Disease hotspots or hot species? Infection dynamics in multi-host metacommunities controlled by species identity, not source location

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Abstract

Pathogen persistence in host communities is influenced by processes operating at the individual host to landscape-level scale, but isolating the relative contributions of these processes is challenging. We developed theory to partition the influence of host species, habitat patches, and landscape connectivity on pathogen persistence within metacommunities of hosts and pathogens. We used this 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 observed metacommunities. 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.

Keywords

maintenance species; reservoir species; source-sink dynamics; metacommunity; metapopulaton; *Batrachochytrium dendrobatidis*; endemic; *Pseudacris regilla*; hotspots; chytrid fungus

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 species within a habitat patch and among patches on a landscape can interact in non-additive ways to

influence pathogen invasion and persistence (Lloyd-Smith *et al.* 2005; Johnson *et al.* 2015; North & Godfray 2017). At the patch-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; Webster *et al.* 2017; Wilber *et al.* 2019). At the landscape-scale, 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 patches (hotspots) versus specific species (maintenance or amplification hosts).

While both variation among host species and across habitat patches influences pathogen invasion and persistence, how these factors interact remains unknown. In a multi-species, single-patch 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-species, multi-patch system, labeling species as maintenance or spillover hosts is made challenging by the added influence of variability among habitat patches –a species potential to maintain a pathogen (i.e. 'maintenance potential') may vary among habitats due to changes in community structure or the physical environment (Haydon *et al.* 2002; Rudge *et al.* 2013; Roberts & Heesterbeek 2020). This context-dependent variability in species maintenance potentials further leads to variability in the potential of individual patches to support a pathogen (i.e. 'source potential'), 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, in part, on the degree to which the maintenance potential of each host species varies with –or is moderate by –patch location.

While the potential of habitat patches to contribute infections across the landscape is ultimately a function of the maintenance potentials of its constituent species, patches can further influence pathogen persistence through their connectivity to other patches in the metacommunity (Park *et al.* 2001; Schreiber & Lloyd-Smith 2009; North & Godfray 2017). For example, depending on the locations of source and sink patches on the landscape, high enough pathogen or host dispersal rates can actually hinder the ability of a pathogen to invade a metapopulation that would otherwise be invasible at lower dispersal rates (Schreiber & Lloyd-Smith 2009; Jousimo *et al.* 2014). Thus, correctly accounting for patch connectivity and pathogen dispersal can fundamentally alter predictions about pathogen invasion across the landscape. Despite this theoretical understanding, few studies have empirically quantified the links among species maintenance potential, patch source potential, and patch connectivity to understand pathogen persistence within a metacommunity (Penczykowski *et al.* 2015). This is a critical next step for understanding the drivers of pathogen 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 susceptible population (Diekmann *et al.* 1990). When $R_0 > 1$, a pathogen can invade a susceptible host population (Keeling & Rohani 2008). In a multi-species, multi-patch system, there is a hierarchy of R_0 values: species-level R_0, patch-level R_0, and landscape-level $R_{0,L}$ (Figure 1A). Maintenance species and source patches are defined by scale-specific values of $R_0 > 1$, while landscape-level $R_{0,L}$ combines the species- and patch-level R_0 values to determine when a pathogen can invade the host metacommunity (i.e. $R_{0,L} > 1$, Fig. 1A; Arino *et al.* 2005, but see Cross *et al.* (2005); North & Godfray (2017)). Theoretically, the species-, patch-, and landscape-level R_0 values, coupled with information on species connectivity and patch connectivity, provide all the information necessary to understand pathogen invasion and persistence within host-pathogen metacommunities. Empirically, however, the parameters required to calculate species- and patch-level R_0 values can be difficult to estimate, particularly 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-patch, multi-species systems.

Here, we first develop multi-patch, multi-species models of host-pathogen metacommunities and then confront these models with commonly-collected pathogen data to address three questions: (1) Are the relative maintenance potentials of host species consistent across habitat patches? (2) How do patch connectivity and pathogen dispersal affect species maintenance and patch source potential in a metacommunity? and (3) What are the relative contributions of maintenance species compared to source patches for determining 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 hundreds of amphibian species worldwide (Kilpatrick *et al.* 2010; Scheele *et al.* 2019). Between 2013 and 2018, 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 and answer our three questions. 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 amphibian species from 77 metacommunities in the East Bay Region of California, USA

