**Title**: Disease hotspots or hot species? Infection dynamics in multi-host metacommunities controlled by species composition, not source location

**Running title**: Maintenance species and metacommunities

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# Abstract

Pathogen persistence in host communities is influenced by a hierarchy of heterogeneities from individual host to landscape-level attributes, but isolating the relative contributions of these heterogeneities is challenging. We developed theory to partition the influence of host species, habitat patches, and landscape connectivity on pathogen persistence within host-pathogen metacommunities. We used the framework to quantify the contributions of host species composition and habitat patch identity on the persistence of an amphibian pathogen across the landscape. By sampling over 11,000 hosts of six amphibian species, we found that a single host species could maintain the pathogen in 91% of the metacommunities we observed. Moreover, this dominant maintenance species contributed, on average, twice as much to landscape-level pathogen persistence compared to the most influential source patch in a metacommunity. Our analysis demonstrates substantial inequality in how species and patches contribute to pathogen persistence, with important implications for targeted disease management.

# Introduction

Many pathogens of conservation and health concern infect multiple host species and occur on landscapes composed of interacting host communities (i.e. 'disease metacommunities'; Paull *et al.* 2012; Miller *et al.* 2013; Johnson *et al.* 2015). Heterogeneity among individuals within a species, among species within a community, and among communities on a landscape can interact in non-additive ways to influence pathogen invasion and persistence (Keeling 1999; Lloyd-Smith *et al.* 2005; Johnson *et al.* 2015; North & Godfray 2017). At the population-scale, individual-level heterogeneity in contacts and susceptibility can result in 'super-spreaders' that contribute disproportionately to pathogen spread (Lloyd-Smith *et al.* 2005). At the community-scale, host species-level differences in population densities, contact rates, and shedding rates dictate contributions to infection dynamics within the community (Mihaljevic *et al.* 2014; Fenton *et al.* 2015; Webster *et al.* 2017). At the landscape-scale, the characteristics of habitat patches and their degree of connectivity can influence pathogen invasion success and persistence (McCallum 2008; Schreiber & Lloyd-Smith 2009; Arino 2009). This creates a challenging yet foundational question: from a control standpoint, what are the relative contributions of heterogeneities across scales in determining pathogen persistence (McCallum & Dobson 2002; Paull *et al.* 2012)? For instance, whether disease management should prioritize strategies such as quarantine, culling, habitat modification, or targeted vaccination will depend critically on the relative influence of specific sites (hotspots) versus specific species (maintenance or amplification hosts).

While both variation among host species and across spatial patches influence pathogen invasion and persistence, how these factors interact remains unknown. In a single-patch, multi-host system, 'maintenance' host species are those that can independently maintain a pathogen and contribute to its spillover into other host species (De Castro & Bolker 2005; McCallum 2012; Webster *et al.* 2017). However, in a multi-patch, multi-host system, labeling species as maintenance or spillover hosts is made challenging by the added influence of habitat patch heterogeneity – a species' maintenance potential may vary among habitats due to changes in community structure or the physical environment (Haydon *et al.* 2002; Paull *et al.* 2012; Rudge *et al.* 2013). This context-dependent variability in species' maintenance potentials further leads to variability in source potential of individual patches, including whether they are 'source' patches capable of independently maintaining a pathogen in isolation from all other patches (McCallum 2008; Schreiber & Lloyd-Smith 2009). As a result, how a pathogen spreads across the landscape will depend on the degree to which host species' maintenance potentials are independent of patch location, are determined by patch location, or are moderated by patch location. While there is a growing theoretical understanding of how community composition can augment or dilute disease risk in host communities (Keesing *et al.* 2006; Mihaljevic *et al.* 2014) and how patch connectivity can promote or inhibit pathogen invasion (Schreiber & Lloyd-Smith 2009;

North & Godfray 2017), few studies have attempted to empirically quantify species' maintenance potential, patch source potential, and their effects on landscape-level pathogen invasion and persistence. This is a critical next step for understanding of the drivers of disease dynamics in multi-species, multi-patch disease systems, which is arguably a common feature of many emerging infections of importance for conservation or society.

The 'maintenance potential' and 'source potential' of a species and patch, respectively, can be defined in terms of the fundamental recruitment number $R_0$. For a single host species in a single patch, $R_0$ defines the number of secondary infections produced over the lifetime of an average infected individual in a fully susceptible population (Diekmann *et al.* 1990). When $R_0 > 1$, a pathogen can invade a fully susceptible host population and the endemic prevalence (if it exists) is a function of $R_0$ (Keelling & Rohani 2008). In a multi-species, multi-patch system, there is a hierarchy of $R_0$ values that describe pathogen invasion and persistence: species-level $R_0$, patch-level $R_0$, and landscape-level $R_{0,L}$ (Fig. 1A). Maintenance species within a patch have species-level $R_0 > 1$ and source patches within a metacommunity have patch-level $R_0 > 1$. Landscape-level $R_{0,L}$ is a combination of species-level and patch-level $R_0$ values and when $R_{0,L} > 1$ a pathogen can deterministically invade a host metacommunity (Fig. 1A; Arino *et al.* 2005, but see Cross *et al.* (2005); North & Godfray (2017)).

Theoretically, the species-level, community-level, and landscape-level $R_0$ values, coupled with species connectivity and patch connectivity, provide all the information necessary to understand how variability in species maintenance potential interacts with patch source potential to affect landscape-level pathogen invasion and persistence. Empirically, however, the parameters required to calculate species-level, community-level, and patch-level $R_0$ values can be difficult to estimate for a single species, much less for multiple species across multiple patches. Fortunately, recent work indicates that many of these difficult-to-estimate parameters, such as the absolute values of transmission coefficients, can be replaced by more commonly estimated parameters such as prevalence and parameter ratios (Rudge *et al.* 2013; Fenton *et al.* 2015). While these approaches have been applied to understand the maintenance potential of hosts in multi-species systems (Rudge *et al.* 2013; Fenton *et al.* 2015), they have yet to be extended to multi-species, multi-patch systems.

Here, we first develop multi-species, multi-patch models and then confront these models with commonly-collected pathogen data to ask the question: do maintenance species contribute more than source patches to pathogen persistence on the landscape? To quantify the contributions of species and patches on pathogen persistence, we focused on interactions between amphibian host species and the fungal pathogen *Batrachochytrium dendrobatidis* (Bd), which is the causative agent of the disease chytridiomycosis and declines in over 500 amphibian species worldwide (Kilpatrick *et al.* 2010; Scheele *et al.* 2019). We compiled infection information on over 11,000 hosts comprising six species of amphibians persisting endemically with Bd

across 139 habitat patches to parameterize a multi-species, multi-patch model. We then used the model to (1) identify the relative contributions of host species to pathogen persistence across patches, (2) quantify the role of among patch connectivity on pathogen persistence, and (3) knockout maintenance species and source patches from metacommunities to assess their relative contributions to landscape-level $R_{0,L}$. The theory we develop provides a quantitative means to assess the contribution of species, patches, and connectivity to pathogen persistence across scales in empirical host-pathogen metacommunities, which is essential information for identifying and implementing effective management strategies.

