

Parasite metacommunities: Evaluating the roles of host community composition and environmental gradients in structuring symbiont communities within amphibians

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Funding information

David and Lucile Packard Foundation; Division of Environmental Biology, Grant/Award Number: 0841758 and 1149308; Division of Graduate Education, Grant/Award Number: 1144083; National Institute of Food and Agriculture, Grant/Award Number: 2014-67012-22272; National Institutes of Health, Grant/Award Number: R01GM109499; Netherlands Organization for Scientific Research, Grant/Award Number: 825.11.036

Handling Editor: Daniel Stouffer

Abstract

1. Ecologists increasingly report the structures of metacommunities for free-living species, yet far less is known about the composition of symbiont communities through space and time. Understanding the drivers of symbiont community patterns has implications ranging from emerging infectious disease to managing host microbiomes.
2. Using symbiont communities from amphibian hosts sampled from wetlands of California, USA, we quantified the effects of spatial structure, habitat filtering and host community components on symbiont occupancy and overall metacommunity structure.
3. We built upon a statistical method to describe metacommunity structure that accounts for imperfect detection in survey data—detection error-corrected elements of metacommunity structure—by adding an analysis to identify covariates of community turnover. We applied our model to a metacommunity of eight parasite taxa observed in 3,571 Pacific chorus frogs (*Pseudacris regilla*) surveyed from 174 wetlands over 5 years.
4. Symbiont metacommunity structure varied across years, showing nested structure in 3 years and random structure in 2 years. Species turnover was most consistently influenced by spatial and host community components. Occupancy generally increased in more southeastern wetlands, and snail (intermediate host) community composition had strong effects on most symbiont taxa.
5. We have used sophisticated but accessible statistical methods to reveal that spatial components—which influence colonization—and host community composition—which mediates transmission—both drive symbiont community composition in this system. These methods allow us to associate broad patterns of community turnover to local, species-level effects, ultimately improving our understanding of spatial community dynamics.

KEYWORDS

amphibians, Bayesian inference, disease ecology, metacommunity, occupancy modelling, parasites, symbionts, trematodes

1 | INTRODUCTION

Evidence from human and wildlife systems illustrates how changes in symbiont community composition—including the mutualists, commensals and parasites that rely on a host—can affect host health and pathogen transmission (Fierer et al., 2012; Johnson, de Roode, & Fenton, 2015). For instance, the use of faecal transplants between human patients, which results in increased gut bacterial diversity, can resolve recurrent *Clostridium difficile* infections (van Nood et al., 2013; Youngster et al., 2014). Similarly, altering the skin microbial community of amphibians has shown potential to protect against the deadly fungus, *Batrachochytrium dendrobatidis* (Harris et al., 2009; Woodhams et al., 2014). Symbiont composition can also affect large-scale patterns of transmission by altering within-host dynamics or by affecting host death rates. In tick-borne diseases such as babesiosis and Lyme disease, for instance, interactions between the two causative agents—*Babesia microti* and *Borrelia burgdorferi*—can promote transmission and lead to more severe disease in humans (Diuk-Wasser, Vannier, & Krause, 2016). Thus, understanding the environmental drivers of symbiont community composition is an important goal, and one for which the field of community ecology has much to offer (Johnson et al., 2015; Mihaljevic, 2012; Seabloom et al., 2015).

Symbiont communities are well-suited for testing general ecological patterns and theories, such as neutral theory, community saturation and island biogeography, among others (Dove, 2006; Krasnov & Vinarski, 2008; Kuris, Blaustein, & Alio, 1980; Kuris & Lafferty, 1994; Poulin, 2007; Poulin, Krasnov, Mouillot, & Thieltges, 2011). Understanding the distribution of symbiont communities also carries the applied benefit of informing host health and symbiont transmission dynamics in wildlife and human systems (Fierer et al., 2012; Johnson & Hoverman, 2012). Metacommunity ecology, which seeks mechanistic understanding of the separate and interactive roles of local and regional processes in shaping communities, offers theory and analytical tools that can be used to explore the factors that affect species composition across space (Holyoak, Leibold, & Holt, 2005; Leibold et al., 2004). By delineating symbiont communities at multiple hierarchical levels (communities within and among host individuals, host populations or even host communities), the application of metacommunity tools can be used to answer applied questions related to individual host health and among-host transmission dynamics, as well as general ecological questions regarding the structuring of communities (Johnson et al., 2015; Mihaljevic, 2012).

There are a variety of emerging statistical tools and frameworks to analyse the effects of environmental gradients on free-living and symbiont community composition, including the use of advanced joint species distribution models and structural equation models (Harris, 2015; Joseph, Preston, & Johnson, 2016; Ovaskainen et al., 2017). One of the most widely used set of statistical tools is derived from metacommunity ecology—the elements of metacommunity structure (EMS, Leibold & Mikkelsen, 2002; Presley, Higgins, & Willig, 2010)—and aims to characterize how communities assemble along environmental gradients, yielding insights into systems ranging from plants to fish to mammals (e.g. de la Sancha, Higgins, Presley, & Strauss, 2014;

Fernandes, Henriques-Silva, Penha, Zuanon, & Peres-Neto, 2013; López-González, Presley, Lozano, Stevens, & Higgins, 2012; Meynard, Boulangeat, Garraud, Mouquet, & Thuiller, 2013; Willig et al., 2011). In this analysis, survey data are compiled into a site-by-species matrix, which is ordinated to arrange the metacommunity by sites that contain similar species compositions and by species with similar distributions among sites. Then, descriptive statistics of the ordinated matrix are analysed to assign a nominal metacommunity structure, such as Clementsian, Gleasonian, Nested, Checker-board or Random. The observed structure gives insight into the mechanisms that influence community assembly in the system. For example, a Clementsian structure suggests that groups of species with similar environmental constraints turnover along a common gradient, whereas a Gleasonian structure suggests that species' occurrences respond to a dominant environmental gradient, but species responses are idiosyncratic, leading to a more continuous gradient of species occurrences. Further statistical tests can be conducted to identify the dominant environmental gradient(s) along which species assemble.

Recently, applications of the EMS have proven useful for understanding symbiont communities. For instance, Richgels, Hoverman, and Johnson (2013) showed that local environmental filters (e.g. abiotic and biotic wetland characteristics, such as surface area and host biomass) more strongly influenced the composition of trematode species in snail hosts compared to more regional-scale process, such as dispersal limitation (i.e. wetland connectivity). Similarly, looking across a large dataset of Sonoran Desert rodents, Dallas and Presley (2014) used EMS methods and variance partitioning to determine that host species traits that influenced habitat quality (e.g. host body size, longevity) were better predictors of parasite composition among host species than traits that influenced parasite colonization opportunities (e.g. host range size, diet breadth, phylogeny). These recent studies highlight the utility of metacommunity approaches for exploring how symbiont communities are structured across space and among hosts. Their results also suggest local habitat filtering may be more important for mediating symbiont community structure compared to more regional-level processes.

