2015; Fallon, Ricklefs, Latta, & Bermingham, 2004; Vidal-Martínez & Poulin, 2003), and even fewer studies have longitudinally tracked parasite community composition across multiple distinct scales to infer the general processes driving assembly.

Here, we compared variation in parasite communities across multiple, discrete biological scales and over time to better characterize the processes driving community composition. We quantified parasite communities (trematodes, nematodes and protists) within two species of amphibian hosts (Pacific chorus frogs *Pseudacris regilla* and California newts *Taricha torosa*), sampled across 10 different ponds within the California Bay Area. By re-visiting each pond throughout host development, we generated a unique dataset on parasite accumulation and

primary succession. Using an additive partitioning approach (Figure 1), we tested the extent to which parasite community composition was driven by differences among host individuals within the same population ( $\beta_{\text{host}}$ ), among host species within the same community ( $\beta_{\text{species}}$ ) or among habitats ( $\beta_{\text{pond}}$ ). We next examined how  $\beta$ -diversity at each of these scales varied across time to gain further insight into how structuring processes changed over the course of primary succession. We also modelled temporal variation in richness ( $\alpha$ -diversity) at each biological scale to better infer whether changes in community composition were operating through species losses (consistent with ecological selection or drift) or through species gain (consistent with dispersal). We expected that, if ecological selection at the habitat or species scale is a major structuring force, we would observe large differences among host species ( $\beta_{\text{species}}$ ) and habitats ( $\beta_{\text{pond}}$ ) relative to null models (Müller & Gossner, 2010). If ecological drift is an important structuring processes, among-host variation ( $\beta_{\text{host}}$ ) would be consistent with or larger than null models, and would increase through time (Püttker, de Arruda Bueno, Prado, & Pardini, 2015). Finally, we expected that if dispersal was not limiting at a particular scale,  $\alpha$ -diversity would increase while  $\beta$ -diversity would decrease through time at that scale (Leibold et al., 2004). Overall, we intend that the application of a consistent framework and terminology can help to identify the drivers of parasite assembly across a range of multi-host, multi-parasite systems, thereby facilitating future comparisons focused on scale-dependent (or invariant) assembly processes related to disease.



**FIGURE 1** Contribution of different biological scales to regional parasite diversity. At the largest scale, regional richness ( $\gamma$ ) is the total number of parasite species summed across all ponds at any given point in time. Regional richness can be partitioned additively into within-host richness ( $\alpha$ -diversity) and turnover at each biological scale ( $\beta$ -diversity) using the equation:  $\gamma = \alpha_{\text{host}}$  (within host) +  $\beta_{\text{host}}$  (between hosts) +  $\beta_{\text{species}}$  (between species) +  $\beta_{\text{pond}}$  (between pond communities). We compared the relative contributions of each component across time

## 2 | MATERIALS AND METHODS

### 2.1 | Field surveys and dissection

Over the summer of 2017 (May–August), we characterized parasite communities within the larvae of two amphibian species (the Pacific chorus frog, *P. regilla*, and the California newt, *T. torosa*). Hosts were sampled from 10 ponds in the California Bay Area (Appendix S1: Figure S1). All ponds were small habitats containing both species of focal amphibian host and the snail species *Helisoma trivolvis* and *Physa* spp. (*Physa acuta* or *Physa gyrina*), which are intermediate hosts for a diversity of trematode species found in amphibians (McCaffrey & Johnson, 2017). Each pond was visited four to five times across the summer, during which we sampled 10–20 individuals of each host species, representing juvenile life stages from post-hatching to peri-metamorphosis (Appendix S1: Figure S2). Previous research in the same system has shown that this sample size is sufficient for estimating parasite richness within a site (Johnson & Hoverman, 2012; Johnson, Preston, Hoverman, & Richgels, 2013). After euthanizing hosts with MS-222, we examined their organs and tissues under an Olympus SZX10 dissection microscope following standard methods (Johnson et al., 2018) to characterize the presence and identity of parasites (Anderson, Chabaud, & Willmott, 2009; Duszynski, Bolek, & Upton, 2007; Gibson, Jones, & Bray, 2002; Schell, 1985; Sleight, 1991). For trematode and nematode infections, we quantified both parasite identity and load (number of parasites per host), whereas for protozoans we noted only presence or absence. We also measured host size (snout–vent length) and developmental stage (Gosner, 1960; Wong & Liversage, 2004).