(Fig. S1). We considered six species of wetland-breeding amphibians: *Pseudacris regilla* (Baird and Girard, 1852) (Pacific tree frog), *Anaxyrus boreas* (Baird and Girard, 1852) (western toad), *Rana catesbeiana* (Shaw, 1802) (American bullfrog), *Rana draytonii* (Baird and Girard, 1852) (California red-legged frog), *Taricha torosa* (Rathke, 1833) (California newt), and *T. granulosa* (Skilton, 1849) (rough-skinned newt). Adult amphibians of all species typically breed in ponds from January to late spring and co-occur as larvae between May and August (Fig. S1, Stebbins & McGinnis 2012). The length of the larval period varies among species (Fig. S1, Johnson *et al.* 2012). Larvae of the native species (*P. regilla*, *A. boreas*, *R. draytonii*, *T. granulosa*, and *T. torosa*) typically mature and leave the pond within the same year, while the non-native *R. catesbeiana* usually requires two or more years to reach metamorphosis (Stebbins & McGinnis 2012). Amphibian communities persist endemically with Bd across multiple interconnected ponds and wetlands with little evidence of Bd-associated pathology. Available information on the biology of these amphibian species coupled with the feasibility of standardized sampling protocols for Bd infection and host density (e.g. Johnson *et al.* 2012; Joseph *et al.* 2016; Stutz *et al.* 2018), 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). Spatially, this meant that all ponds were no more than two kilometers away from at least one other pond within a metacommunity. 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 spatiotemporal 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 with an average of six ponds per metacommunity. There were 139 unique ponds sampled across six years and, on average, each pond was sampled in four years, for a total of 496 unique pond-by-year combinations.

From May through August in 2013–2018, crews sampled amphibian communities over the course of two visits per pond. During the first visit (early summer), standardized dipnet surveys were used to estimate the density of larval amphibians for each species (for details see Johnson *et al.* 2013; Joseph *et al.* 2016). During the second visit (mid summer), we used standardized methods to swab the skin of metamorphosing anurans or late-stage larvae (caudates) to assess Bd infection status and Bd load using quantitative polymerase chain reaction (qPCR) with a standardized TaqMan assay (Boyle *et al.* 2004; Hyatt *et al.* 2007). qPCR for Bd was run on each sample in triplicate to quantify measurement error (DiRenzo *et al.* 2018). 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. While adult amphibians were present and occasionally captured during surveys, the sampling protocols 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 developed a dynamic model to address our three questions regarding the contributions of host species and habitat patches 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 directly model Bd load as there was little evidence for load-dependent mortality in this system. 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)

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

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. λ_{ip} is the shedding rate of Bd zoospores into the environment of species i in patch p. γ_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 ν_{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. Host death rate is given by d_{sp} and is species and patch specific.

The parameter ϕ_s is the within-season dispersal rate for host species s (i.e. the rate at which individuals of species s leave a patch) and c_{jp} is the probability that a host moves from patch p to patch j. 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. The area ratio $\frac{A_j}{A_p}$ converts the total number of individuals leaving patch j in a time step to the appropriate density units in 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 $R_{0, s, p} = \frac{\beta_{sp} \lambda_{sp} S^*_{sp}}{b_{sp} \gamma_p}$,

where S^*_{sp} is the density of susceptible hosts of species s in patch p before infection arrives and b_{sp} is the loss rate from the infected class such that $b_{sp} = d_{sp} + \nu_{sp}$ (Fig. 1B). Note that if we included Bd-induced mortality at some constant rate a_{sp}, this would be additively included into b_{sp}.

At equilibrium, algebraic manipulations of equation 1 show that

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

The variable Π^*_{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. In Appendix S2, we discuss why an approximate equilibrium assumption is appropriate for the within-season dynamics of this amphibian-Bd system.

Finally, 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). As a result, 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 pathogen persistence, *relative* to the other species that have been sampled.

Linking empirical data to maintenance species and source patches

We fitted statistical models that accounted for false absences to estimate Bd load, Bd prevalence Π^*_{sp} and host density N^*_{sp} for species s in patch p (models described in Appendix S3; Miller *et al.* 2012; Joseph *et al.* 2016; DiRenzo *et al.* 2018). We assumed that host zoospore 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 species-level $R_{0, s, p}$ estimates. Finally, because our model assumed that amphibians were sharing the same pool of zoospores, patch-level $R_{0, s, p}$ could be directly calculated as $R_{0, p} = \sum_{s \,\in\, \text{Species}} R_{0, s, p}$ (Rudge *et al.* 2013).

Question 1: Are the maintenance potentials of host species consistent across patch locations?