# Materials and Methods

## Study system and data collection

Between 2013 and 2018, we examined the within-season Bd maintenance potential of six amphibian species found in 77 metacommunities in the East Bay Region of California (Contra Costa, Alameda, and Santa Clara counties). We considered six species of wetland-breeding amphibians: *Pseudacris regilla* (PSRE), *Anaxyrus boreas* (ANBO), *Rana catesbeiana* (RACA), *Rana draytonii* (RADR), *Taricha torosa* (TATO), and *Taricha granulosa* (TAGR). Adult amphibians of all species typically breed in ponds from January to late spring and co-occur as larvae and metamorphs between May and August (Fig. S1, Stebbins & McGinnis 2012). The length of the larval period varies among species (Fig. S1, Johnson *et al.* 2012). PSRE, ANBO, TAGR, and TATO larvae typically mature and leave the pond within the same year, while RACA and RADR can overwinter as larvae (Stebbins & McGinnis 2012). Amphibian communities persist endemically with Bd across multiple interconnected ponds and wetlands with little evidence of Bd epidemics. Moreover, the biology of the amphibian species in these communities is well-understood and the communities are amenable to standardized sampling protocols for Bd infection and host density (e.g. Johnson *et al.* 2012; Joseph *et al.* 2016; Stutz *et al.* 2018). These attributes make this amphibian-Bd system ideal to link with multi-species, multi-patch pathogen models.

We defined a metacommunity as a potentially interconnected network of ponds and wetlands among which amphibians could move. Each pond represented a patch in the metacommunity. We defined metacommunities such that they closely corresponded to administratively delineated parks and properties (Johnson *et al.* 2016). Our rationale was that properties provided a connected stretch of habitat within which amphibians could potentially disperse. In addition, we considered the same spatial metacommunity sampled over multiple years as different spatio-temporal metacommunities. We assumed that between season amphibian migrations and pond dynamics (e.g. ponds drying) largely uncoupled pathogen dynamics between years. The 77

metacommunities were comprised of between one to 26 ponds and there were 139 unique ponds sampled across six years (496 unique pond by year combinations).

From May through August in 2013-2018, crews sampled amphibian larvae and metamorphs using standardized dip net surveys (for details see Johnson *et al.* 2013). Standardized skin swabs were taken from each sampled amphibian to assess Bd infection status and Bd load using quantitative polymerase chain reaction (qPCR, Boyle *et al.* 2004). qPCR for Bd was run on each sample in triplicate to quantify measurement error (DiRenzo *et al.* 2018). Additional dip net surveys were conducted to estimate density of amphibian larvae and metamorphs (Joseph *et al.* 2016). As the Bd and density sampling was all within a season, we focused our analysis on within season Bd dynamics and not between season dynamics. Moreover, while adult amphibians were present and occasionally captured in dip net sweeps, the surveys were not designed to sample adult amphibians. We discuss the implications of excluding adults in Appendix S1.

## A multi-species, multi-patch model of pathogen dynamics

We used a dynamic model to (1) compute species-level maintenance potential and patch-level source potential in order to (2) decompose how species and patches contributed to Bd persistence on the landscape within a season. We considered a multi-species, multi-patch (S)usceptible-(I)nfected-(S)usceptible model with infection from an environmental zoospore pool $Z$ for host species $s = 1, \ldots, H$ and patches $p = 1, \ldots, P$ (Fig. 1B). Bd is transmitted between hosts via a motile, aquatic zoospore stage (Longcore *et al.* 1999). Consistent with previous Bd models, we assumed that amphibians acquired infection directly from an aquatic zoospore pool into which infected amphibians shed Bd zoospores (Mitchell *et al.* 2008; Briggs *et al.* 2010). We did not consider a load-dependent model of the pathogen dynamics within the host (e.g., Briggs *et al.* 2010). As there was little evidence in this system of load-dependent Bd-induced mortality occurring at a rate that affected host population dynamics, we chose to use a simpler model that did not directly account for Bd load. We did, however, use Bd load as a proxy for shedding rates of infectious zoospores, as described below.

The multi-species, multi-patch model we consider is (Fig. 1B)

$$\begin{aligned}
\frac{dS_{sp}}{dt} &= f(N_{sp}) - d_{sp}S - \beta_{sp}S_{sp}Z_p + \nu_{sp}I_{sp} + \phi_s \sum_{j \in P}(-c_{jp}S_{sp} + c_{pj}S_{sj}\frac{A_j}{A_p}) \\
\frac{dI_{sp}}{dt} &= \beta_{sp}S_{sp}Z_p - (\nu_{sp} + d_{sp})I_{sp} + \phi_s \sum_{j \in P}(-c_{jp}I_{sp} + c_{pj}I_{sj}\frac{A_j}{A_p}) \\
\frac{dZ_p}{dt} &= \sum_{i \in S} \lambda_{ip}I_{ip} - \gamma_p Z_p
\end{aligned} \tag{1}$$

where $S_{sp}$ and $I_{sp}$ are the densities of susceptible and infected hosts, respectively, of species $s$ in patch $p$. $Z_p$ is the density of zoospores in the zoospore pool in patch $p$. The term $\beta_{sp}Z_p$ is the force of infection for

species $s$ in patch $p$. $\lambda_{sp}$ is the species- and patch-specific shedding rate of Bd zoospores into the environment and $\gamma_p$ is the patch-specific decay rate of the zoospores in the environment. We assumed all hosts in a patch share the same pathogen pool and that the pathogen pool is well-mixed. The parameter $\nu_{sp}$ is the species and patch-specific recovery rate of an infected host. Host birth rate is given by the generic function $f(N_{sp})$ where $N_{sp} = S_{sp} + I_{sp}$ and is species and patch specific. We assumed that Bd infection does not affect host reproduction. Host death rate is given by $d_{sp}$ and is species and patch specific.

The parameter $\phi_s$ is the within-season species-specific dispersal rate (i.e. the rate at which individuals of species $s$ left a patch) and $c_{jp}$ is the probability that a host moves from patch $p$ to patch $j$. We let $c_{jj} = 0$ such that a species does not remain in the same patch if it moves. The $P \times P$ matrix $\mathbf{C}$ contains $c_{jp}$ movement probabilities and is irreducible – all patches were accessible to all other patches in a finite time (Arino 2009). We assumed that both infected and susceptible individuals can disperse, that infection does not affect dispersal, and that infection status does not change during dispersal. Finally, $A_p$ is the area of patch $p$.

**Species-level $R_{0,s,p}$**

Given equation 1, species-level $R_{0,s,p}$ of species $s$ in patch $p$ is given by $R_{0,s,p} = \frac{\beta_{sp}\lambda_s S^*_{sp}}{b_{sp}\gamma_p}$, where $S^*_{sp}$ is the density of susceptible hosts of species $s$ in patch $p$ before infection arrives and $b_{sp} = d_{sp} + \nu_{sp}$ (Fig. 1B). Note that if we included Bd-induced mortality at some constant rate $\alpha_{sp}$, this would be additively included into $b_{sp}$.