### 2.2 | Richness and composition across biological scale and time

To examine how parasite richness varied with biological scale and sampling date, we quantified host-level richness ( $\alpha_{\text{host}}$ ) as the number of parasite taxa within an individual host, population-level richness ( $\alpha_{\text{population}}$ ) as the number of parasite taxa across all individuals of a given host species at a given pond and habitat-level richness ( $\alpha_{\text{pond}}$ ) as the number of parasite taxa totalled across both host species at a given pond. Regional richness ( $\gamma$ ) was estimated as the total number of parasite taxa across all ponds. We quantified  $\alpha_{\text{host}}$ ,  $\alpha_{\text{population}}$ ,  $\alpha_{\text{pond}}$  and  $\gamma$  separately for each time point and modelled richness as a function of time separately for each biological scale, using GLMM. We included polynomial terms for sample date to test whether richness accumulation was linear or unimodal and selected the model that minimized Akaike's information criterion (AIC) values (Appendix S1). We used indicator species analysis in the package INDICESPECIES for R (DeCáceres & Legendre, 2009), to determine whether certain parasite species were associated with particular time points ('indicator species analysis'), including early or late summer. The code for this and all subsequent statistical analyses are available at figshare (<https://doi.org/10.6084/m9.figshare.11809461>).

### 2.3 | $\beta$ -diversity across biological scale and time

To quantify how differences among parasite communities (i.e. turnover or  $\beta$ -diversity) changed with time, we estimated pairwise dissimilarity metrics using Jaccard's distance (Jaccard, 1912), which is based on presence–absence data (Appendix S1). We estimated between-host turnover ( $\bar{\beta}_{\text{J,host}}$ ) as the average pairwise dissimilarity between individuals of the same species collected in the same pond on the same visit. Between-species turnover ( $\bar{\beta}_{\text{J,species}}$ ) was the average difference between *P. regilla* and *T. torosa* parasite communities at a given site-visit, and between-habitat turnover ( $\bar{\beta}_{\text{J,pond}}$ ) was the average difference in parasite communities among ponds. We calculated all three metrics separately at each time point. Using a separate linear mixed model for each biological scale, we quantified the relationship between Jaccard's  $\beta$ -diversity and sample date (Appendix S1).

Because Jaccard's  $\beta$ -diversity metric is sensitive to total taxonomic richness and thus should not be used to compare turnover across scales, we used an additive partitioning approach to compare  $\beta$ -diversity among hosts, species and communities (Crist et al., 2003; Gering, Crist, & Veech, 2003; Johnson et al., 2016; Lande, 1996; Veech & Crist, 2010). This approach partitions regional parasite diversity ( $\gamma$ ) into scale-specific values of turnover ( $\beta$ -diversity) and richness ( $\alpha$ -diversity) using the formula:  $\gamma = \alpha_{\text{host}}$  (within host) +  $\beta_{\text{host}}$  (between hosts) +  $\beta_{\text{species}}$  (between species) +  $\beta_{\text{pond}}$  (between habitats; Figure 1). We used the function *adipart* in the R package VEGAN (Oksanen et al., 2018), which implements random permutations of species occurrence data to produce estimates of significance relative to a null model. The null distribution was generated using 1,000 random permutations which hold site-level richness constant and randomly distribute parasite species across sites relative to their abundance (Crist et al., 2003). We present the difference between observed values ( $\bar{\alpha}_{\text{host,obs}}$  and  $\bar{\beta}_{\text{host,obs}}$ ) and mean null simulation values ( $\bar{\alpha}_{\text{host,sim}}$  and  $\bar{\beta}_{\text{host,sim}}$ ) to evaluate whether observed diversity differed from random chance and then assessed how the proportional contribution of each component to total  $\gamma$ -diversity varied with time as hosts progressively developed and infections accumulated.

$\beta$ -diversity estimates can be influenced by false absences, which are more likely when detection probability is low (e.g. due to rarity or small sample size). Consequently differences in  $\beta$ -diversity across scales could, in part, be driven by the fact that rare species might have higher detection rates at some scales than others. Therefore, we evaluated the sensitivity of the above analyses to the inclusion of rare species by re-running the analyses without rare species, as well as using the Bray–Curtis abundance-based dissimilarity metric (Appendix S1).