We began our analysis with the assumption that patches were unconnected within a metacommunity (i.e. $\phi_s = 0$). We then calculated relative and absolute $R_{0,s,p}$ values for all species across across patch-by-year combinations. Under the assumption of no connectivity, the only parameters needed to calculate species-specific $R_{0,s,p}$ were Bd prevalence, relative density, and relative shedding rates for the different amphibian species within a patch (equation 2). If one species consistently had higher relative $R_{0,s,p}$ values than another, this was evidence that relative species maintenance potential for that species pair was independent of patch location. We used a two-sided binomial test to test if relative maintenance potentials of species were consistent across patches by comparing whether one species consistently had a larger species-level $R_{0,s,p}$ than another species.

Question 2: How does patch connectivity affect species maintenance and patch source potential?

Equation 2 shows that accounting for the connectivity of patches can change our conclusions about the consistency of species maintenance potential and patch source potential within a metacommunity. Here we give a summary of how we included connectivity into our model. The complete methods are described in Appendix S4.

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 describes 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, there were many values for r_{sp} 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. In other words, if $R_{0,s,p} < 0$ for a value of r_{sp}, then the observed levels of prevalence, Bd loads, and host density were not consistent with an endemic equilibrium state of the multi-species, multi-patch model. For example, high levels of host dispersal would tend to homogenize species-level density and pathogen prevalence among patches, such that observing highly variable equilibrium host densities and prevalences among patches at endemic equilibrium would be inconsistent with high levels of host dispersal.

We 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 drew 10,000 parameter sets of plausible $H \times P\ r_{sp}$ parameters and computed the species-level $R_{0,s,p}$ for all species and patches using equation 2 (Appendix S4). For each species s in patch p, we ensured that we drew a plausible r_{sp} value (i.e. one such that $R_{0,s,p} > 0$) by setting equation 2 to zero and solving for $r_{sp} = \phi_s/b_{sp}$ (Appendix S4). For the results presented below, we used both the median $R_{0,s,p}$ values from the 10,000 plausible parameter sets and the maximally connected plausible parameter set. We defined the maximally connected plausible parameter set for a

metacommunity as the set where each r_{sp} was at its maximum plausible value (Appendix S4).

Question 3: What are the contributions of maintenance species compared to source patches for pathogen persistence?

For our final question, we sought to quantify the relative contributions of maintenance species and source patches to landscape-level $R_{0,L}$. For each metacommunity, 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 (see Appendix S5 for details). We performed this simulated removal experiment over the plausible sets of r_{sp} values for a metacommunity. We defined the most influential source patch in a metacommunity as the patch with the largest patch-level $R_{0,p}$, given a set of plausible r_{sp} parameters. We performed this *in silico* removal experiment on 61 metacommunities that had more than one habitat patch and more than one amphibian species.

Results

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

Overall, *P. regilla* was observed in 82% of patch-by-year combinations (405 / 496), *T. torosa* in 67% (334 / 496), *T. granulosa* in 28% (137 / 496), *A. boreas* in 28% (138 / 496), *R. draytonii* in 13% (65 / 496), and *R. catesbeiana* in 11% (56 / 496). Median species richness per patch was between 2 and 3, depending on the year. *P. regilla* and *T. torosa* were present in 74 and 70 of 77 metacommunities, respectively, while *R. draytonii*, *T. granulosa*, *A. boreas*, and *R. catesbeiana* were all found in less than 50% of the 77 metacommunities (37, 36, 32, and 27 metacommunities, respectively). *Pseudacris regilla* and *T. torosa* also had higher estimated larval densities relative to *R. draytonii*, *A. boreas*, *T. granulosa*, and *R. catesbeiana*, although density estimates varied substantially across years (Fig. 2A).

Bd was detected in 73% of patches that were sampled from 2013–2018. *Rana draytonii* generally had the highest Bd prevalence, followed by *P. regilla* and *A. boreas* (Fig. 2B). Observed prevalence was the lowest for *T. torosa* and *T. granulosa* (Fig. 2B). Prevalence estimates varied across years, with 2014 showing a substantially lower prevalence for most species (Fig. 2B). Within a year, mean Bd load given infection was generally significantly higher in *A. boreas*, *P. regilla*, and *R. draytonii* compared to *T. granulosa* and *T. torosa* (95% credible intervals of log load differences between these species were significantly different than 0, but not in year 2014; Fig. 2C). Loads detected in *R. catesbeiana* were generally not significantly different from those in other species.

Question 1: Are the maintenance potentials of host species consistent across patch locations?