If equation 1 is at equilibrium, we can re-write $R_{0,s,p}$ as

$$R_{0,s,p} = \frac{\beta_{sp}\lambda_s N^*_{sp}}{b_{sp}\gamma_p} = \frac{1 + \frac{\phi_s}{b_{sp}} \sum_{j \in \text{Patches}} (c_{jp} - c_{pj} \frac{A_j}{A_p} \frac{\Pi^*_{sj}}{\Pi^*_{sp}} \frac{N^*_{sj}}{N^*_{sp}})}{(1 - \Pi^*_{sp})(\sum_{i \in \text{Species}} \frac{\lambda_{ip}}{\lambda_{sp}} \frac{\Pi^*_{ip}}{\Pi^*_{sp}} \frac{N^*_{ip}}{N^*_{sp}})} \quad (2)$$

The variable $\Pi^*_{sp}$ is the equilibrium Bd prevalence and $N^*_{sp}$ is the equilibrium density of species $s$ in patch $p$. If it holds, the equilibrium assumption is useful because one can calculate $R_{0,s,p}$ without needing hard-to-estimate parameters such as species-specific absolute transmission rates (Rudge *et al.* 2013; Fenton *et al.* 2015). One can instead use more commonly collected parameters such as host density, Bd prevalence and Bd infection load.

A useful property of equation 2 is that the ratio between two species-level $R_{0,s,p}$ values from the same patch $p$ depends only on the parameters relating to the two species being compared (Appendix S1). In this case, if one does not have the necessary data on other community members that are potentially important for the persistence of Bd, one can still analyze the contribution of each species to persistence, relative to the other species that have been sampled.

### The endemic equilibrium assumption

In this study, we had snapshots of data from each pond during each season and thus could not conclusively test whether or not particular sites were in approximate equilibrium within a season. However, Fenton *et al.* (2015) showed that calculations of $R_0$ using this approach are relatively robust to deviations from the equilibrium assumption if prevalence and host density are fluctuating about a mean value through time. Biologically, our sampling period was generally after the influx of adult amphibians for breeding and before the efflux of metamorphs from the pond, such that we did not expect densities to vary drastically within the sampling period. Moreover, pooling prevalence estimates across the sampled months showed no consistent peaks in prevalence during the sampling season for the six species considered (Fig. S2), suggesting that an approximate endemic equilibrium assumption is not strongly violated for this system.

### Linking empirical data and $R_{0,s,p}$

We fitted statistical models that accounted for measurement and observation error to estimate Bd load, Bd prevalence $\Pi^*_{sp}$ and host density $N^*_{sp}$ for species $s$ in patch $p$ (models described in Appendix S2; Miller *et al.* 2012; Joseph *et al.* 2016; DiRenzo *et al.* 2018). We assumed that host shedding rate was proportional to Bd load (DiRenzo *et al.* 2014) and estimated the shedding rate ratios $\frac{\lambda_{ip}}{\lambda_{sp}}$ for species $s$ and $i$ in patch $p$ as the ratio between estimated mean Bd loads for species $s$ and $i$ in patch $p$. We calculated $R_{0,s,p}$ using equation 2, propagating the uncertainty in the parameter estimates. The results we present use the median $R_{0,s,p}$ estimates.

## Contributions of host species and habitat patches in unconnected metacommunities

We began our analysis with the assumption that patches were unconnected on the landscape (i.e. $\phi_s = 0$). We made this assumption so that we could compare how including connectivity changed species maintenance potential and patch source potential. Under this assumption, the only parameters needed to calculate species-specific $R_{0,s,p}$ are Bd prevalence, relative density, and relative shedding rates for the different amphibian species within a patch (equation 2). Moreover, because our model assumed that amphibians were sharing the same pool of zoospores, patch-level $R_{0,p}$ could be directly calculated as $R_{0,p} = \sum_{s \in \text{Species}} R_{0,s,p}$ (Rudge *et al.* 2013). We calculated relative and absolute $R_{0,s,p}$ values for our analysis of unconnected patches.

## Contributions of host species and habitat patches in connected metacommunities

Our study contained 77 metacommunities within which amphibian species could move. Equation 2 shows that accounting for the connectivity of the metapopulations can change our conclusions about the nature of species maintenance potential and patch source potential. Here we give a summary of how we included connectivity into our model. The complete methods are described in Appendix S3.

Given a metacommunity of connected patches, there were multiple connectivity parameter sets that were equally "plausible" given observed patterns of prevalence, Bd loads, and host density. By "plausible" we mean that $R_{0,s,p} \geq 0$ for all species and patches in the metacommunity. To address this challenge, we explored the plausible set of connectivity parameters to determine how the maintenance potential of a species and source potential of a patch varied over the plausible parameter space. The key unknown connectivity parameter in the model was the ratio between species-specific dispersal rate and the loss rate from the infected class, $r_{sp} = \phi_s / b_{sp}$. This parameter gives the expected number of patches to which an infected individual of species $s$ that disperses from patch $p$ moves to over its time infected. As this parameter could not be uniquely inferred from snapshot data, we instead allowed $r_{sp}$ to vary across all species and patches within a metacommunity and explored how species maintenance potential and patch source potential changed across plausible values of $r_{sp}$, compared to an assumption of no dispersal (i.e. $r_{sp} = 0$).

For each metacommunity with $H$ species and $P$ patches, we randomly drew $H \times P$ $r_{sp}$ parameters and computed the species-level $R_{0,s,p}$ for all species and patches in a metacommunity using equation 2 (Appendix S3). For a single parameter set of $H \times P$ $r_{sp}$ values, each vector $R_{0,s,\cdot}$ of length $P$ was associated with $P$ $r_{sp}$ values, one entry for each patch occupied by species $s$ in the metacommunity. If any $R_{0,s,\cdot} < 0$, this indicated that the parameter vector $r_{s\cdot}$ was not plausible given the model and data. Using a rejection algorithm, we identified which parameter sets were plausible and computed species-level and patch-level absolute and relative $R_0$ values for these parameter sets and compared them to species- and patch-level $R_0$ values calculated with no connectivity. We repeated this 100,000 times for each metacommunity. The plausible connectivity parameter sets were the subset of the 100,000 parameter sets that were not rejected. We defined the most connected plausible parameter set as the set where the mean $r_{sp}$ was maximized across habitat patches for species $s$ in a metacommunity.