## 3 | RESULTS

### 3.1 | Field surveys and parasite community

We quantified the richness and community composition of parasites from 959 individual hosts (445 *T. torosa*, 514 *P. regilla*) from 10 ponds across 3 months of sampling. The majority of hosts ( $n = 795$ ; 82%)

were infected by at least one parasite. On average, ponds contained 6.2 parasite taxa per visit. We identified 18 distinct taxa of parasites, 11 of which were present in >1% of hosts (six digenetic trematodes, two nematodes and three protists; Appendix S1: Table S1). The most common parasite was the trematode *Ribeiroia ondatrae* (present in 44% of *P. regilla* and 48% of *T. torosa*), followed by the trematode *Echinostoma* spp. (59% of *P. regilla* and 16% of *T. torosa*). Some parasites were specialists (e.g. the trophically transmitted nematode *Chabaudgolvania* sp. was only found in *T. torosa*, whereas two protists [*Opalina ranarum* and *Nyctotherus cordiformis*] and the nematode *Gyrrincola batrachiensis* were only found in *P. regilla*). Other parasites (e.g. the trematodes *R. ondatrae* and *Manodistomum syntomentera*) infected both host species at roughly equal proportions.

### 3.2 | Richness and composition across biological scale and time

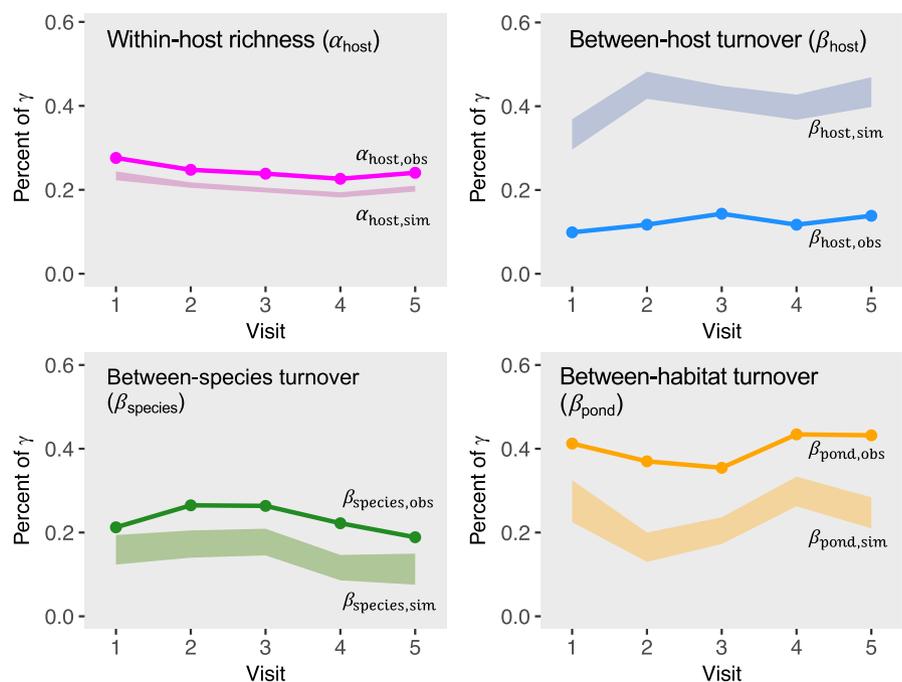
Richness showed a nonlinear relationship with time at both the host- and population-levels (Appendix S1: Figure S3). The top model for predicting host-level richness ( $\alpha_{\text{host}}$ ) included significant terms for host species, an interaction between visit and species and a quadratic term for visit. This model showed improved fit over the next best model, which used visit as a linear term ( $\Delta\text{AIC} = -10.47$ ). Therefore, hosts accumulated parasites nonlinearly with respect to time, with richness peaking in late June to mid-July. The median richness within *P. regilla* hosts was three parasites, which was significantly higher than *T. torosa* (median = 1; estimate =  $-1.65 \pm 0.15$ ;  $p < 0.0001$ ; Appendix S1: Figure S3). The best performing model for predicting population-level richness ( $\alpha_{\text{population}}$ ) included significant terms for host species, an interaction between visit and species and a second-order polynomial term for visit. Similarly, within-population