When EMS methods rely on binary occurrence data, however, imperfect detection of species at surveyed sites often results in structure misclassification (Mihaljevic, Joseph, & Johnson, 2015). In other words, suboptimal sampling of cryptic, rare or otherwise difficult to detect species can lead to ordinated matrices that obscure the true structure of the metacommunity, ultimately impeding our understanding of underlying biology. Additionally, to discern which environmental gradients might lead to observed patterns in species turnover, many studies using EMS implement univariate correlation tests between the site-by-species matrix ordination scores and a suite of environmental covariates. However, this strategy collapses a wealth of information, including species-specific responses to environmental covariates and the simultaneous influence of multiple covariates, into one or two component axes. Importantly, Jackson, Turner, Pearson, and Ives (2012) showed that models that estimate species-specific responses are better able to detect influential environmental gradients compared to common approaches that collapse the community into smaller

dimensions (e.g. redundancy analysis, canonical correspondence analysis [CCA] and non-metric multidimensional scaling [NMDS]).

In this study, we combine three emerging methods in metacommunity ecology—multivariate statistics, detection-error correction and the EMS—in a cohesive analysis to evaluate the roles of space, habitat filtering and host community composition on symbiont occupancy and species turnover. We utilize an extensively surveyed amphibian–symbiont system that consists of eight parasite taxa, most of which are digenetic trematodes, and their intermediate amphibian and snail host communities. Several of these symbionts cause moderate to severe pathology, making an understanding of symbiont community composition of great importance in this system (Koprivnikar et al., 2012). We hypothesized that host community composition would limit symbiont occupancy across sampled wetlands, given that these symbionts have complex life cycles and rely on a variety of host taxa, such as snails, larval amphibians and terrestrial vertebrates. We also expected that wetland isolation or regional location would limit symbiont occupancy via effects on colonization opportunities. Finally, we suspected that local habitat filtering—beyond effects manifesting on the host communities—could act to influence symbiont occupancy to a lesser extent, likely through effects on the survival or spread of parasite free-living stages (Richgels et al., 2013). By using and further developing tools to evaluate metacommunity structure, our overarching aim was to apply ecological theory developed for free-living communities to better understand the determinants of symbiont community variation across space and time.

2 | MATERIALS AND METHODS

2.1 | Natural history

During the aquatic larval life stage, amphibians can acquire a variety of helminth and protozoan symbionts, whose effects range from benign to severely pathogenic (Koprivnikar et al., 2012; Schotthoefer et al., 2011). The majority of the parasites found in larval amphibians are digenetic trematodes, which have complex life cycles requiring multiple host species (Combes, Bartoli, & Théron, 2002; Koprivnikar et al., 2012; Poulin & Cribb, 2002). While trematode species can have a variety of host types, modes of transmission, modes of movement, and other life-history characteristics, we briefly introduce those that are most relevant to the taxa found in wetland habitats in California (Johnson et al., 2016). A typical life cycle consists of a reproductive adult within a definitive host, typically a mammal, bird, amphibian or reptile, which deposits trematode eggs into the wetland via host faeces. The eggs hatch (or are first consumed) and the next life stage infects a snail host, in which the trematodes reproduce asexually. A free-living stage typically emerges from the snail host and infects another intermediate host (e.g. snail, larval insect, fish or amphibian host) within the aquatic environment. These second intermediate hosts are eaten by the trematode's definitive host to complete the life cycle. Often these trematodes are relatively host-specific in their use of snail intermediate hosts but have a larger suite of alternative downstream hosts. The pathological effects of these trematodes on

their amphibian hosts vary by parasite load and by parasite species. For instance, *Ribeiroia ondatrae*, which penetrates the developing limb bud of tadpoles, can cause mortality in tadpoles and severe limb malformations, even with low loads (Johnson, Kellermanns, & Bowerman, 2011). In contrast, *Alaria* spp., which is found non-specifically throughout amphibian tissues, causes limited pathology even at very high loads (Johnson & Hoverman, 2012; Johnson, Lunde, Ritchie, & Launer, 1999). The two protist taxa identified in this study, *Opalina* spp. and *Nyctotherus* spp., develop within the amphibian host's small intestine, from which cyst stages are expelled into the wetland with host faeces (El Mofty & Smyth, 1964). Consumption of the cyst stage initiates a new infection. More detailed information about symbiont natural history, life cycle and taxonomy can be found in Appendix S1.

2.2 | Sampling methods

We surveyed 174 wetlands and 3,571 amphibian hosts across the Bay Area of California during the summers (July–August) of 2009–2013, following the sampling design presented in Richgels et al. (2013) and Johnson, Preston, Hoverman, and Richgels (2013) (Figure 1). These wetlands harbour up to six amphibian species, five snail species, and many symbiont species that utilize multiple intermediate and definitive host species within the wetlands. Here, we focus on the symbiont communities of the Pacific chorus frog, *Pseudacris regilla*, which is the most commonly occurring frog, is often found in large numbers, and harbours a diverse suite of macro- and micro-parasites (Johnson & Hoverman, 2012). Note that we use the inclusive term “symbiont,” which generally includes mutualists, commensals and parasites that rely on a host. We define a local symbiont community to be all the symbiont taxa that reside within a wetland, which we delineate as the local habitat patch. Thus, we amalgamate the within-host symbiont community of each sampled frog to a local, wetland-level symbiont community. Then, the symbiont metacommunity for a given year consists of all of the wetlands surveyed within that year.

During field surveys of each wetland, c. 10 recently metamorphosed *P. regilla* were collected (range 8–29, median 10) by hand and subsequently examined for symbionts (Johnson et al., 2013; Appendix S1). For each individual host, we carefully examined all host organs and tissues, identifying and quantifying all encountered symbionts. Larval trematodes (metacercariae and mesocercariae) were mechanically excysted (if necessary) and identified to genus or species using morphological features (Hartson, Orlofske, Melin, Dillon, & Johnson, 2011; Johnson et al., 2016). We encountered 18 unique taxa of trematode and protist species. However, because we were interested in associating symbiont community composition with wetland-specific characteristics, we limited our dataset to include only *P. regilla* individuals that harboured parasite types acquired during larval development. We therefore excluded individuals infected with symbionts acquired in the terrestrial habitat or after hosts transition from herbivory to carnivory with metamorphosis. This ensured that hosts collected from a wetland likely did not migrate from some other source. Thus, we removed five trematode (primarily adults) and three nematode taxa; we removed an additional two trematode taxa found in <1% of hosts, leaving a final

