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SYMPOSIUM

Advancing Theory Underlying Diversity-Disease Relationships: Competence in the Context of Life History, Demography, and Disease

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Synopsis Biodiversity loss can increase parasite transmission via the dilution effect when two criteria are met. First, if communities consist of hosts that span a gradient of competence, from highly competent species that amplify transmission to low-competence species that decrease transmission. Second, if biodiversity loss is non-random, such that low-diversity communities possess a disproportionately high number of highly competent hosts. Infection is then predicted to spread more efficiently in low-diversity (high competence) communities. These criteria offer a compelling direct connection between biodiversity loss and disease. Evaluating the processes underlying these criteria can provide insight into how commonly they are met, and when we can expect to observe parasite dilution. By pairing recently published competence values and high-resolution infection data from a multi-host multi-parasite system (five amphibian species and four trematode taxa), we evaluated core assumptions embedded in the dilution effect criteria: (1) Infection outcomes are governed by species competence; (2) community assembly is non-random; and (3) life history mediates an indirect connection between competence and community assembly. We found that competence was a strong predictor of infection in natural systems for the majority of host-parasite interactions. Community assembly order of amphibians was also predictable based on the spatiotemporal commonness of each species. While amphibian life history characteristics were associated with competence (with faster pace-of-life characteristics tied to higher levels of competence), we did not observe an association between life history characteristics and spatiotemporal patterns of commonness. Consequently, there was an idiosyncratic relationship between competence and assembly order. Simulations demonstrated that, even when the competence-assembly order relationship is absent, average community competence can still decline with species richness, as long as the most common species (first to assemble) has relatively high competence. By connecting life history, demography, competence, and infection, we found strong empirical support for some of the assumptions underlying the dilution effect; for those that were not met, we gained novel insight into the pathways through which community structure may lead to dilution.

Introduction

Pronounced declines in biodiversity, alongside increases in the emergence and spread of several infectious diseases, have motivated over two decades of research on how biodiversity might constrain infection. Growing from foundational models on the dilution effect (Ostfeld and LoGiudice 2003; Keesing et al. 2006), the field of diversity-disease theory has amassed hundreds of theoretical and empirical studies spanning diverse ecological systems and interactions (Civitello et al. 2015; Halliday et al. 2020; Mahon et al. 2024). This body of work has transformed our understanding of how and to what degree ecological communities can regulate pathogen spread (Johnson et al. 2015; Rohr

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et al. 2020; Keesing and Ostfeld 2021), as well as how the influence of ecological communities—and resulting disease outcomes—can be modified by scale (Halliday and Rohr 2019; Rosenthal et al. 2021; Liu et al. 2023; Strauss et al. 2024). But while a few notable systems have yielded robust and extensive evidence that community structure constrains disease (Allan et al. 2009; Keesing et al. 2010; Halliday et al. 2023; Johnson et al. 2024), our mechanistic understanding of how diversity-disease relationships unfold across systems is still in development. Much of diversity-disease literature consists of correlational studies that explore associations between measures of species diversity and measures of infection. These studies represent a valuable and essential step in assessing the generality of the theory. To expand our mechanistic insight, scientists are now encouraging research efforts that move beyond correlation and carefully investigate the processes that underlie disease dilution (Johnson et al. 2015; Luis et al. 2018; Rohr et al. 2020; Halsey 2019).

Species losses can increase parasite transmission when two criteria are met: (1) if communities consist of host species that span a gradient of competence—from higher competence species that act as parasite sources to lower-competence species that act as parasite sinks (where competence is the capacity of the host to support infection, given exposure [Stewart Merrill and Johnson 2020]). And (2) if biodiversity loss (the extirpation of species) is non-random, such that low-diversity communities possess a disproportionately high number of competent hosts (Ostfeld and LoGiudice 2003; Joseph et al. 2013; Johnson et al. 2015). When these criteria are met, parasites are predicted to spread more efficiently in low-diversity (higher average competence) communities, generating a direct negative relationship between biodiversity and transmission. Embedded in these two criteria are a series of assumptions that, when tested, can offer insight into the generality of diversity-disease associations.