## Simulated knockouts: The effect of removing maintenance species and source patches on landscape-level $R_{0,L}$

In our final analysis, we sought to directly answer the question: how much does landscape-level $R_{0,L}$ change when we remove a particular species in the metacommunity compared to when we remove the most influential

source patch? Up to this point, our calculations of $R_{0,s,p}$ and $R_{0,p}$ did not require any assumptions about the loss rate of hosts from the infected class, $b_{sp}$. However, calculating landscape-level $R_{0,L}$ for an amphibian metacommunity required the ratios between the rates at which hosts left the infected class (i.e. $b_{ij}/b_{sp}$ for $i, s = 1, \ldots, S$, $j, p = 1, \ldots, P$, Appendix S4). We made the following two assumptions about the relative values of $b_{sp}$. First, we assumed that recovery rates from Bd infection were inversely related to load, such that individuals with higher loads had a lower probability of clearing infection (Wilber *et al.* 2016; Ohmer *et al.* 2017). Second, we assumed loss of infection $\nu_{sp}$ occurred at a faster rate than background host mortality $d_{sp}$ such that we could approximate $b_{ij}/b_{sp}$ as a ratio of estimated mean Bd loads for species $s$ in patch $p$ $\mu_{sp}$: $\frac{b_{ij}}{b_{sp}} = \frac{1}{1/\mu_{sp}} \frac{\mu_{ij}}{} = \frac{\mu_{sp}}{\mu_{ij}}$. In Appendix S4, we considered different assumptions about the magnitude of background mortality rate and our overall results were insensitive to our assumptions.

Over the plausible connectivity space, we calculated how much landscape-level $R_{0,L}$ changed when we removed a particular species in the metacommunity compared to when we removed the most influential source patch. We defined the most influential source patch in a metacommunity as the patch with the largest $R_{0,p}$, given a set of plausible connectivity parameters. We performed this *in silico* removal experiment on 61 metacommunities that had more than one habitat patch and more than one amphibian species (Appendix S4).

# Results

## Patterns of host density, Bd prevalence, and Bd load across patches

PSRE hosts were observed in 82% of patch by year combinations (405 / 496), TATO in 67% (334 / 496), TAGR in 28% (137 / 496), ANBO in 28% (139 / 496), RADR in 13% (65 / 496), and RACA in 12% (60 / 496). PSRE and TATO were present in 74 and 70 out of 77 metacommunities, respectively. RADR, TAGR, BUBO, and RACA were all found in less than 50% of the 77 metacommunities (37, 36, 32, and 27 metacommunities, respectively). PSRE and TATO had higher estimated median amphibian densities per sweep than RADR, ANBO, TAGR, and RACA, although density estimates showed substantial variation across years (Fig. 2A).

Bd was detected in 73% of patches that were sampled from 2013-2018. Conditional on a host being present at a patch, RADR generally had the highest Bd prevalence, followed by PSRE and ANBO (Fig. 2B). Observed prevalence was the lowest for TATO and TAGR (Fig. 2B). Prevalence estimates varied across years, with 2014 showing a substantially lower non-zero prevalence for PSRE, RADR, and ANBO (Fig. 2B). Within a year, mean Bd load given infection was generally significantly higher in ANBO, PSRE, and BUBO

compared to TAGR and TATO (95% credible intervals of log load differences between these species were significantly different than 0, but not in year 2014; Fig. 2C). RACA loads given infection were generally not significantly higher or lower than other species.

## Species maintenance potential and patch source potential in amphibian metacommunities

**Within a patch, PSRE was the most important amphibian host species for the persistence of Bd**: The relative $R_{0,s,p}$ of PRSE was larger than other amphibian species in 81% of the patches in which the amphibian species co-occurred (488 / 604 instances of PSRE co-occurring with other amphibian species within a patch; Fig. 3). Of the 116 instances where PSRE had a lower relative $R_{0,s,p}$ to another species in the community, 36% were with ANBO, 27% were with TATO, 18% were with RADR, and 11% were with RACA.

We also examined the absolute values of species-specific $R_0$ across habitat patches, given the assumption that metamorphs and tadpoles are the primary contributors to Bd dynamics within a season. Absolute values of $R_0$ were highest for PSRE (median $R_{0,s,p} = 1.09$), followed by RADR ($R_{0,s,p} = 0.36$), ANBO ($R_{0,s,p} = 0.35$), RACA ($R_{0,s,p} = 0.17$), TATO ($R_{0,s,p} = 0.02$), and TAGR ($R_{0,s,p} = 0.006$) (Fig. 4). The ranking of species-level $R_{0,s,p}$ values were largely consistent across years, though median magnitudes changed.

**The majority of host communities had at least one maintenance host species and PSRE was almost always a maintenance host when it was present**: Of the 496 patch-year combinations sampled, 125 had median $R_0$ estimates where all species-specific $R_{0,s,p}$ values were less than one, but community-level $R_0$ was greater than one (i.e. an obligate host community, Fig. 5). In 65 of these 125 obligate host communities, Bd was not empirically observed, but low levels of Bd load and prevalence were inferred given a non-zero probability of Bd detection error from the Bd load model (see Appendix S2, Fig. 5). Of the 371 non-obligate host communities, 9% had multiple host species with $R_{0,s,p} > 1$ (i.e. facultative communities). Eighty-eight percent of facultative communities were comprised of PSRE and either ANBO or RADR. The other 91% of non-obligate communities (339 communities) had only one species with $R_{0,s,p} > 1$ (i.e. spillover communities) and all other species (if any were present) had $R_{0,s,p} < 1$. In the non-obligate communities where PSRE was present, PSRE was a maintenance host 88% of the time (265 / 301; Fig. 5).

**Under plausible levels of connectivity, multiple source patches contributed to Bd persistence and PSRE was the dominant maintenance host**: Under the assumption of no connectivity, all patches within a metacommunity had to be, by definition, source patches – if Bd was present and endemic and the

patch was not connected to any other patch then it must be a source patch. However, connectivity can alter the relative maintenance and source potential of a species and patch, respectively. We found that across the plausible parameter space of connectivity, the importance of PSRE as a maintenance host within patches was largely unchanged (Fig. 3, Fig. 4). Considering the median $R_{0,s,p}$ values predicted from the plausible parameter space for $r_{sp}$ for each species in each of the 77 metacommunities, the relative $R_{0,s,p}$ of PRSE was larger than other amphibian species in 80% (482 / 604 combinations) of the patches in which the amphibian species co-occurred (Fig. 3).

While species maintenance potential did not change over the plausible connectivity space, patch source potential did (e.g. Fig. 5). However, even under the most connected plausible parameter scenario 53 of the 61 metacommunities with more than one patch had two or more source patches contributing to Bd persistence (e.g. Fig. 5).

**Removing PSRE from metacommunities led to larger decreases in landscape-level $R_{0,L}$ than removing the most influential source patch**: Over the plausible range of connectivity, removing PSRE led to, on average, a 43% larger reduction in landscape-level $R_{0,L}$ compared to removing the largest source patch (95% confidence interval from single sample t-test: [10%, 63%], Fig. 6). In contrast, removing any of the other five amphibian species was significantly less effective, on average, at reducing landscape-level $R_{0,L}$ than removing the the most influential source patch (Fig. 6). In five of the 61 metacommunities with more than one patch and one species, removing the most influential source patch reduced landscape-level $R_{0,L}$ more than removing any particular species (Fig. 6).