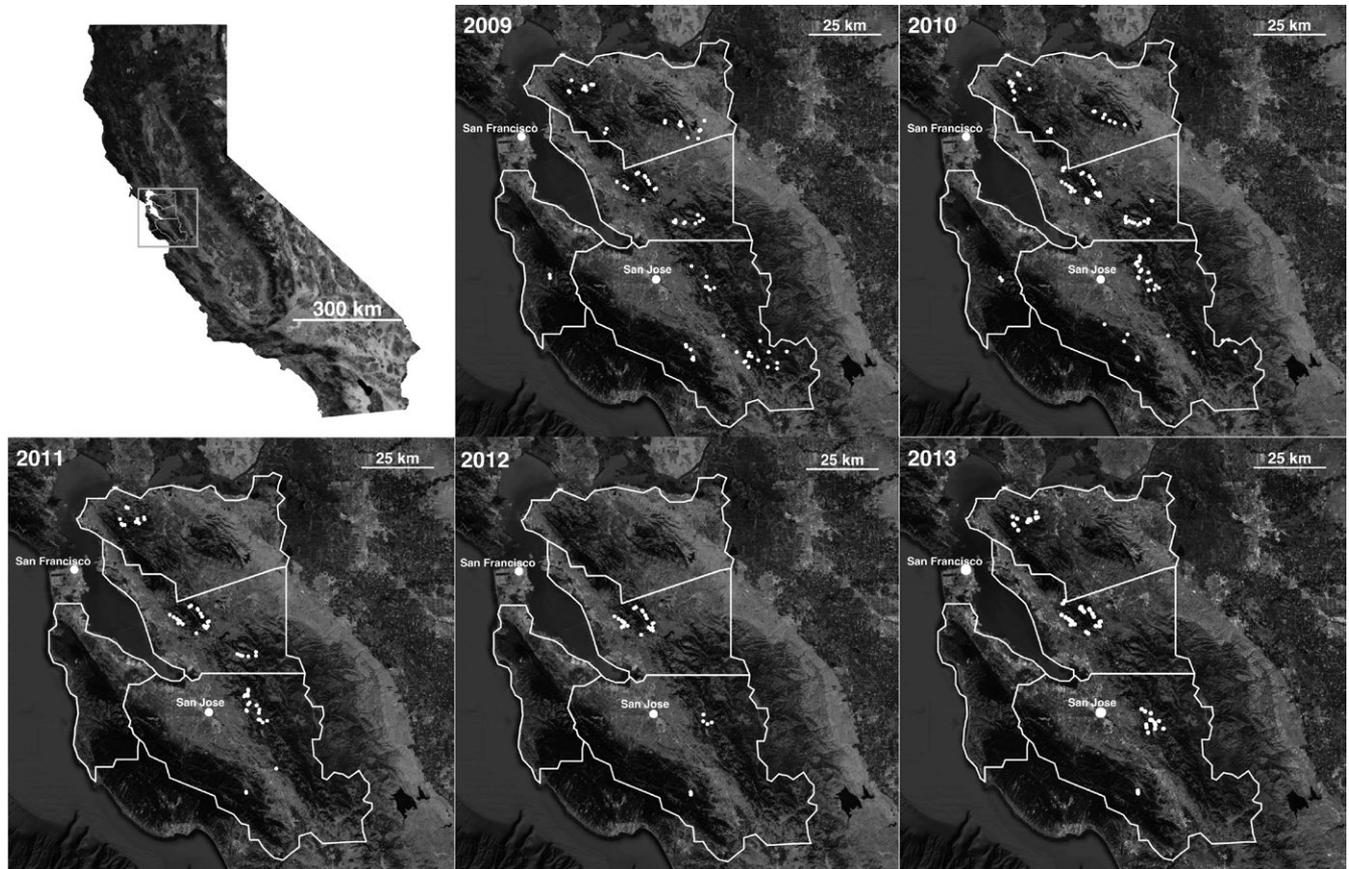


FIGURE 1 Map of the study region. White points represent sampled wetlands. Note that not all wetlands were sampled in all years

symbiont pool of six trematodes and two protists (Table 1). Within survey years, any symbiont taxon found in <5% host individuals was also removed from the metacommunity analysis to reduce bias in metacommunity statistics, such that the symbiont pool ranged from five to eight taxa among years.

2.3 | Ecological drivers of symbiont occurrence

Based on previous research and ecological theory (Hartson et al., 2011; Schotthoefer et al., 2011), we carefully selected a suite of wetland-level covariates to explain symbiont occurrence and turnover, which we grouped into three categories: spatial characteristics, habitat filtering and host community composition (Table 2). We selected spatial features that could influence the colonization rates of symbionts (i.e. measures of dispersal limitation). The spatial category consists of wetland latitude (Lat) and the percentage of area within a 1 km buffer of each wetland that was occupied by wetland (WET; based on 2006 natural land cover database [NLCD] imagery). To deal with zero-inflation in the WET statistic, we created a binary indicator variable, WET_z, which indicates whether the respective value of WET is zero. Thus, the model estimates one categorical effect when WET = 0 and one linear effect when WET >0, a strategy that preserves the linear relationship assumption. We also note that latitude was negatively correlated with longitude (Pearson's $r = .74$), such that our more northern sites were also more western sites.

We categorized additional wetland features as contributing to habitat filtering, in that these characteristics could influence the symbionts' abilities to persist in the habitat. These local abiotic and biotic characteristics included pond permanence (binary: ephemeral or permanent), wetland area, water conductivity, pH and the percentage of the shoreline vegetated, which were all measured at the time of sampling. Additionally, we included the percentage of area within a 1 km buffer that was covered in forest (Forest), also based on 2006 NLCD imagery, to serve as a proxy for human encroachment.

Our third covariate category included information on local amphibian and snail host community composition, which is important for symbiont transmission dynamics. Specifically, we included estimates of the total density of both larval amphibians and snails (Amph_Density, Snail_Density), and the total amphibian and snail species richness (Amph_Rich, Snail_Rich). We suspected that these metrics of composition could influence parasite transmission via the probability of contacting appropriate hosts. We also included the incidence of each amphibian and snail species as unique binary covariates in order to distinguish effects of host composition from the effects of specific host species. More details about amphibian and snail sampling can be found in Appendix S1. We note that we did not include the incidence of *P. regilla*, because it was necessarily present at all sites, nor did we include the incidence of *Helisoma trivolvis*, because this snail species was present at >94% sites, and inclusion of this covariate hindered model convergence.

TABLE 1 Parasite taxa used in this study

Animalia			
	Platyhelminthes		
		Trematoda	
			Echinostomida
			Echinostomatidae
			<i>Echinostoma</i> spp. (ECHI)
			Snail Host: <i>Helisoma trivolvis</i> , <i>Physa</i> spp., <i>Lymnaea</i> spp., <i>Radix</i> spp.
			Intermediate Host: Amphibians
			Definitive Host: Birds, mammals
			Cathaemasiidae
			<i>Ribeiroia ondatrae</i> (RIB)
			Snail Host: <i>Helisoma trivolvis</i>
			Intermediate Host: Amphibians, Fish
			Definitive Host: Birds, some mammals
		Plagiorchiida	
			Cephalogonimidae
			<i>Cephalogonimus</i> spp. (CEPH)
			Snail Host: <i>Helisoma trivolvis</i>
			Intermediate Host: Amphibians
			Definitive Host: Amphibians
			Ochetosomatidae
			<i>Manodistomum syntomentera</i> (MANO)
			Snail Host: <i>Physa</i> spp.
			Intermediate Host: Amphibians
			Definitive Host: Snakes
		Strigeidida	
			Diplostomatidae
			<i>Alaria</i> spp. (ALAR)
			Snail Host: <i>Helisoma trivolvis</i>
			Intermediate Host: Amphibians
			Paratenic Host: Non-canids that eat infected amphibians
			Definitive Host: Canids
			<i>Fibricola</i> spp. (FIB)
			Snail Host: <i>Physa</i> spp.
			Intermediate Host: Amphibians
			Definitive Host: Raccoons, other mammals
Protista			
	Ciliophora		
		Heterotrichea	
			Heterotrichida
			Nyctotheridae
			<i>Nyctotherus</i> spp. (NYCT)
			Host: Amphibians
	Heterokontophyta		
		Opalineae	
			Opalinida
			Opalinidae
			<i>Opalina</i> spp. (OPAL)
			Host: Amphibians