Within a patch, *P. regilla* was consistently the most important amphibian host species for the persistence of Bd: The relative $R_{0,s,p}$ of *P. regilla* was larger than other amphibian species in 82% of the patches in which the amphibian species co-occurred (489 / 600 instances of *P. regilla* co-occurring with other amphibian species within a patch;

Fig. 3). *P. regilla* was statistically more likely to have a higher species-level $R_{0, s, p}$ than all five species with which it co-occurred (Fig. 3). Of the 111 instances where *P. regilla* had a lower relative $R_{0, s, p}$ to another species in the community, 38% were with *A. boreas*, 29% were with *T. torosa*, 19% were with *R. draytonii*, and 8% were with *R. catesbeiana*.

The majority of host communities had at least one maintenance host species and *P. regilla* was almost always a maintenance host when it was present: Of the 496 patch-by-year combinations sampled, 126 had estimates where all species-specific $R_{0, s, p}$ values were less than one, but patch-level $R_{0, p}$ was greater than one (i.e. an obligate host community, Fig. 4). In 66 of these 126 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 S3, Fig. 4). Of the 370 communities that were not 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 *P. regilla* and either *A. boreas* or *R. draytonii*. The other 91% of non-obligate communities (338 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 *P. regilla* was present, *P. regilla* was a maintenance host 89% of the time (267 / 300; Fig. 4).

Question 2: How does patch connectivity affect species maintenance and patch source potential?

Under plausible levels of connectivity, multiple source patches contributed to Bd persistence and *P. regilla* 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 *P. regilla* as a maintenance host within patches was largely unchanged (Fig. 3). Under plausible levels of connectivity, the relative $R_{0, s, p}$ of *P. regilla* was larger than other amphibian species in 81% (483 / 600 combinations) of the patches in which the amphibian species co-occurred (Fig. 3).

While species maintenance potential did not change across plausible connectivity parameters, patch source potential did (e.g. Fig. 4). However, even under the maximally connected plausible parameter scenario 51 of the 62 metacommunities with more than one patch had two or more source patches contributing to Bd persistence (e.g. Fig. 4).

Question 3: What are the contributions of maintenance species compared to source patches for pathogen persistence?

Removing *P. regilla* 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 *P. regilla* led to, on average, a 53% larger reduction in landscape-level $R_{0,L}$ compared to removing the largest source patch (95%

confidence interval from single sample t-test: [33%, 85%], Fig. 5). 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 most influential source patch (Fig. 5). In six 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. 5).

Discussion

Understanding how different scales 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 identifying the relative effects of 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 scales of heterogeneity contributing 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 sources of heterogeneity (e.g. species-level and patch-level heterogeneity), a single source of heterogeneity can disproportionately contribute to pathogen persistence.

A key challenge that multi-species communities pose for disease management is that the identity of maintenance species can vary across habitat patches, making pathogen management strategies habitat-dependent (Rudge *et al.* 2013; Webster *et al.* 2017). Quantifying the degree to which maintenance potential depends on the species and not the habitat can help identify when specific-specific management can reduce disease on the landscape. In our study, we found that the Pacific tree frog (*P. regilla*) was consistently the dominant maintenance host across patches. This was reflected in higher relative values of species-level $R_{0,s,p}$ when *P. regilla* co-occurred with other amphibian species. However, we did find that in some communities other amphibian species were predicted to be maintenance hosts. Of particular interest in amphibian-Bd systems is the effect that the invasive American bullfrog *R. catesbeiana* 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 *P. regilla*, *A. boreas*, or *R. draytonii* when these species co-occurred. Moreover, while bullfrogs were predicted to be maintenance hosts in 17 patches under a no connectivity scenario, bullfrogs did not remain a maintenance host in six of these source patches when we included patch connectivity. This was in contrast to the patches where *A. boreas* and *R. draytonii* 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 their importance 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, in our study, while *P. regilla* had a higher density than *R. draytonii* in all patches where they co-occurred, it tended to have a lower Bd prevalence and load relative to *R. draytonii*; as a result, *P. regilla* was the more important maintenance host in only 65% of these patches. 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 are 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.

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, heterogeneity in species maintenance potential across habitat patches can lead to heterogeneity in patch source potential, which can interact with patch connectivity through source-sink dynamics to affect pathogen persistence within a metacommunity (Schreiber & Lloyd-Smith 2009; North & Godfray 2017). Equation 2 and Fig. 4 illustrate this point –depending on the level of connectivity and variability in host prevalence and density across patches, species-level $R_{0, s, p}$ values can increase or decrease as connectivity increases and can do so at different rates across species and patches. Thus,

for example, hosts that were predicted to be maintenance species at low levels of connectivity may no longer be maintenance species at high levels of connectivity. Testing the effects of connectivity on our predictions of species maintenance potential, we found minimal changes in relative species maintenance potential compared to no connectivity. While we did observe significant changes in patch source potential as connectivity increased, even at maximum plausible levels of connectivity we found that 82% (51 / 62) of the amphibian-Bd metacommunities observed in this system were most consistent with a weakly connected network of more than one source patch.