# Discussion

Understanding how multiple levels of heterogeneity in host-parasite systems interact can improve the efficiency of managing human and wildlife diseases (Lloyd-Smith *et al.* 2005; Paull *et al.* 2012; Webster *et al.* 2017). By focusing management on super-spreading individuals (Lloyd-Smith *et al.* 2005), highly competent host species (Kilpatrick *et al.* 2006), or source patches on the landscape (Paull *et al.* 2012), the effort required to mitigate pathogen impacts can be greatly reduced. In this study, we used a widely-applicable theoretical framework to isolate different levels of heterogeneity leading to pathogen persistence in multi-species, multi-patch host-pathogen systems. We linked this framework to empirical pathogen data from over 11,000 hosts comprising six species across 77 metacommunities to identify to roles of species, patches and connectivity on pathogen persistence at the landscape-level. We found that pathogen persistence in multi-species, multi-patch metacommunities was primarily driven by a single maintenance host species, rather than particular source

patches and among patch connectivity. Our study contributes to broader theory on host-pathogen dynamics by illustrating that even in host-pathogen systems with multiple levels of heterogeneity (e.g. species-level and patch-level heterogeneity), a single-level of heterogeneity can disproportionately contribute to pathogen persistence.

In our study, we found that the Pacific tree frog (PSRE) was generally the dominant maintenance host across patches. This was reflected in both higher absolute values of species-level $R_{0,s,p}$ for PSRE and higher or equal relative values of $R_{0,s,p}$ when PSRE co-occurred with other amphibian species. However, a key challenge that multi-species communities pose for disease management is that the identity of maintenance species can vary across communities, making pathogen management strategies habitat-dependent (Rudge *et al.* 2013; Webster *et al.* 2017). While the dominant community type that we observed was one where PSRE was a maintenance host, we also found that in some observed communities other amphibians species were predicted to be maintenance hosts. Of particular interest in amphibian-Bd systems is the effect that the invasive American bullfrog RACA has on Bd persistence (Garner *et al.* 2006; Adams *et al.* 2017). We found that, while infected with Bd in this system, bullfrogs were not consistently more important relative maintenance hosts than PSRE, ANBO, or RADR when these species co-occurred. Moreover, while bullfrogs were predicted to be maintenance hosts in 20 patches under a no connectivity scenario, bullfrogs did not remain a maintenance host in seven of these source patches when we included patch connectivity. This was in contrast to the patches where ANBO and RADR were maintenance hosts and remained maintenance hosts with or without connectivity. Taken together, our results suggest that bullfrogs are not disproportionately more influential on within-season Bd dynamics in an average patch than other amphibian species found in this system. However, given the multi-year tadpole stages of bullfrogs we cannot rule out the importance of bullfrogs in between-season Bd dynamics.

Empirical studies often identify host maintenance potential using independent comparisons of host characteristics such as prevalence, pathogen load, disease-induced mortality, and host density (e.g. Reeder *et al.* 2012; Stockwell *et al.* 2016; Brannelly *et al.* 2018; Hudson *et al.* 2019). While a useful approach, the challenge with independently using these characteristics to identify maintenance hosts is that it becomes hard to compare maintenance potential among multiple species within a community. For example, is a host with higher density and lower prevalence a more important maintenance host than a host with lower density and higher prevalence? Previous work in multi-species systems has shown how these commonly-collected characteristics can be linked to an established quantitative measure of maintenance potential, $R_0$ (Rudge *et al.* 2013; Fenton *et al.* 2015), and we generalized this approach to multi-species, multi-patch host-pathogen systems. Note that computing $R_0$ within and across habitat patches does require assumptions that need to be checked (Keelling & Rohani 2008; Fenton *et al.* 2015). However, when done systematically it provides

an unambiguous way to relate characteristics that are suggestive of a maintenance host to a quantitative measure of maintenance potential across species and patches.

Identifying host maintenance potential in multi-host communities can have important conservation implications for managing disease impacts. While Bd was not a cause of conservation concern in our system, it is in many other multi-species amphibian communities (Scheele *et al.* 2019). In Central and South America, for example, amphibians have experienced drastic Bd-induced declines and particular species have been implicated as disproportionately contributing to infection risk (Schloegel *et al.* 2010; DiRenzo *et al.* 2014). However, we not aware of any studies in amphibian-Bd systems that have quantified maintenance hosts by synthesizing the multiple dimensions of host and pathogen characteristics into a single, theoretically-supported metric of maintenance potential: species-level $R_0$ (see Canessa *et al.* 2019, for an example with the pathogen *Batrachochytrium salamandrivorans*). The approach developed in Fenton *et al.* (2015) and extended here provides a feasible way to use data often collected in amphibian-Bd systems with multiple host species to promote theoretically informed amphibian management where Bd is a conservation concern.

While our study primarily focused on the dominant maintenance host across communities, community assembly and composition can also affect community-level disease risk (e.g. $R_{0,p}$, Dobson 2004; Keesing *et al.* 2006). In this study, we made the assumption that pathogen transmission occurred from a well-mixed environmental zoospore pool, amphibians had equal access to the pool, and gaining an infection did not deplete the pool. This assumption meant that, given species-level $R_{0,s,p}$ values, patch-level $R_{0,p}$ was simply a summation of these values. More generally, however, moving from species-level $R_{0,s,p}$ values to patch-level $R_{0,p}$ values requires understanding inter-specific overlap in direct or indirect contact and the dynamics of pathogen depletion in the environment (Fenton *et al.* 2015). When these factors are important for the pathogen dynamics of a system, the relationship between community composition, species-level $R_{0,s,p}$ values, and patch-level $R_{0,p}$ values can be non-additive, with changes in the species composition of a patch augmenting or diluting patch-level $R_{0,p}$ (Dobson 2004).

When habitat patches are unconnected, identifying species maintenance potential is key for understanding pathogen dynamics within a patch (Fenton *et al.* 2015). However, when patches are connected, variability in species maintenance potential across habitat patches can make patch-level heterogeneity a more important driver of pathogen dynamics than species-level heterogeneity. Thus, the major question that we wanted to answer in this study was: do species contribute more than patches to the persistence of a pathogen on the landscape? Answering this question is important as most empirical applications of epidemiological theory have considered the role of heterogeneity on disease dynamics at a single scale (Bansal *et al.* 2007; Schreiber & Lloyd-Smith 2009; Rudge *et al.* 2013), but few studies consider how different scales of heterogeneity interact to affect pathogen persistence (Paull *et al.* 2012). An advantage of our theoretical framework is that at

endemic equilibrium species-level $R_{0,s,p}$ and patch-level $R_{0,p}$ can be linked to landscape-level $R_{0,L}$ entirely through unitless parameter ratios and probabilities (Appendix S4). Just as with the multi-species models that our approach extends (Rudge *et al.* 2013; Fenton *et al.* 2015), this is useful because hard-to-estimate rates such as transmission rates, pathogen decay rates, and dispersal rates are not needed. Therefore, multi-patch, multi-species models can be more easily linked with commonly-collected empirical data to identify how different scales of heterogeneity affect pathogen persistence.