TABLE 2 Wetland-level covariates used in the statistical model

Category	Covariate	Description
Spatial	Lat	Latitude of the wetland
	WET	Percentage of the 1-km radius from Lat-Long position that is occupied by wetlands (based on 2006 NLCD—natural land cover database—imagery)
	WET_z	Binary identification of WET with zero values (see main text)
Habitat filtering	Permanent	Binary descriptor of wetland permanence
	Area	Area of the pond as assessed by GPS
	Veg_s	Percentage of the shore which had vegetation
	Forest	Percentage of the 1 km radius from Lat-Long position that is covered in forest (based on 2006 NLCD—natural land cover database—imagery)
	Cond	Conductivity (uS/cm) measured using Yellow Springs Instruments 556 Multi Probe System
	pH	pH measured using Yellow Springs Instruments 556 Multi Probe System
Host community	Amph_Density	Amphibian larval density, estimated with dip net surveys
	Snail_Density	Snail density, estimated with dip net surveys
	Amph_Rich	Amphibian species richness
	Snail_Rich	Snail species richness
	AMCA	Incidence of <i>Ambystoma californiense</i> (California tiger salamander)
	ANBO	Incidence of <i>Anaxyrus boreas</i> (western toad)
	RACA	Incidence of <i>Rana catesbeiana</i> (American bullfrog)
	RADR	Incidence of <i>Rana draytonii</i> (California red-legged frog)
	TATO	Incidence of <i>Taricha torosa</i> (California newt)
	GYRA	Incidence of <i>Gyraulius parvus</i>
	LYMN	Incidence of <i>Lymnaea columella</i>
	PHYSA	Incidence of <i>Physa</i> spp. (mix of <i>P. acuta</i> and <i>P. gyrina</i>)
	RADIX	Incidence of <i>Radix auricularia</i>

2.4 | Statistical overview

We developed a multispecies occupancy model to determine how the covariates influenced wetland-level occupancy rates of parasite taxa, while correcting for detection error. Our overall goal was to determine the most important environmental drivers of symbiont composition across space via model selection and to subsequently understand how these drivers influence the structure of the symbiont metacommunity in each year. In particular, we are interested in identifying environmental gradients that strongly affect species turnover in the symbiont community.

Our statistical routine is rooted in a recently developed extension of the EMS framework—detection error-corrected elements of metacommunity structure (DECEMS; Mihaljevic et al., 2015). Briefly, DECEMS overcomes bias imposed by imperfect detection, which may be of particular importance for parasites, by accounting for the probability of detecting each species to estimate the “true” occupancy of each species. Then, we estimate metacommunity structure using the posterior samples of the estimated occupancy of each species at each site. This allows for a more rigorous exploration of uncertainty in categorical metacommunity structures. Moreover, the multispecies occupancy model estimates species-specific covariate effects, a more powerful tool for inferring the impact of covariates on species

turnover (Jackson et al., 2012). We describe each part of this process in detail below. Data and code available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.mf202> (Mihaljevic, Hoye, & Johnson, 2017).

2.5 | The occupancy model

Our multispecies occupancy model is based on the statistical framework proposed by Jackson et al. (2012); however, we extend the model to account for detection error in a Bayesian framework. Importantly, Jackson et al. (2012) showed that, by estimating species-specific covariate effects, the model outperforms many standard methods used to identify environmental drivers of species turnover, such as CCA and NMDS.

Our data consist of the number of frogs in which each symbiont taxon is observed at each wetland, assembled into the vector y_q :

$$y_q \sim \text{Binom}(z_q p_{n[q]}, j_q)$$

Here $q = 1, \dots, NM$, where N is the number of symbiont taxa and M is the number of sites. y_q is then assumed to follow a binomial distribution. $p_{n[q]}$ represents the probability of detecting species, n , when it is present; and j_q is the number of frogs sampled from a given wetland, which allows us to account for sampling effort and

therefore estimate detection rates. In our case, the detection probability can be interpreted as the average prevalence of a symbiont within a site (i.e. the average per cent of the larval *P. regilla* population expected to be infected with a given parasite species within a wetland). z_q then represents the “true” occurrence of the species at a given wetland, taking values of zero or one. Therefore, even if a species is truly present, a low detection probability could lead to an observed absence at the wetland. z_q is estimated as a Bernoulli random variable with probability, ψ_q , the species-specific probability of occurrence at a wetland:

$$z_q \sim \text{Bern}(\psi_q)$$

The species-specific occurrence probabilities, ψ_q , are then linearly related to the covariates:

$$\psi_q = \text{logit}^{-1}(\alpha_{n[\text{year}][q]} + \mathbf{B}_{n[q]} \mathbf{X}_{\text{site}[q]})$$

The site-specific covariates are stored in matrix, $\mathbf{X}_{\text{site}[q]}$, which is multiplied by the vector of species-specific slopes (i.e. covariate effects), $\mathbf{B}_{n[q]}$. We allow the species-specific, baseline occurrence probabilities, $\alpha_{n[\text{year}][q]}$, to vary annually (i.e. a random effect of year on the intercept). Each intercept, $\alpha_{n[\text{year}][q]}$, and each slope, $\beta_{n[q]}$, is assumed to be distributed normally with means, μ_α and μ_β , and variances, $\sigma_{\text{intercept}}^2$ and σ_{slope}^2 , respectively. Thus, the model is able to generate bias-corrected, species-specific estimates of covariate effects by accounting for detection error.

In particular, we are interested in using the model to identify environmental gradients that strongly affect spatial turnover in the symbiont community. This means we are interested in identifying covariates with significant random effects; in other words σ_{slope}^2 for the covariate is significantly greater than zero. This would suggest that symbiont species respond to the covariate differentially, leading to turnover in composition among wetlands along a gradient of the covariate. We are also interested in identifying covariates that have significant fixed effects; in other words, μ_β for the covariate differs significantly from zero. This would demonstrate that the covariate has significant effects on occurrence that are consistent across most symbiont species (i.e. consistently positive or negative covariate effects among species). Because the model estimates species-specific covariate effects, we can also associate changes in symbiont composition to taxon-specific effects (more below).

We ran the model using a Bayesian approach to inference and parameter estimation, relying on Markov chain Monte Carlo (MCMC) sampling in which we iteratively sample from the posterior. All models were run in the open-source software JAGS (Just Another Gibbs Sampler; <http://mcmc-jags.sourceforge.net/>) via the open-source statistical software, R (R Core Team, 2014). We used uninformative priors and ran each model with three MCMC chains. Models were run with an initial 80,000 iteration adaptation phase, followed by an 80,000 iteration burn-in period, and then 1,500 iterations were stored, thinning by 50 iterations, for a total of 235,000 iterations per model run. We assessed convergence using the potential scale reduction factor, \hat{R} (Gelman, 1996). An example model statement is provided in Appendix S2. We equate “significance” to effects that are reliably

non-zero, meaning that their 95% highest density interval does not overlap zero.