The first assumption is that species competence is the key factor controlling infection. That is, when predicting the capacity of an ecological community to support infection, we assume that this average capacity arises from the species identities comprising it and their underlying competence values. However, infection outcomes can be shaped by several processes outside of the host-parasite interaction itself. Parasite (or vector) choice behaviors, as well as host avoidance or sickness behaviors, can shape which host species or individuals are exposed to infection, with habitat-specific factors and stochasticity further modifying when and where a host encounters infective stages (Kilpatrick et al. 2006; Sears et al. 2015; Johnson et al. 2019; Payne et al. 2025). Such differences in exposure have strong potential to overwhelm the importance of competence for shaping infection, potentially decoupling competence-infection relationships. In such a case, how competence is distributed within communities would make a weak contribution to transmission. An improved version of this first assumption may then be that species competence, given comparable exposure, controls infection. By testing the assumption that natural infections averaged across the landscape—and over varying exposure regimes—are reflective of species competence values, we can explore how often the first criterion for disease dilution is met.

Non-random biodiversity loss carries a second core assumption: species vary predictably in their probability of loss (i.e., sequence of extinction versus persistence during community disassembly [Ostfeld and LoGiudice 2003]). In the context of species extinctions, early ecological stress theory proposed that a species' vulnerability to stressors was, in part, shaped by life history strategy (Rapport et al. 1985). Fast pace-of-life (r-selected) organisms that invest heavily in current reproduction and have general niche requirements were predicted to be more resilient to environmental stress than slower pace-of-life (K-selected) species that invest in maintenance (future reproduction) and possess specific niche requirements. More recently, this theory has been broadened to account for population trends beyond vulnerability and resilience. That is, pace of life is thought to be a key factor shaping species' demographic and distributional patterns, such that fast pace-of-life species may be expected to occur more frequently over time, through space, and across communities (Cardillo et al. 2008). Probing relationships between pace of life, spatiotemporal distributions, and commonness across communities can therefore ground-truth our assumption that species loss is non-random.

Whether non-random diversity loss results in a disproportionately high number of competent hosts rests on a third and final assumption. For this pattern to emerge, a species' likelihood of persisting during community disassembly must be related to its capacity to transmit infection (Young et al. 2013; Johnson et al. 2015). As before, life history theory underlies this assumption (Johnson et al. 2012; Joseph et al. 2013). Species with fast pace-of-life strategies are thought to allocate energy to current reproduction at the cost of long-term maintenance, including immunity and parasite resistance (Lee 2006; Cronin et al. 2010; Previtali et al. 2012). Conversely, slow pace-of-life organisms may invest heavily in immune defense to increase lifespan and maximize their potential for future reproduction. Life history tradeoffs between reproduction and immunity can then generate a powerful (albeit indirect) association between commonness across the landscape and competence for infection (Valenzuela-Sanchez et al. 2021). This triad of associations is at the heart of the dilution effect (Keesing et al. 2006). Testing each link can ground diversity-disease theory in ultimate evolutionary drivers, and in doing so, solidify expectations for its generality.

In our past research on amphibian-parasite interactions, we have demonstrated that the average competence of amphibian communities declines with increasing species richness, as is assumed by the dilution effect (Johnson et al. 2013; Johnson et al. 2024). Indeed, richness-associated changes to amphibian community composition and amphibian densities fundamentally shape infection success at the whole wetland scale for four dominant parasite taxa (Johnson et al. 2024). Yet, questions remain on the underlying processes generating these competence-infection patterns. Do species identities (and their associated competence values) reliably predict natural infections across the landscape? What aspects of amphibian demographic patterns produce the assembly orders that underlie richness-competence associations? And can these phenomena be traced back to life history characteristics of the amphibian hosts? To advance theory on the dilution effect, we combine new metrics of competence with high-resolution infection data and a suite of published life history characteristics (egg size, larval period, adult body size, and lifespan) to address the following hypotheses: (1) field infections across the landscape are shaped by species-level competence estimates; (2) species' demographic patterns (commonness in space and time) underly community assembly order; and (3) life history mediates an indirect connection between competence and community assembly.