Using our theoretical framework, we found that 85% of the amphibian-Bd metacommunities observed in this system were most consistent with a weakly connected network of source patches. To understand the implications of this metacommunity structure on pathogen persistence at the landscape-level, we systematically removed either the dominant maintenance species or source patch in a metacommunity, *in silico*. Over the plausible range of connectivity, knocking out the dominant maintenance species on average reduced landscape-level $R_{0,L}$ twice as much as knocking out the primary source patch in the metacommunity. As PSRE was the dominant maintenance species in most metacommunities, knocking out PSRE was the most effective strategy for reducing landscape-level $R_{0,L}$ for Bd. In contrast, knocking out RACA was generally less effective for reducing landscape-level $R_{0,L}$ than removing the most influential source patch. Note that our *in silico* removal of a species does not necessarily mean killing the species. Any mechanism that removed the potential for a species to contribute to Bd transmission, such as treatment, could similarly affect landscape-level $R_{0,L}$. Overall, we found that despite heterogeneity in species maintenance potential across habitat patches, patch-level heterogeneity was less important than species-level heterogeneity for landscape-level pathogen persistence.

By partitioning the contributions of two levels of heterogeneity, species and patch heterogeneity, to landscape-level pathogen persistence, this study takes an important step toward understanding the effects of heterogeneity across scales on pathogen dynamics (Paull *et al.* 2012). The model we develop is applicable to other multi-species, multi-patch systems and is amenable to asking additional theoretical questions to further unravel the hierarchy of heterogeneities driving host-pathogen dynamics.

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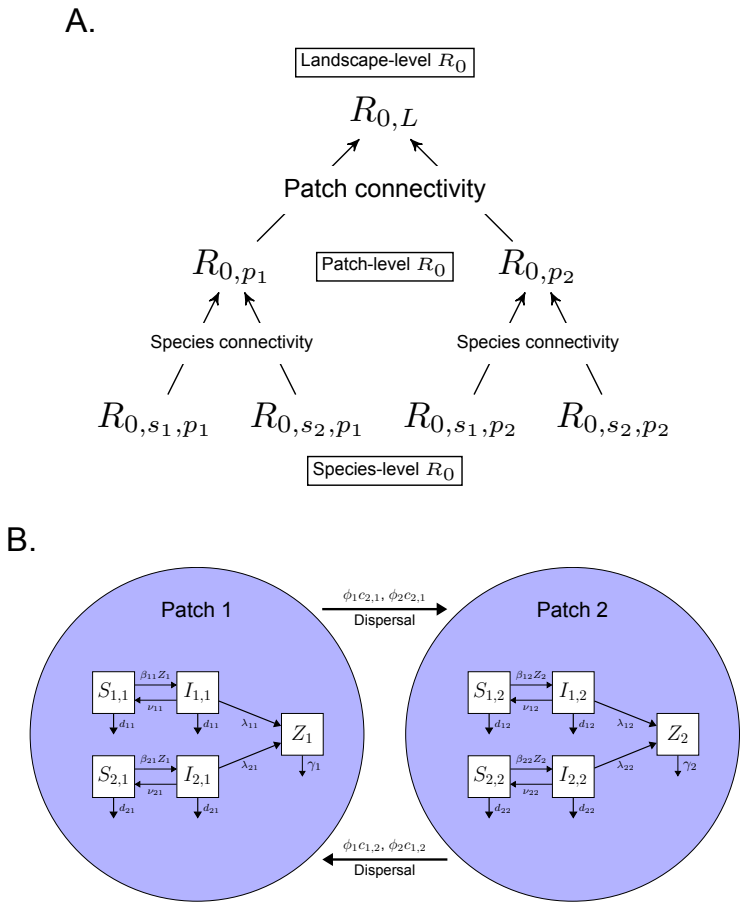


Figure 1: **A.** The partitioning of a multi-species, multi-patch system into species-level $R_{0,s,p}$, patch-level $R_{0,p}$, landscape-level $R_{0,L}$, species connectivity (e.g. the off-diagonals of a Who-Acquired-Infection-From-Whom (WAIFW) matrix, Dobson 2004), and patch connectivity. In this example, there are two species and two patches on the landscape. **B.** The multi-species, multi-patch pathogen model used to partition the importance of maintenance species and source patches on pathogen persistence in a metacommunity (equation 1). The diagram uses two species and two patches as an example.

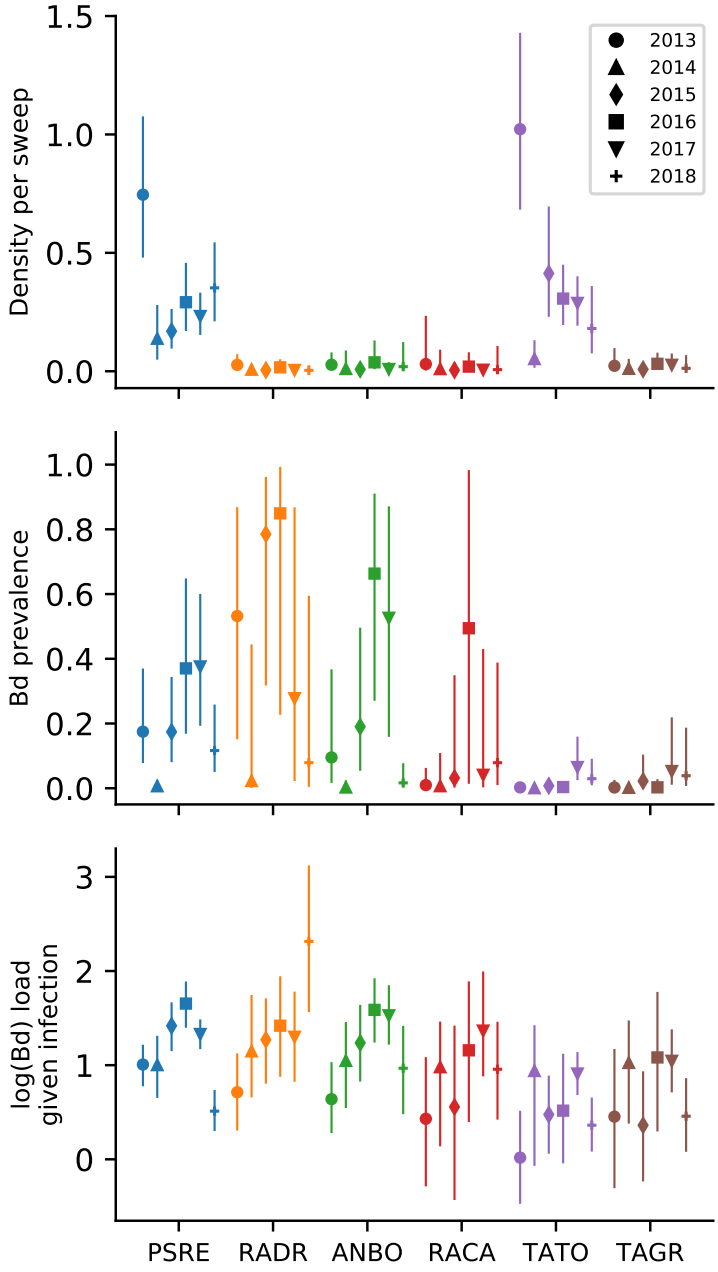


Figure 2: **A.** Median estimated amphibian density per net sweep after accounting for false absences across six years, 139 sites and six amphibian species. **B.** Median estimated prevalence after accounting for false detection and measurement error. **C.** Median estimated mean log(Bd) load conditional on infection after accounting for detection error. For all figures, the error bars are 95% credible intervals about the estimated median. Different shapes represent different years.