2.6 | Model selection: Within-sample and out-of-sample prediction

For the 2009–2012 data, we created models that included all nested subsets of our covariate categories, such that the “SpatHabHost” model included all covariates, while, for example, the “SpatHost” model included only the spatial and host community-related covariates (see Tables 1 and 3). For each one of these nested models, we calculated a Bayesian metric of within-sample predictive accuracy, the Watanabe–Akaike information criteria (WAIC). WAIC is analogous to AIC in that lower values of WAIC indicate better models; however, whereas AIC estimates a penalty for complex models using the raw number of parameters in the model, the WAIC uses the variance of the posterior samples. WAIC has several advantages over other Bayesian-type information criteria, and is the preferred metric for occupancy models (Hooten & Hobbs, 2014; Watanabe, 2013).

We calculated the WAIC for data subsets of each model. Specifically, we calculated a WAIC for each symbiont taxon (using the data for that taxon across all years), and then a WAIC for each year of the model (using the data for all species within a year), and then the total WAIC for the model. This allows us to understand how well the model predicts (within-sample) data for each taxon individually and for each year individually. We also compared our covariate models to a null model that only included the intercepts (species-specific baseline probabilities). It should be noted that this model is far less complex than the covariate models. This could lead to lower WAIC scores even though the within-sample prediction (i.e. likelihood) is generally worse than the covariate models’.

We also explored how well our statistical models were able to predict out-of-sample data. Here, we used additional data from 55 wetlands sampled in 2013, and we calculated the receiver operating characteristic area under the curve (ROC AUC) (Zipkin, Grant, & Fagan, 2012). In brief, this metric is generated by comparing (1) the estimated occurrence probabilities in 2013 generated from the covariate effects estimated from the 2009–2012 dataset to (2) the estimated “true” occupancy from a model that only uses the 2013 dataset. AUC values greater than 0.5 show that the model is discriminating occupancy with greater than 50% certainty (i.e. better than a coin toss). This Bayesian form of AUC has the advantage of allowing for an exploration of model prediction while accounting for imperfect detection. It should also be noted that AUC does not include a penalty for model complexity.

2.7 | Estimating metacommunity structure based on the model output

For each year (2009–2012) and for the combined 2009–2012 dataset, we used the “best” model (based on year-wise WAIC selection, Table 3) to estimate metacommunity structure. For the 2013 metacommunity, we used the model with the highest median AUC. From each of these models, we compiled posterior estimates of true occupancy, z_q ,

TABLE 3 WAIC model selection. We have bolded the best models in each column based on a difference in WAIC (Δ WAIC >2). Note that italicized WAIC scores are scores that are marginally better than the null model (Δ WAIC <2)

Model	Species												
	ALAR	ECHI	FIB	CEPH	MANO	NYCT	OPAL	RIB	Year			Full	
Spat	527.47	1,517.23	95.89	684.65	394.07	566.05	1,235.78	1,239.17	1,700.18	2,263.40	1,812.15	484.59	6,260.32
Hab	534.90	1,517.37	96.66	684.71	398.21	573.53	1,239.93	1,239.99	1,701.16	2,275.60	1,824.87	483.67	6,285.30
Host	530.37	1,517.31	93.09	684.91	394.60	565.54	1,244.38	1,240.09	1,701.22	2,279.82	1,805.67	483.59	6,270.30
SpatHab	532.27	1,517.71	97.41	684.56	397.16	570.83	1,237.19	1,240.05	1,702.53	2,269.39	1,821.34	483.93	6,277.19
SpatHost	529.73	1,517.33	93.28	684.45	396.42	564.62	1,248.01	1,240.85	1,701.87	2,280.48	1,808.08	484.27	6,274.69
HabHost	532.71	1,517.44	93.79	685.87	396.52	571.08	1,253.51	1,240.47	1,703.17	2,292.32	1,812.38	483.52	6,291.39
SpatHabHost	532.08	1,517.37	94.62	684.85	397.10	570.23	1,252.85	1,240.15	1,702.01	2,289.06	1,814.95	483.23	6,289.26
Null	528.78	1,516.99	95.63	683.25	393.40	568.51	1,234.97	1,239.92	1,698.34	2,267.79	1,810.91	484.40	6,261.44

ECHI, *Echinostoma* spp.; RIB, *Ribeiroia ondatrae*; CEPH, *Cephalogominus* spp.; MANO, *Manodistomum syntomentera*; ALAR, *Alaria* spp.; FIB, *Fibricola* spp.; NYCT, *Nyctotherus* spp.; OPAL, *Opalina* spp.

into posterior site-by-species matrices, Z_{post} (Mihaljevic et al., 2015). We created 300 Z_{post} matrices for each year, and for each matrix, we calculated the three EMS—coherence, turnover and boundary clumping. Based on these metrics, we assigned a categorical metacommunity structure to each Z_{post} . Thus, we are able to generate pseudo-posterior estimates of each element of metacommunity structure and an overall probability distribution of metacommunity structure. In other words, we are able to determine the posterior probability that a metacommunity exhibits any given structure type. We generated the EMS using the package METACOM (version 1.4.6) in R, which relies heavily on the VEGAN package (version 2.4-3) (Dallas, 2014; Oksanen et al., 2013). The details of calculating these metrics have been reviewed extensively elsewhere (e.g. Leibold & Mikkelsen, 2002; Mihaljevic et al., 2015; Presley et al., 2010). Data and code available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.mf202> (Mihaljevic et al., 2017).

3 | RESULTS

3.1 | Surveys

Larvae of six amphibian species were detected: *Taricha torosa* (California newt), *Ambystoma californiense* (California tiger salamander), *Rana catesbeiana* (American bullfrog), *Anaxyrus boreas* (western toad), *Rana draytonii* (California red-legged frog) and our focal host *P. regilla* (Pacific chorus frog). Across all sites, we encountered five snail taxa: *Radix auricularia*, *Lymnaea columella*, *H. trivolvis*, *Gyraulus parvus* and *Physa* spp. (mix of *P. acuta* and *P. gyrina*), of which *H. trivolvis* and *Physa* spp. function as first intermediate hosts for many of the trematode species (McCaffrey & Johnson, 2017). Amphibian richness at each site ranged from one to all six species with a mean of 3.1, while snail richness ranged from none to five taxa, with a mean of 2.1.

3.2 | Environmental drivers of species turnover

Based on WAIC model selection, the spatial and host community composition components consistently influenced symbiont taxa occurrence and, consequently, overall community composition, whereas the models with habitat filtering showed little support (Table 3). The within-sample model selection approach was largely validated by the AUC analysis using the 2013 data, where models with combinations of spatial and host components out-competed the null model for three out of the eight taxa (Table S1 in Appendix S2). All models, including the null with estimated baseline occurrences, showed relatively high predictive accuracy (median AUC for all models were greater than 0.76).

The effect of spatial covariates was driven by wetland latitude, which had a negative slope across all taxa (i.e. a negative fixed effect $\mu_{\beta} < 0$), meaning that overall occupancy probability increased in southeastern wetlands (Table 4, Figure 1). There was also a negative effect of latitude on *Alaria* spp. and *Nyctotherus* spp. individually (Table 4). Indeed, based on WAIC selection, for *Nyctotherus* spp., the models with combinations of spatial and/or host components outperformed the null model, and the model with spatial components was marginally better than the null for *Alaria* spp.