parasite richness was higher in *P. regilla* populations (median = 5) than in *T. torosa* populations (median = 2, estimate =  $-1.42 \pm 0.34$ ;  $p < 0.0001$ ). While habitat-level richness ( $\alpha_{\text{pond}}$ ) exhibited a similarly unimodal relationship, the best model was a null model, indicating that visit was a poor predictor of parasite richness within ponds. Regional richness ( $\gamma$ ; aggregated over all ponds) did not change over time (estimate [visit] =  $0.009 \pm 0.09$ ;  $p = 0.92$ ).

Of 11 parasite taxa, four were strongly associated with a particular time point or group of time points based on indicator species analysis (Appendix S1: Figure S4). The protozoan *Tritrichomonas augustus* was associated with the first and second visits ( $p = 0.003$ ), and the nematode *G. batrachiensis* was associated with the first through third visits ( $p = 0.001$ ). Two trematode parasites, *Echinostoma* spp. and *Gorgoderina* sp., were 'late season' parasites, associated with the third through fifth visits ( $p = 0.001$  and  $p = 0.02$  respectively).

### 3.3 | $\beta$ -Diversity across biological scale and time

Additive partitioning of diversity (Figure 1) revealed that differences among habitat patches ( $\beta_{\text{ponds}}$ ) had the strongest influence on regional parasite diversity ( $\gamma$ ), and were considerably greater than the effects of differences between host species ( $\beta_{\text{species}}$ ) or among individual hosts ( $\beta_{\text{host}}$ ; Figure 2). Among-habitat turnover averaged over all visits ( $\bar{\beta}_{\text{pond,obs}}$ ) accounted for 40% of regional parasite diversity, and ponds were significantly less similar than expected from a null model ( $\bar{\beta}_{\text{pond,obs}} - \bar{\beta}_{\text{pond,sim}} = 0.16$ ;  $p < 0.001$ ). When rare species were removed, the same overall pattern remained, but  $\bar{\beta}_{\text{pond,obs}}$  declined to 29%. Within-host parasite richness ( $\bar{\alpha}_{\text{host}}$ ) was the second largest contributor to regional diversity, accounting for 25% of regional parasite diversity, which was slightly higher than expected ( $\bar{\alpha}_{\text{host,obs}} - \bar{\alpha}_{\text{host,sim}} = 0.040$ ;  $p < 0.001$ ). Differences among



**FIGURE 2** Additive partitioning of regional parasite richness ( $\gamma$ ). Each panel shows the observed contribution of each level to overall regional parasite richness (solid line), compared to null simulations where parasites are distributed randomly (illustrated by a shaded ribbon showing the 95% CI of simulations). Differences among communities or ponds ( $\beta_{\text{pond}}$ ) represented the largest contribution to regional parasite richness and variation among individual hosts in the same population ( $\beta_{\text{host}}$ ) represented the smallest contribution to regional parasite richness

host species ( $\bar{\beta}_{\text{species}}$ ) accounted for 23% of regional parasite diversity and were only slightly less similar ( $\bar{\beta}_{\text{species,obs}} - \bar{\beta}_{\text{species,sim}} = 0.08$ ;  $p < 0.001$ ) than predicted by null models. Finally, differences among host individuals within the same population ( $\bar{\beta}_{\text{host}}$ ) accounted for just 12% of regional diversity, and individuals were much more similar in their parasite communities than predicted by null models ( $\bar{\beta}_{\text{host,obs}} - \bar{\beta}_{\text{host,sim}} = -0.29$ ;  $p = 0.001$ ). Therefore, turnover between habitat patches (ponds) accounted for the highest percentage of regional diversity, followed by within-host richness, between species at the same site and between hosts of the same population (Figure 2).