Pathogen dynamics within a metacommunity are driven by processes operating across scales (Paull *et al.* 2012). However, most empirical applications of epidemiological theory have considered the role of processes operating at a single scale on emergent disease dynamics (e.g. how does individual heterogeneity in contact rates affect pathogen invasion? Bansal *et al.* 2007; Schreiber & Lloyd-Smith 2009; Rudge *et al.* 2013). The theoretical developments in this study, combined with a large spatial dataset, provided us the unique opportunity to test the relative contributions of species- and patch-level processes to disease persistence in a metacommunity. When we systematically removed either the dominant maintenance species or source patch in a metacommunity *in silico*, we found that removing the dominant maintenance species on average reduced landscape-level $R_{0,L}$ twice as much as removing the primary source patch in the metacommunity. As *P. regilla* was the dominant maintenance species in most metacommunities, removing *P. regilla* was the most effective strategy for reducing landscape-level $R_{0,L}$ for Bd. 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 $R_{0,L}$.

There were two reasons for the larger effects of *P. regilla* removal than habitat patch removal on landscape-level $R_{0,L}$. First, because *P. regilla* maintenance potential was consistent across patches, removing *P. regilla* consistently removed the most important species for Bd persistence within a patch. Second, because *P. regilla* was widely dispersed on the landscape, the source potentials of many patches within a metacommunity were affected by *P. regilla* removal. In contrast, just removing a widely-dispersed species (e.g. *T. torosa*) or a species with high maintenance potential (e.g. *R. draytonii*) was significantly less effective at reducing $R_{0,L}$ than removing the most influential source patch. These results highlight the importance of identifying how consistent species maintenance potentials are across habitat patches, as this can help determine whether landscape-level management of pathogens might be most effective at the species or patch scale.

The model we develop is applicable to other multi-species, multi-patch systems and is amenable to asking additional theoretical questions to further unravel how multiple sources of heterogeneity drive host-pathogen dynamics. Just as with the multi-species models that our approach extends (Rudge *et al.* 2013; Fenton *et al.* 2015), our model is particularly useful at the interface between theory and data because hard-to-estimate rates such as transmission, pathogen decay, and dispersal 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.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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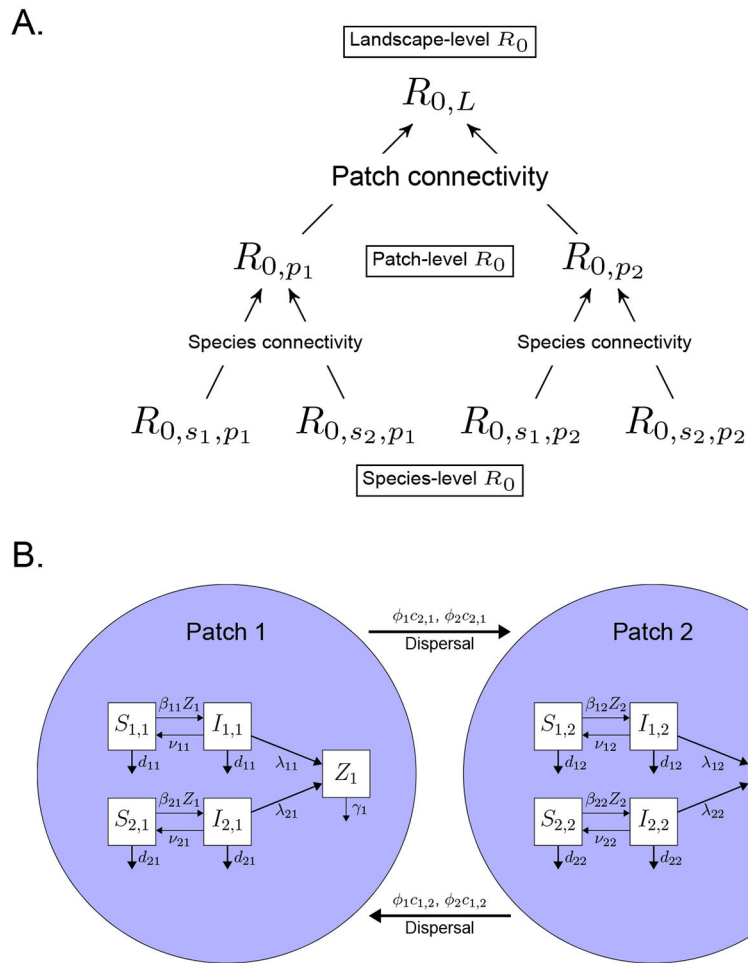
A.