TABLE 4 Covariate effects estimated by the full model ("SpatHabHost"). Only covariate effects that differ from zero (based on the 95% highest density interval [HDI]) are shown. Full tables of covariate effects and their 95% HDI, for each statistical model, are shown in Appendix S2. Note that the effect of AMCA is italicized because it had a significant random effect ($\sigma > 0$). However, this effect was driven by a marginally significant effect on CEPH

Category	Covariate	ALAR	CEPH	ECHI	FIB	MANO	NYCT	OPAL	RIB	μ	σ
Spatial	Lat	-0.44					-0.49			-0.28	
	WET										
	Wet_z										
Habitat Filtering	Permanent Area										
	Veg_s										
	Forest										
	Cond	-0.42			-0.57	-0.47					
	pH										
Host Community	Amph_Density										
	Snail_Density										
	Amph_Rich										
	Snail_Rich	1.42	2.00	1.82	1.55	2.28	1.33	1.12	1.55	1.63	
	AMCA		-0.97								0.75
	ANBO										
	RACA		-1.01			-1.19					0.82
	RADR		0.95								0.62
	TATO										
	GYRA	-1.13	-0.98	-1.35	-1.33	-1.74		-1.19	-1.39	-1.26	
	LYMN	-1.36	-1.13	-1.16	-1.37		-1.31	-1.23	-1.16	-1.23	
PHYSA	-1.3	-1.02				-1.17		-0.99	-0.89		
RADIX	-1.81	-1.93						-1.92	-1.8		

ECHI, *Echinostoma* spp.; RIB, *Ribeiroia ondatrae*; CEPH, *Cephalogonimus* spp.; MANO, *Manodistomum syntomentera*; ALAR, *Alaria* spp.; FIB, *Fibricola* spp.; NYCT, *Nyctotherus* spp.; OPAL, *Opalina* spp.

The effect of host community composition on symbiont composition was more complex. First, each symbiont's occupancy probability increased with snail species richness, likely due to an increased probability that their required intermediate snail host would occupy sites with more snail species (Table 4). However, individual symbiont taxa also had idiosyncratic, negative responses to the presence of alternative snail host species. For instance, *Alaria* spp., *Cephalogonimus* spp. and *R. ondatrae*, which all use *H. trivolvis* as an intermediate host, had negative responses to the presence of all other snail species. Similarly, *Fibricola* spp. and *Manodistomum syntomentera*, which use *Physa* spp. as intermediate hosts, showed negative responses to the presence of some non-physid snail species (Table 4).

While neither larval amphibian density nor richness had significant effects on the symbiont community, the presence of particular amphibian species was associated with some symbionts' occupancy probabilities. *Cephalogonimus* spp. showed a negative response to the presence of *R. catesbeiana*, but a positive response to the presence of *R. draytonii*. The presence of *R. catesbeiana* was also negatively associated with the occupancy of *M. syntomentera*.

Based on WAIC analysis, the effects of the spatial and host community composition components were strongest for *Alaria* spp., *Fibricola* spp. and *Nyctotherus* spp., and were strongest in explaining overall community composition in 2010 and 2011. In the AUC predictive analysis using 2013 data, we noticed that models that included the habitat filtering covariates also out-competed the null model for some taxa (Table S1 in Appendix S2). This is likely because the AUC analysis does not penalize for model complexity, and the statistical model showed a significantly negative effect of water conductivity for three of the eight symbiont taxa. In Appendix S2, we show the covariate effect estimates and their 95% highest density interval (HDI) for all nested models, but we note that these estimates are largely consistent across models (e.g. the effect of latitude is similar in magnitude across all models that include the spatial components).

3.3 | Metacommunity structure influenced by species-specific effects

While metacommunity structure did vary from year to year, years that showed non-random structure showed nested structure (Table 5,

TABLE 5 Yearly metacommunity structure and associated statistics. For coherence, turnover and boundary clumping, we display the median posterior value for each statistic, based on measurements from 300 Z_{post}

Dataset	Number of sites	Number of taxa	Structure type			Coherence		Turnover		Boundary clumping	
			Nested	Checker-board	Random	Embedded abs.	Null mean	Replacements	Null mean	Morista's I	
2009	75	7			1.000	175	169.27	3,026	5,183.65	1.13	
2010	98	7	0.617	0.007	0.377	155.5	211.86	2,147.5	9,295.82	1.7	
2011	61	8	0.860		0.140	102	132.01	1,296	4,495.64	1.68	
2012	27	5	0.070		0.930	18	23.97	205	340.91	1.34	
2013	55	7	0.983	0.003	0.013	22	81.51	0	2,142.94	1.28	
Combined ('09-'12)	261	8	0.843		0.157	646	801.7	17,264.5	81,001.92	2.65	

Figure 2). We saw nested structures in 2010 (62% probability of nested structure), 2011 (86%) and 2013 (98%), as well as in the combined 2009–2012 dataset (84%). In 2009, the structure was definitively random, with 100% of the 300 Z_{post} showing this random structure. Similarly, in 2012, in which we only had 27 sampled wetlands, we also saw predominantly random structures (93%). Interestingly, we see that in our statistical model, we had the strongest model support in 2010 and 2011, and these years also had the highest probabilities of non-random metacommunity structures. Compared to 2009 and 2012, *Nyctotherus* spp. and *Alaria* spp. were more prevalent in 2010 and 2011 (Figure 2). Similarly, *Fibricola* spp. was only found at high prevalence in 2011. These three symbiont taxa had the strongest model support for the effects of hosts and spatial components. Thus, it is likely that the presence of these three taxa, for which we have strong model support, also contribute strongly to coherent metacommunity structure in this system.

4 | DISCUSSION

Applications of metacommunity theory to host–symbiont distributional patterns remain rare, despite the value of metacommunity tools for understanding how and why symbiont community composition changes over space and time. Here we integrated three emerging tools from metacommunity research—multispecies statistical modelling, detection-error correction and the EMS—to explore how symbiont communities varied in space and time, using parasites within populations of a pond-developing frog as our study system. In most years, the symbiont communities of *P. regilla* exhibited nested metacommunity structure across wetlands, although some years showed random structures. By decomposing community-level changes into symbiont-specific responses, our analyses suggest that both spatial components and components of the host community composition are the most important drivers of species turnover in this system. Particularly, southeastern sites had higher occupancy probability across symbionts, and symbionts responded to various aspects of the snail and amphibian intermediate host community composition, somewhat idiosyncratically. Nonetheless, metacommunity structure and the strength of environmental gradients varied among years, likely due to yearly variation in the parasite species pool, variability in species-specific responses to covariates and unmeasured environmental factors.