Differences in parasite community composition between host species ( $\bar{\beta}_{\text{J,species}}$ ) weakened over the summer (estimate =  $-0.06 \pm 0.02$   $p = 0.005$ ), such that species at the same site became more similar in their parasite communities over time. Between-host differences ( $\bar{\beta}_{\text{J,host}}$ ) did not change over time (estimate =  $-0.02 \pm 0.01$ ;  $p = 0.20$ ), indicating that individuals within the same population did not become more or less similar in their parasite communities over the season. Overall, *T. torosa* individuals had lower  $\bar{\beta}_{\text{J,host}}$  values than *P. regilla* (estimate =  $-0.16 \pm 0.03$ ;  $p < 0.0001$ ); therefore, *T. torosa* individuals shared more parasites with other members of their population than did *P. regilla*. Differences among habitat patches ( $\bar{\beta}_{\text{J,pond}}$ ) did not change appreciably over time (estimate =  $-0.01 \pm 0.02$ ;  $p = 0.64$ ). These patterns were robust to the dissimilarity metric used, as well as the inclusion of rare species (Appendix S1).

## 4 | DISCUSSION

Despite increasing interest in describing how parasite community composition changes across habitats, host species and individuals (Johnson, de Roode, & Fenton, 2015; Pedersen & Fenton, 2007; Seabloom et al., 2015), comparatively few studies have investigated the drivers of compositional differences (i.e. 'parasite community assembly') especially across both biological scale and time. In this study, we compared patterns of parasite composition across nested biological scales and used repeated sampling over a temporal window of host development to derive insight into the potential roles of drift, dispersal and ecological selection. This integration of scales indicated that parasite communities were more different across habitat patches than across host species, and that individuals within the same population contained highly similar parasite communities. Differences among habitat patches (i.e. ponds) were consistent with dispersal limitation, whereas within communities, high rates of dispersal appeared to erode individual and species-level differences. Our study illustrates that, as a whole, dispersal processes can play a strong role in structuring parasite communities, but that rates of dispersal strongly differed across scales.

Based on additive partitioning of regional diversity, hierarchical differences in parasite community between ponds ( $\beta_{\text{ponds}}$ ) comprised the majority (40%) of regional level diversity, more than differences between host species ( $\beta_{\text{species}}$ ; 23%) or individuals ( $\beta_{\text{host}}$ ; 12%). Habitat-level differences ( $\beta_{\text{ponds}}$ ) were significantly greater at

each time point than expected by chance (Figure 2), suggesting that parasites were distributed non-randomly across ponds. These differences were, in part, driven by false negative detections of rare parasite species; when they were removed, the contribution of  $\beta_{\text{ponds}}$  was lower (28%). Differences among ponds could be the result of ecological selection if sites filter out certain parasite taxa based on abiotic or biotic conditions. For example, the only two ponds that lacked a common trematode parasite (*Cephalogonimus americanus*) were also the only ponds with American bullfrog (*Rana catesbeiana*) larvae, which are a less competent host that could reduce *C. americanus* abundance (Johnson et al., 2013). Consequently, the host community could represent one possible selection mechanism driving parasite community composition, as previously reported in similar studies (Johnson et al., 2013; Krasnov, Shenbrot, Mouillot, Khokhlova, & Poulin, 2005; Maestri, Shenbrot, & Krasnov, 2017; Mihaljevic, Hoyer, & Johnson, 2017). More broadly, our results are consistent with a large body of work indicating that ecological selection can strongly structure parasite communities across localities (e.g. Dallas & Presley, 2014; Krasnov et al., 2015; Warburton, Kohler, & Vonhof, 2016). To further elucidate the role of ecological selection, interannual variation could be assessed; differences among ponds that are stable across years and correlate strongly to environmental factors could point to important selection mechanisms shaping parasite community composition.