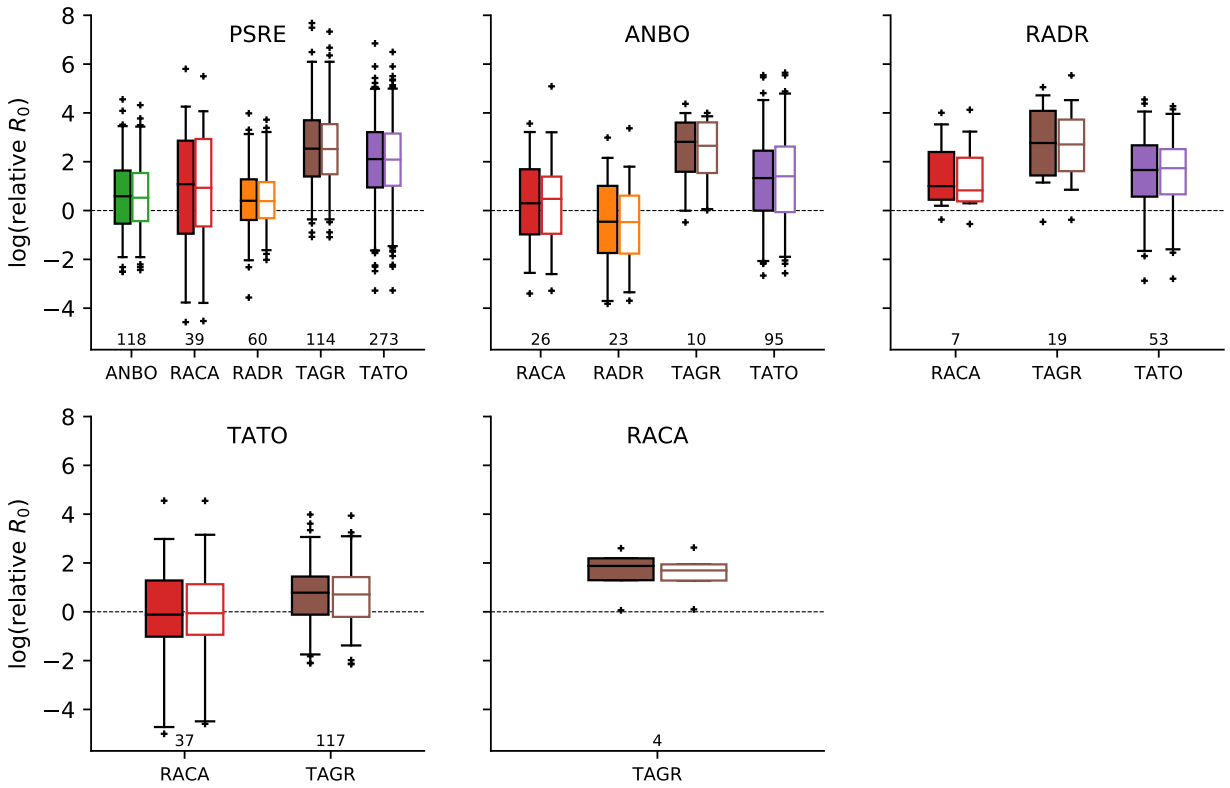


Figure 3: Relative species-level $R_0$ values within a patch calculated using equation 2 with $r_{sp} = 0$ (filled boxplots) and using the median $R_{0,s,p}$ from the plausible set of dispersal rate to loss of infected rate ratios $r_{sp}$ (unfilled boxplots). As an example of the labeling, the "ANBO" x-label of the plot titled "PSRE" shows the distribution of the ratios of PSRE $R_{0,s,p}$ values to ANBO $R_{0,s,p}$ values for patches where PSRE and ANBO were both present. A value larger than zero indicates that the relative maintenance potential of PSRE is greater than ANBO for that comparison. The numbers on the plots give the number of patches where both species were found. The bars give the medians, the boxes given the upper and lower quartiles, the whiskers give the 2.5 and 97.5 percentiles, and "+"s show points outside of these percentiles.

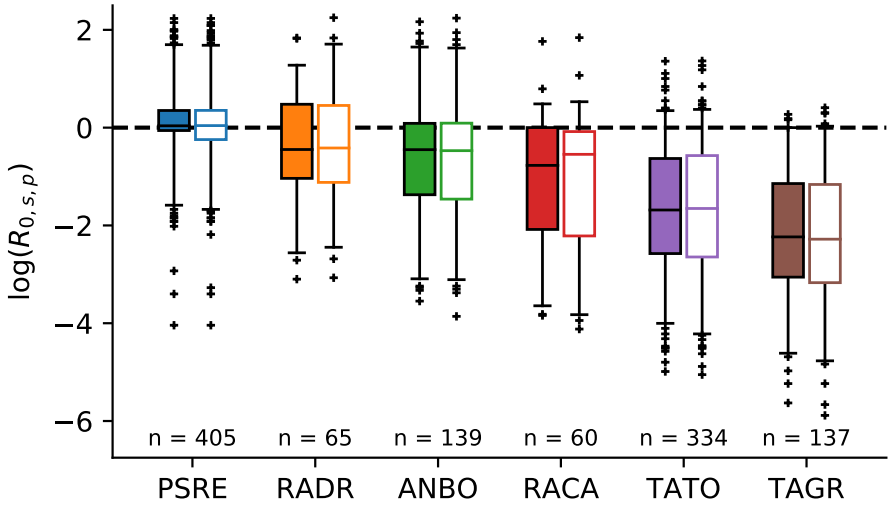


Figure 4: The absolute species-level $R_{0,s,p}$ values calculated using equation 2 when there was no connectivity (i.e. dispersal rate to loss of infected rate ratio was $r_{sp} = 0$, filled boxplots). The median species-level $R_{0,s,p}$ values under plausible connectivity (unfilled boxplots). The bars give the medians, the boxes given the upper and lower quartiles, the whiskers give the 2.5 and 97.5 percentiles, and "+"s show points outside of these percentiles. The sample sizes give the number of patch by year combinations where a species was found. The most noticeable difference between no connectivity and connectivity predictions is that the distribution of absolute $R_{0,s,p}$ values for PSRE shifts down as fewer patches are source patches in the plausible connectivity scenario.