B.

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 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.
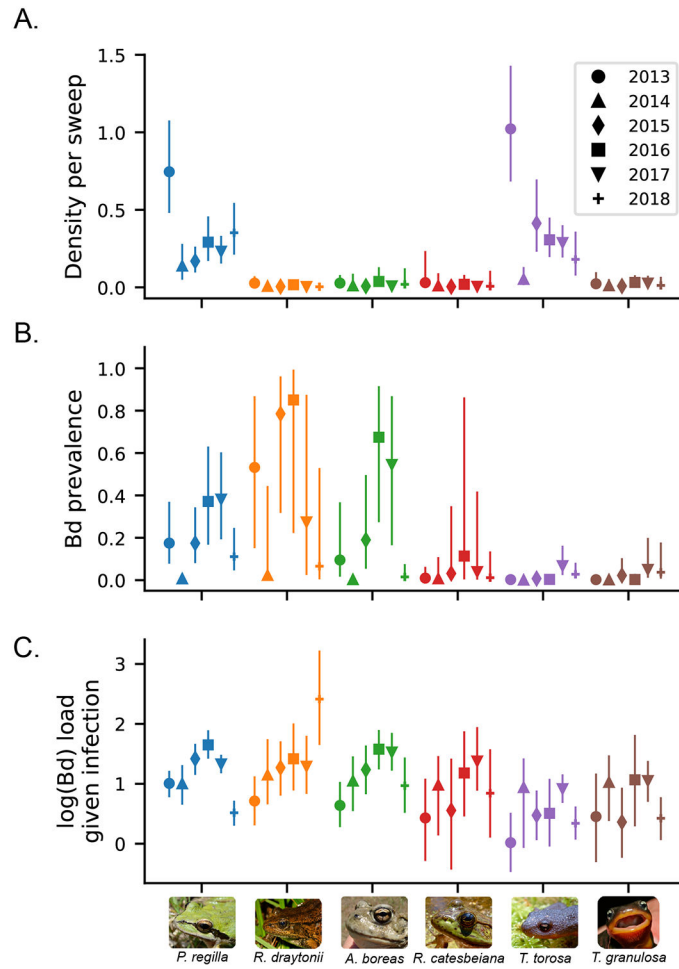
Figure 2: A.
Median estimated amphibian density per dip net sweep after accounting for false absences across six years, 139 patches and six amphibian species. **B.** Median estimated prevalence after accounting for false absences. **C.** Median estimated mean log(Bd) load conditional on infection after accounting for measurement error. For all figures, the error bars are 95% credible intervals about the estimated median. Different shapes represent different years. The species on the x-axis are Pacific tree frog (*P. regilla*), western toad (*A. boreas*), American bullfrog (*R. catesbeiana*), California red-legged frog (*R. draytonii*), California newt (*T. torosa*), and rough-skinned newt (*T. granulosa*).
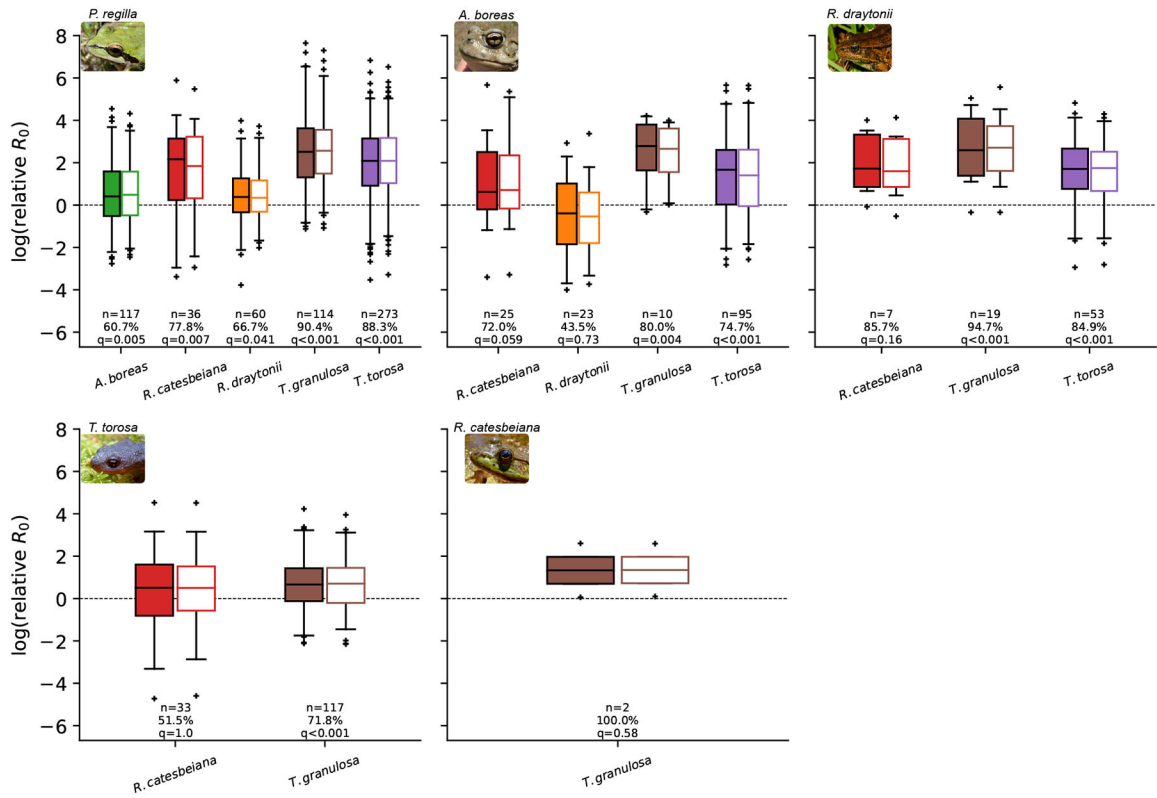
Figure 3:

Relative species-level $R_{0,s,p}$ values within a patch calculated using equation 2 with no connectivity (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 "*A. boreas*" x-label of the plot titled "*P. regilla*" shows the distribution of the ratios of *P. regilla* $R_{0,s,p}$ values to *A. boreas* $R_{0,s,p}$ values for patches where *P. regilla* and *A. boreas* were both present. A value larger than zero indicates that the relative maintenance potential of *P. regilla* is greater than *A. boreas* for that comparison. '*n*' gives the number of patches where both species were found, '%' gives the percent of comparisons where relative log $R_{0,s,p}$ values were greater than zero, and '*q*' gives the *p*-value corrected for false discovery rate (Benjamini & Hochberg 1995) from a binomial test with the null hypothesis that species are equally likely to have a higher species-level $R_{0,s,p}$ within a patch. The bars give the median relative $R_{0,s,p}$ values, 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.
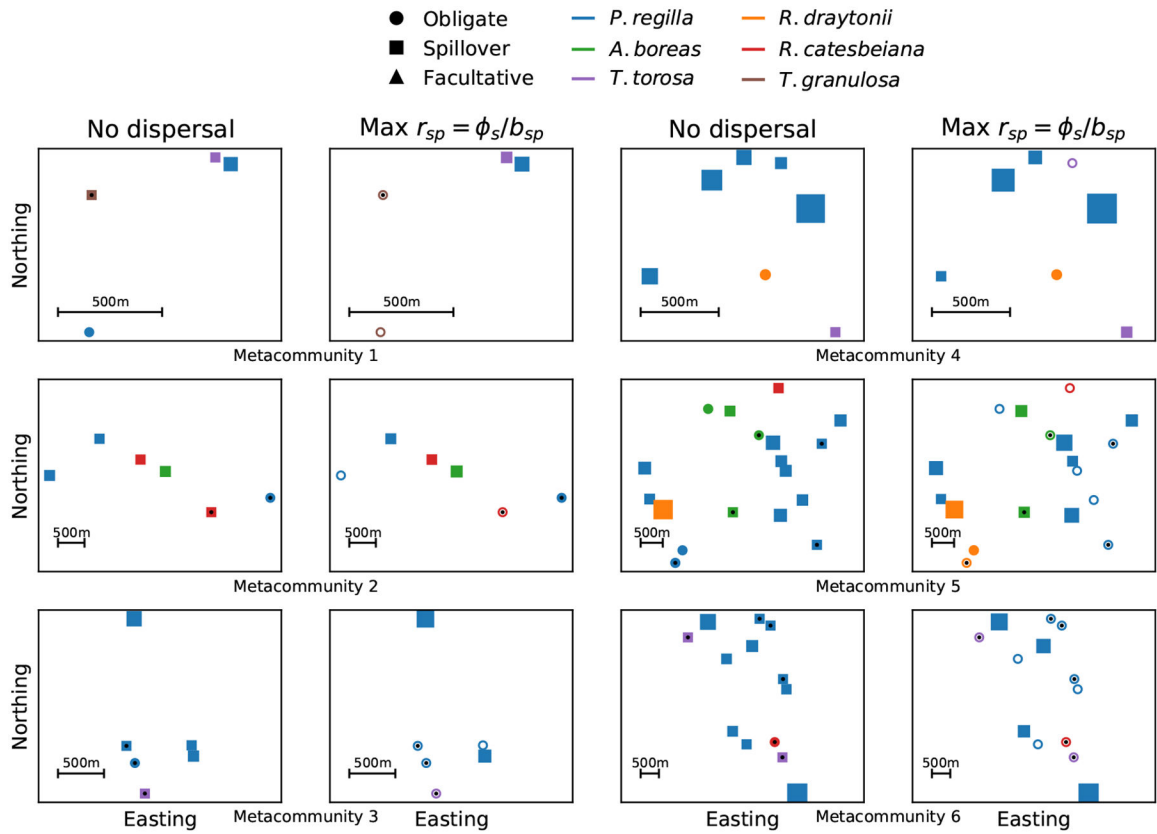
Figure 4:

Six representative metacommunities 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 using a UTM projection. The color of the point indicates which amphibian has the highest species-level $R_{0,s,p}$ in the patch. 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 patches (Appendix S3).
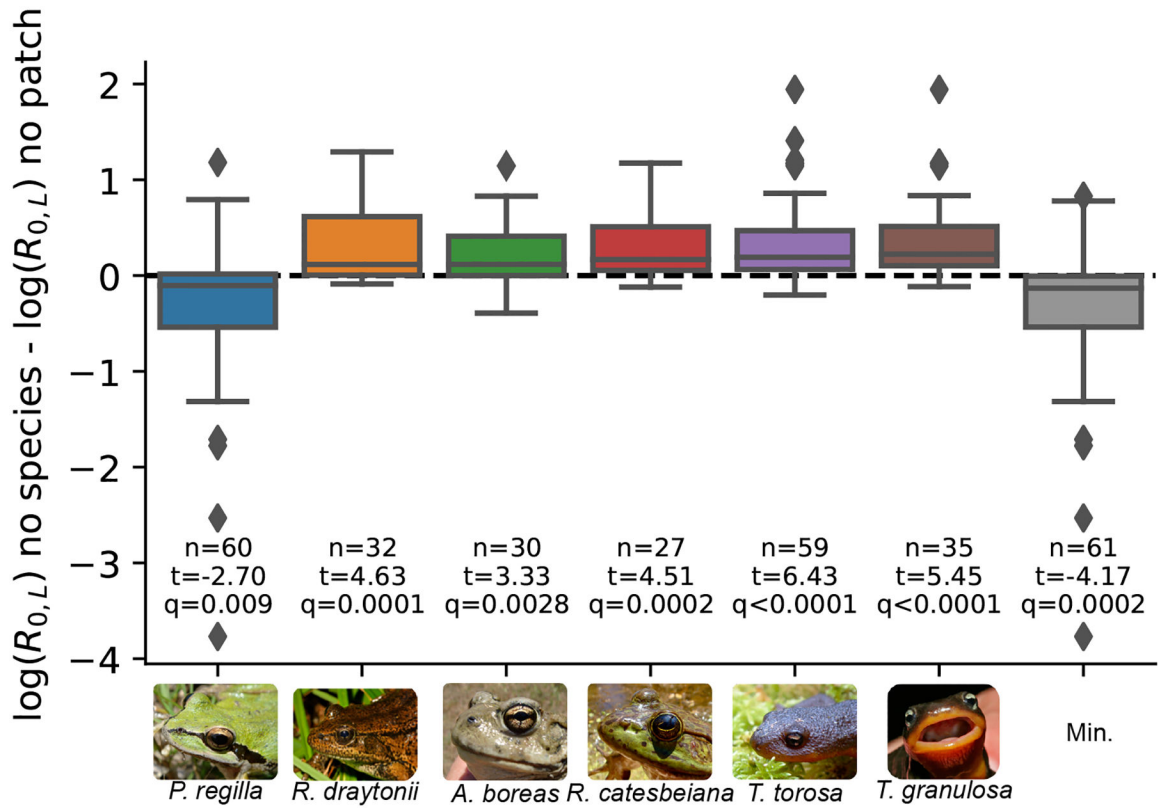
Figure 5:

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 $\log\left(\frac{R_{0,L}^{\text{no species}}}{R_{0,L}^{\text{no patch}}}\right)$ 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 $\log\left(\frac{R_{0,L}^{\text{no species}}}{R_{0,L}^{\text{no patch}}}\right)$ 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 $R_{0,L}$.