Differences among ponds could also be generated by dispersal limitation; for instance, ponds lacking certain parasites may have not been colonized, even if suitable conditions for that parasite's survival exist. However, differences among pond communities were consistent over time, using both Jaccard's distance and additive partitioning approaches (Figure 2), and pond-level richness remained stable over time (Appendix S1: Figure S3), suggesting that dispersal did not occur during the sampling window at levels high enough to attenuate differences in pond parasite communities. As such, lack of dispersal during the sampling season created stable differences among sites. Parasites are spread from site-to-site through the movement of hosts (Price, 1980). Despite the large dispersal potential of parasites within vagile hosts, host activity may be seasonal or infrequent, limiting colonization opportunities. Indeed, variation in definitive host activity is known to limit dispersal (Kuris & Lafferty, 1994), and parasite communities are often strongly structured by this dispersal limitation at landscape scales (Hartson, Orlofske, Melin, Dillon, & Johnson, 2011; Smith, 2001; Thieltges et al., 2010). Moreover, habitat-level factors can strongly influence the activity of hosts and therefore the probability of dispersal (Hartson et al., 2011; Sousa & Grosholz, 1991) making parasite dispersal across sites a non-neutral process. Consequently, relationships between geographic distance and community dissimilarity, which are commonly used to infer dispersal limitation in free-living communities (Cottenie, 2005; Soininen et al., 2007), may not be expected for parasite communities structured by dispersal (Poulin, 2003; Thieltges et al., 2010). This is analogous to animal-dispersed plants, wherein dispersal is driven by the active habitat selection of seed-dispersers rather than neutral processes (Jones et al., 2015). Correspondingly,

habitat characteristics could strongly influence parasite community composition, but via non-neutral dispersal mechanisms, rather than selection. Tracking parasite dispersal more directly, for instance by monitoring or manipulating host movement (Wood, Summerside, & Johnson, 2019), could thus be an important tool for further evaluating the role of dispersal limitation in driving among-site variation in parasite communities.

In addition to high variation across sites, host species also demonstrated significant and non-random differences in parasite community composition. Differences between the parasite communities of *P. regilla* and *T. torosa* ( $\beta_{\text{species}}$ ) were greater than expected by chance (Figure 2). Therefore, ecological selection appeared to play a role in structuring the parasite communities among different host species, consistent with other systems (e.g. Dallas & Presley, 2014; Friggens & Brown, 2005; MacColl, 2009). Indeed, almost half (5/11) of the parasite taxa in this study were strict specialists on one host (Appendix S1: Table S1) and previous studies (Johnson et al., 2016) have demonstrated that host diversity is an important driver of regional parasite diversity in this same system. Intriguingly, differences among host species ( $\beta_{\text{species}}$ ) decreased over time, revealing that *P. regilla* and *T. torosa* within the same site became more similar in their parasite communities. This pattern appeared driven by a combination of decreasing selection and increasing dispersal pressure over time. Specialist parasites (protozoans and nematodes) tended to peak earlier in the season (Appendix S1: Figure S4); this observation was supported by indicator species analysis showing that both early season parasites were specialists with direct life cycles. On the other hand, generalist parasites in this study were all digenetic trematodes requiring a snail intermediate host, meaning that infections occurred later in development, after snails began shedding infectious trematode stages around June (Paull & Johnson, 2014). Host species became more similar due to the accumulation of infections by generalist parasites, which reached high prevalences later in summer. Therefore, high dispersal of generalist parasites led to the homogenization of the two host species over time, and specialist parasites became less common through time, weakening the relative importance of selection. This differs from free-living communities, wherein specialist taxa often appear to colonize later in succession (Helsen, Hermý, & Honnay, 2016; Piechnik, Lawler, & Martinez, 2008; Ravel, Violle, & Munoz, 2012).

We found little evidence of heterogeneity among individual hosts; hosts within the same population shared significantly more parasites than expected by chance (Figure 2). Low  $\beta$ -diversity at this scale can result from high dispersal rates ('propagule pressure'), which acts to homogenize communities (Leibold et al., 2004; Qian, 2009), and it is well-established that dispersal to individual hosts can be high in pond ecosystems given the high biomass of infectious forms produced by trematodes (Lambden & Johnson, 2013; Preston, Orlofske, Lambden, & Johnson, 2013). Many parasites reached high prevalences within host populations, including numerous taxa that reached 100% prevalence (Appendix S1: Figure S4), indicating a lack of dispersal limitation to individual hosts. Our evidence differs from previous studies documenting