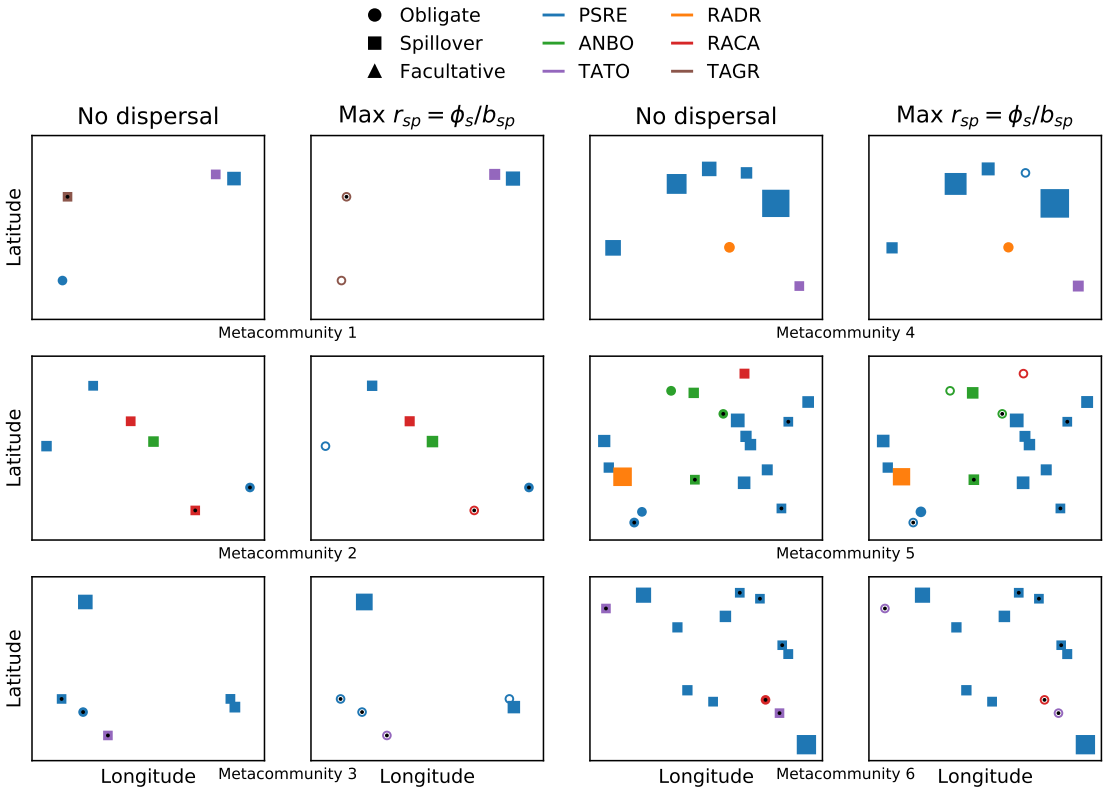


Figure 5: Six representative metacommunities and patch source potentials given no dispersal and maximum plausible connectivity for each species in a metacommunity (Max $r_{sp} = \phi_s/b_s$). Each point represents the spatial location of a patch within the metacommunity. The color of the point indicates which amphibian has the highest $R_{0,s,p}$ in the site. If the point is filled, the patch-level $R_{0,p}$ is greater than 1 and the patch is a source patch. If the point is not filled, the patch-level $R_{0,p}$ is less than 1 and the patch is a sink. The shape of the point indicates what type of community is found in the patch. Circle = an obligate community where $R_{0,s,p} < 1$ for all species, Square = A spillover community where $R_{0,s,p} > 1$ for only one species, and Triangle = a facultative community where $R_{0,s,p} > 1$ for more than one species. The size of the point represents a scaled measure of patch-level $R_{0,p}$ when patch-level $R_{0,p} > 1$. Finally, points with small black dots indicate patches where Bd was not observed for any species. Our statistical model for Bd load accounted for detection error, such that there was some probability that Bd was present, but at low prevalence in these patches. We used the model-predicted prevalence given detection error when making inference for these sites (Appendix S2).

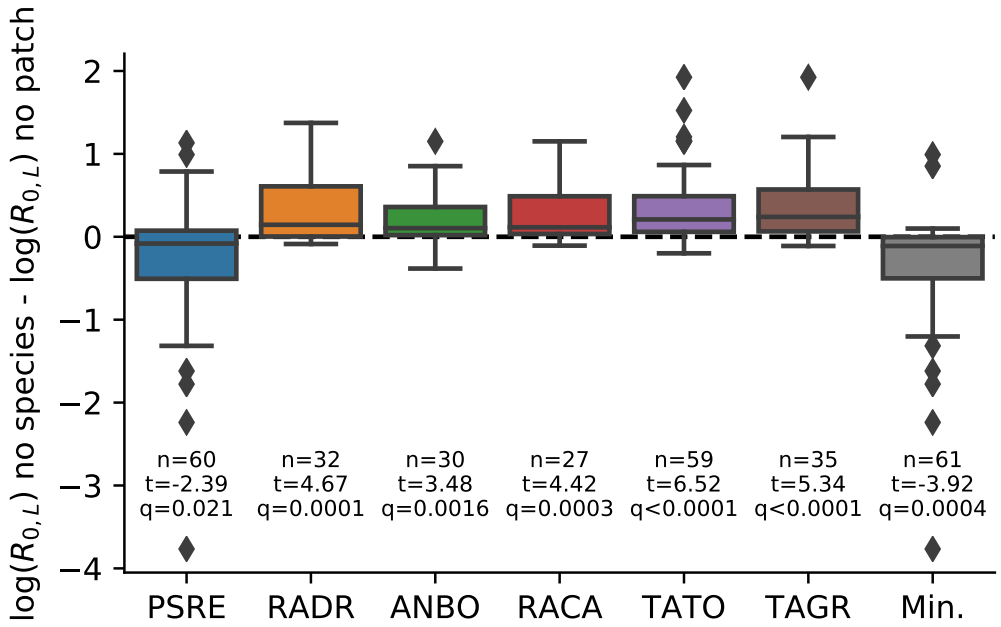


Figure 6: The effect of removing a species on landscape-level $R_{0,L}$ compared to removing the most influential source patch for 61 metacommunities with at least two patches and two species. Negative values indicate a larger reduction in landscape-level $R_{0,L}$ when a species is removed compared to when the most influential source patch is removed from the metacommunity. The sample sizes give the number of metacommunities out of 61 where a species was present. The $t$-statistics are from single sample t-tests testing the null hypothesis that the ratio $\log(\frac{R_{0,L}\text{no species}}{R_{0,L}\text{no patch}})$ is significantly different than zero. The $q$ value is the significance value of the single sample t-test, after adjusting for multiple comparisons using the false discovery rate correction (Benjamini & Hochberg 1995). The gray boxplot "Min." shows the minimum ratio $\log(\frac{R_{0,L}\text{no species}}{R_{0,L}\text{no patch}})$ across all species within a metacommunity. The dashed line indicates where removing a species and removing the most influential source patch had the same effect on landscape-level $R_{0,L}$.

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