4.1 | Environmental gradients

We found strong evidence that a wetland's spatial position in the landscape affected parasite occurrence probabilities and spatial turnover. In general, symbionts tended to have higher probabilities of occurrence at the southeastern wetlands, which were situated in larger areas of undeveloped land relative to those in the northwest portion of our sampling design (Figure 1). Based on a simple species–area relationship (Rosenzweig, 1995), one might expect that these southeastern areas have a higher diversity of vertebrate, definitive host species, which often results in higher colonization rates for symbionts and a more

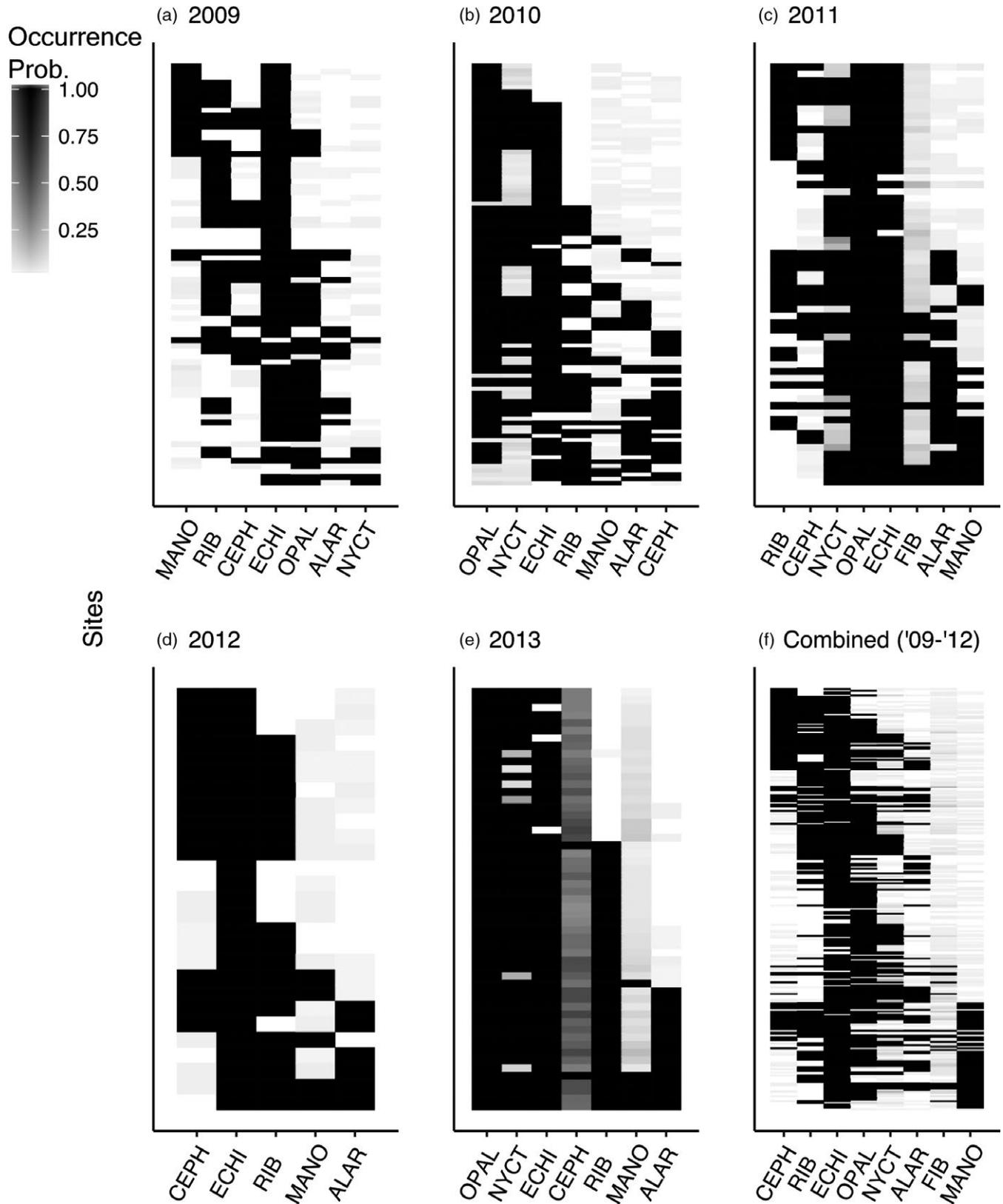


FIGURE 2 Metacommunity structures for each of the 4 years of sampling. Panels consists of the ordinated metacommunity matrix for a given year, where wetlands are rows and symbiont species are columns. This matrix is filled based on the probability of occurrence for each symbiont at each wetland, where black represents 100% probability of occurrence (i.e. the symbiont was observed). The legend in the upper left shows how the colours in the matrix match the probabilities of occurrence. ECHI, *Echinostoma* spp.; RIB, *Ribeiroia ondatrae*; CEPH, *Cephalogonimus* spp.; MANO, *Manodistomum syntomentera*; ALAR, *Alaria* spp.; FIB, *Fibricola* spp.; NYCT, *Nyctotherus* spp.; OPAL, *Opalina* spp.

diverse symbiont species pool (Hechinger & Lafferty, 2005; Hechinger, Lafferty, Huspeni, Brooks, & Kuris, 2007). Thus, spatial position likely influences the symbionts' abilities to colonize via effects on definitive host species, which are the primary mode through which trematodes move between sites. We unfortunately do not have data on the vagile definitive hosts that can transport parasite eggs across the landscape, often wading birds and carnivorous mammals, including raccoons and canids. Future studies could employ camera traps or bird and mammal scat surveillance to explain more variability in the wetland-level community composition of symbionts with complex life cycles.

Snail community composition, and in particular, snail species richness was a strong driver of symbiont occupancy probability. All taxa in our system responded positively to snail species richness, likely due to an increased probability that any given intermediate snail species would be present at higher snail richness. We also sampled sites with zero snail species, meaning that, inevitably, a non-zero richness would increase the chances of finding trematode parasites, given their reliance on these intermediate (or definitive) hosts. More surprisingly, many of the symbiont species responded negatively to the presence of non-host snail congeners. For instance, the symbionts that use *H. trivolvis* as intermediate host (*Alaria* spp., *Cephalogonimus* spp., and *R. ondatrae*) responded negatively to the presence of many other snail taxa, and a similar pattern held for the symbionts that use physid snails. Previous research in our system and others has shown while host diversity "begets" symbiont diversity (Hechinger & Lafferty, 2005; Johnson et al., 2016), the presence of alternative, non-host species can decrease the transmission of symbionts due to a variety of mechanisms (Johnson & Thieltges, 2010; Keesing, Holt, & Ostfeld, 2006). For instance, alternative snail hosts reduce transmission via failed infection events in unsuitable (i.e. "decoy") or low competency hosts (reviewed in Johnson & Thieltges, 2010). Additionally, the presence of congeners influences the competitive dynamics within the snail community. In our system, competition among snail species affects the overall densities, relative abundances, survival and fecundity of snails, which consequently reduces parasite transmission, at least for *R. ondatrae* (Johnson et al., 2012). Thus, snail richness and the identity of snail host species within a wetland both play important roles for explaining symbiont community composition.

The composition of alternative amphibian hosts had a smaller impact on symbiont community composition compared to snail composition. Notably, however, the occupancy probability of *Cephalogonimus* spp. and *M. syntomentera* declined in the presence of *R. catesbeiana*, the American bullfrog, which is an introduced species in this region. *Rana catesbeiana* is known to negatively affect the occurrence and abundance of other amphibian species' larvae in our system (Boone, Semlitsch, Little, & Doyle, 2007; Preston, Henderson, & Johnson, 2012), and functions as a "low competence" host for several of these parasites (Johnson et al., 2013). Another interesting finding was that the occurrence of the trematode parasite *Cephalogonimus* spp. correlated positively with the presence of the amphibian host, *R. draytonii*. Although we do not know the exact species identity of this symbiont, parasites in this genus use amphibians as definitive hosts. Our results suggest that future studies should examine the potential role

of the California red-legged frog in the life cycle of this understudied symbiont.