high heterogeneities among hosts (Paull et al., 2012), driven by selection (e.g. host traits influencing susceptibility or exposure risk; Johnson, Nelson, & Dick, 2005), dispersal (e.g. spatial variation in exposure risk; Calabrese, Brunner, & Ostfeld, 2011) or interactions between dispersal and drift (e.g. priority effects; Budischak et al., 2016). Overall, parasite interactions and variation in host competency or exposure risk did not appear to be important processes in this system. We note, however, that by sampling similarly aged, non-reproductive hosts within similar habitats, our approach effectively limited several of the sources of intra-host variability in parasite communities. In natural populations containing a mixture of different larval cohorts, differences among individuals would likely be larger, with younger individuals supporting more protozoan infections, and older individuals supporting more trematode infections. Hosts at intermediate stages of development supported the most diverse parasite communities, as evidenced by the unimodal relationship between richness and time (Appendix S1: Figure S3). Finally, the low divergence among host individuals indicated that drift was not a strong structuring force, since drift is expected to increase divergence over time (Gilbert & Levine, 2017). Drift can represent a powerful stochastic force driving community dissimilarity (Hubbell, 2001) and is expected to operate more strongly when community sizes are small, such as the within-host scale (Vellend, 2010). The most prevalent parasites in this system, digenetic trematodes, do not reproduce within our focal amphibian hosts, requiring a definitive host to complete reproduction; thus demographic fluctuations and thus the influence of drift were likely dampened at the within-host scale. This suggests that, unlike in free-living species, the effect of drift for parasites may be more important at larger scales which encompass the entire parasite life cycle. The role of drift has received relatively little attention in parasite community ecology (Seabloom et al., 2015), but its scale dependency may represent an important future avenue of research.

Empirical data from hierarchically nested parasite communities provide opportunities to understand how ecological processes vary over biological scale and enable syntheses across community ecology. However, key differences among these study systems present challenges for integrating free-living and parasite community ecology. For example, within parasite community ecology, the use of multiple, alternative sets of terminologies to describe assembly have led to both confusion and a disconnect from community ecology generally. For instance, parasitologists may refer to parasites as being limited by 'encounter filters' or 'compatibility filters' (Combes, 2001) or evaluate the role of 'host-level' processes such as host age, sex or body size in driving community composition (Blaylock, Holmes, & Margolis, 2011). Yet mechanistically such traits can affect community composition through dispersal (e.g. if larger hosts experience greater colonization Kuris, Blaustein, & Alio, 1980), selection (e.g. if body size correlates with immune function; Venesky et al., 2012) or drift (e.g. if larger hosts contain larger parasite communities more resistant to stochastic extinctions; Guégan & Huguény, 1994). Additionally, the same

process may be referred to by multiple names depending on the scale of study—for instance, dispersal may be called ‘transmission’ when parasites disperse to hosts, but may be referred to as ‘colonization’ when that host or population is previously uninfected (Bush, Lafferty, Lotz, & Shostak, 1997). The concept of ‘transmission’ further tends to combine both selection and dispersal-based processes (McCallum et al., 2017), making it challenging to compare with assembly processes in free-living ecology. As empirical data on parasite communities accumulate, using a common language about the underlying processes will further facilitate comparisons across studies and biological scales, improving links with free-living community ecology.

Studies of parasite community ecology have generated numerous fundamental insights into how parasite community composition alters disease dynamics (Johnson et al., 2015), but understanding how those communities arise is still difficult with observational studies in natural populations. Using additive partitioning is one way to make direct, cross-scale comparisons in nested communities, and we have used this approach herein to compare processes acting at the within-host, within-population and within-pond level. We additionally demonstrate that comparing communities over a temporal window, especially over primary succession, can aid in disentangling process and pattern. Community assembly mechanisms influence important facets of infectious disease-causing agents: where they are, when they arrive and at what scales they are most limited. A process-based approach therefore improves our ability to predict where parasites will spread and at what scales they may be appropriately managed.

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## AUTHORS' CONTRIBUTIONS

W.E.M., T.M.-G. and P.T.J.J. designed the study; W.E.M., T.M.-G. and D.M.C. collected the data; W.E.M. analysed the data; W.E.M. led the writing of the manuscript. All authors contributed to editing and reviewing the manuscript and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data and R code necessary to reproduce analyses are archived on figshare. Data: <https://doi.org/10.6084/m9.figshare.11809242.v2> (Moss, McDevitt-Galles, Calhoun, & Johnson, 2020a); R code:

<https://doi.org/10.6084/m9.figshare.11809461.v2> (Moss, McDevitt-Galles, Calhoun, & Johnson, 2020b).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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