We also note that the null model, which estimates baseline occurrence but no covariate effects, had significant predictive ability for both within-sample and out-of-sample data. This is not surprising for a number of reasons. First, baseline occurrence probability still provides a great deal of information about the system and must be estimated from a large amount of data (i.e. the average number of wetlands a symbiont is expected to occupy in any given year); in other words, the null is not agnostic. Accordingly, the null model was able to predict our "unobserved" 2013 with >70% accuracy. A truly agnostic null would assume each symbiont taxa to have a 50% chance of occupying any given site. However, we wanted to assess how well we could explain occupancy with specific covariates, above and beyond baseline occurrence. Second, occurrences of two of the symbionts (*Echinostoma* spp. and *Opalina* spp.) constituted 55% of all observations in the dataset and were nearly ubiquitous in most years, making it difficult to associate their occurrence with any particular gradient; thus, our covariate models could only really explain the remaining 45% of data. Therefore, the fact that we have support for covariate models above our relatively informative null model is a significant achievement.

4.2 | Metacommunity structure

We found nested metacommunity structures in most years, and non-coherent (random) structures in others. Nested structures result from a pattern in which species poor sites tend to have a subset of taxa found in more speciose sites. There are many biological and statistical mechanisms that can lead to a nested metacommunity, such as species specializing on nested subsets of a shared environmental gradient. Random structure (i.e. the lack of coherence) could indicate that there is not a dominant environmental gradient structuring the community, that species respond randomly to any given gradient (or that multiple gradients obscure a cohesive pattern) or that we do not have a large enough species pool or a large enough number of sites to detect an existing pattern (Gotelli, 2000; Presley et al., 2010). Particularly relevant to 2012, a smaller number of wetlands and species leads to a smaller and sparser matrix, which results in less power to detect patterns (Gotelli & Graves, 1996; Ulrich & Gotelli, 2013). Similarly, a depauperate species pool could cause the EMS analysis to struggle to differentiate between structure types (Gotelli, 2000). These same arguments, however, apply to us finding nested patterns. Specifically, sparse matrices could lead to a higher rate of false positives (type I error). It should also be noted that even if the EMS statistics show random structure, other statistical methods of detecting nestedness could indeed indicate nested patterns (e.g. the nestedness metric based on overlap and decreasing fill) (Almeida-Neto, Guimaraes, Guimaraes, Loyola, & Ulrich, 2008).

The nested structures are not easily linked to the dominant environmental gradients found in our statistical routine, and were likely influenced by highly prevalent species and species-specific responses to different environmental gradients. For example, in 2010, the symbiont metacommunity had a c. 60% probability of having nested structure.

Although the distributions of *R. ondatrae*, *M. syntomentera*, *Alaria* spp. and *Cephalogonimus* spp. were nested within the broad distributions of three other symbionts, there were also many instances in which these species did not occur with one another. Additionally, there was not a single covariate to which these taxa responded consistently that might be different from the other more broadly distributed taxa. The ambiguity in structure identity could thus be the result of species' occurrences responding to different environmental gradients that are spread variably across the landscape, rather than a coherent response to a single gradient.

Among years, variation in metacommunity structure was likely the result of local or regional changes in environmental condition. While we did not attempt to explain inter-annual variability in structure with our statistical analyses, such patterns could be influenced by variation in sampling effort (i.e. number of wetlands sampled), weather and temporal turnover in the regional parasite community. For instance, spring rainfall in the study area was relatively high in 2009 and 2010, while 2011 and 2012 experienced rainfall well below average and were the beginning of a severe drought in California (NOAA National Climatic Data Center). Variation in these climatic patterns could influence survival, reproduction or movement behaviour of definitive and intermediate hosts, altering local and regional parasite colonization and persistence probabilities from year to year (e.g. Vacher, Vile, Helion, Piou, & Desprez-Loustau, 2008). Additionally, even if a small number of important environmental gradients consistently affect parasite community structure in our study system, the relative magnitudes of their effects could vary in response to regional climatic conditions. And, given that our statistical method is meant to find the simplest model to explain the data, any covariates with small effects could get discounted from the top models, leaving only the covariates with greatest effects.

5 | CONCLUSIONS

For symbiont communities, metacommunity theory and emerging statistical tools offer methods to explore the impacts of local environmental filtering, such as host composition, and regional processes, such as dispersal limitation, on multi-scale symbiont distributions. In turn, symbionts offer a unique ecological community with which to evaluate metacommunity theory. Here, we used the EMS, embedded within a rigorous and novel statistical routine, to explore how environmental gradients and host composition affects symbiont community turnover through space and time. By sampling a large number of individual hosts across numerous replicate wetlands and over time, our results indicated that the symbiont metacommunity within *P. regilla* exhibited mostly nested structure but that this structure was not consistent in all years. Local symbiont composition responded most strongly to variation in host community composition and the geographic placement of wetlands, which likely influences definitive host diversity. Our results are also relevant to other systems of symbionts that include species with complex life cycles. These symbionts rely on multiple host species that often utilize vastly different environments.

Predicting the symbiont composition in any one environment will require integrating the effects of symbiont colonization and transmission across environment types. Thus, further understanding symbiont community dynamics across space and time will require a synthesis of ecological and evolutionary dynamics that occur at multiple spatial scales. An emphasis on building analytical tools and methods that link dynamics across scales should be a priority in this field.

ACKNOWLEDGEMENTS

We thank the many field and laboratory technicians that helped collect data for this project: Dana Calhoun, J. Gregory, Brett Goodman, Dan Preston, Katherine Richgels, Travis McDevitt-Galles, Kathy Hixon, Kendra Gietzen, Patrick Hoffman, Jeff McFarland, Margaret Boyle, Don Larson, Allison Price, Ian Buller, Bryan LaFonte, Jason Lambden, and Emily Hannon. We are also thankful for the collaboration of the East Bay Regional Parks, East Bay Municipal Utility District, Santa Clara County Parks, Hopland Research and Extension Center, Blue Oak Ranch Reserve (especially Michael Hamilton), California State Parks, The Nature Conservancy, Open Space Authority and Mid-peninsula Open Space for access to lands and resources. J.R.M. was supported by a National Science Foundation Graduate Research Fellowship (DGE 1144083) and by a USDA NIFA Postdoctoral Fellowship (2014-67012-22272). B.J.H. was supported by a Rubicon fellowship from the Netherlands Organization for Scientific Research (825.11.036). P.T.T.J. gratefully acknowledges the National Science Foundation (DEB-0841758 and DEB-1149308), the National Institutes of Health (R01GM109499) and the David and Lucile Packard Foundation for funding.

AUTHORS' CONTRIBUTIONS

All authors conceived the ideas; J.R.M. and P.T.T.J. collected the data; all authors designed methodology; J.R.M. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data and code available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.mf202> (Mihaljevic et al., 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Mihaljevic JR, Hoyer BJ, Johnson PTJ. Parasite metacommunities: Evaluating the roles of host community composition and environmental gradients in structuring symbiont communities within amphibians. *J Anim Ecol*. 2018;87:354–368. <https://doi.org/10.1111/1365-2656.12735>