Methods

Study system and data

We focus our work on natural communities of amphibians that are commonly infected by trematodes in the East Bay region of California. The trematode species in our system are aquatic parasites with complex life cycles that involve sequential movement from snail first intermediate host to larval amphibian second intermediate host to vertebrate definitive host (Schell 1985). Infection of larval amphibians occurs when swimming cercariae are released from snails; cercariae seek an amphibian host, penetrate its tissue upon contact, and develop into metacercariae or mesocercariae (depending on the parasite's taxon) inside the amphibian's tissue. Trematodes within the tissue persist as the amphibian matures and undergoes metamorphosis, and can be transmitted to a vertebrate predator when the amphibian is consumed by the predator. Our study conducts analyses on previously published data for this system, which comprises five amphibian hosts (western toad *Anaxyrus boreas* [ANBO]; Pacific chorus frog *Pseudacris regilla* [PSRE]; American bullfrog *Rana catesbeiana* [RACA]; rough-skinned newt *Taricha granulosa* [TAGR]; California newt *Taricha torosa* [TATO]) and four trematode parasites (*Alaria marcinae* [ALMA]; *Cephalogonimus* sp. [CESP]; *Echinostoma* spp. [ECSP]; *Ribeiroia ondatrae* [RION]). Laboratory-derived competence values for each of the twenty host-parasite interactions were published in Stewart Merrill et al. (2022), and associated field infections and demographic patterns (site occupancy) were quantified for 11 years and 902 communities in Johnson et al. (2024). We unite these datasets to ask new questions on the drivers of community competence patterns. Our analyses go beyond these past studies in important ways. First, while Stewart Merrill et al. (2022) developed novel measures of competence to help explain community-level infection outcomes in Johnson et al. (2024), we now ask how well a given species' competence value predicts its landscape-level pattern of infection. Second, there have been few studies (including those from which we derive data) that have united robust measurements of competence, demographic patterns underlying assembly order, and species life history traits in a single study for multiple parasites. Our analyses integrate all three pieces of information to test underlying assumptions of diversity-disease theory.

How well are field infections explained by species-level competence estimates?

Our recent metric of competence sought to incorporate information that is epidemiologically relevant (and potentially essential) to understanding natural infection patterns (Stewart Merrill et al. 2022). In particular, our metric incorporated: (1) variation in exposure (where competence was integrated over a range of ecologically realistic doses), (2) pre-transmission mortality (where competence was scaled based on the likelihood of host death prior to the point of transmission), and (3) parasite-specific responses (where competence for a given host was measured separately for different parasite taxa). Because our metric builds upon lower-information estimates, we can ask whether the addition of information gets us closer to predicting infection in natural systems.

We compared three laboratory estimates of a host species' capacity to support a given parasite infection. Our lowest information estimate, initial susceptibility, is the percentage of administered cercariae that develop into encysted metacercariae (or mesocercariae) in the host 36 h after exposure to one standard dose

(20 cercariae per amphibian). This metric is typical of a rapid infection assay and excludes variation in exposure, and the possibilities of infection clearance or pre-transmission mortality. Our moderate information estimate, dose-integrated susceptibility, is the percentage of administered cercariae over a range of exposure doses that persist as encysted metacercariae (or mesocercariae) in the host (for this estimate, amphibians were assessed for infection 20 days after exposure). This estimate therefore incorporates variation in exposure and provides time for clearance of infection to occur, but does not include pre-transmission mortality. Finally, our highest information estimate, dose-integrated competence is the percentage of cercariae across a range of exposure doses that become transmittable metacercariae (with the hosts remaining alive) 20 days after exposure. Values for each estimate and host-parasite interaction are published in Stewart Merrill et al. (2022).

To assess the performance of the three estimates outlined above, we evaluated associations between each estimate and natural infection levels in the field. Mean infection levels (number of metacercariae/mesocercariae per host) for each host-parasite interaction were quantified from individual infection data published in Johnson et al. (2024). From this dataset, we excluded amphibians collected from sites that did not have cercariae present (zero-exposure sites) and we excluded any amphibians with infection loads greater than 200 (because the exposure doses in Stewart Merrill et al. 2022 ran to a maximum of 200 cercariae per host). Excluding amphibians with loads over 200 did not meaningfully reduce our sample sizes. This exclusion resulted in retention of 99.6% of individuals assessed for *Alaria marcinae* (3418/3429), 99.9% assessed for *Cephalogonimus* sp. (5232/5234), 97.0% assessed for *Echinostoma* spp. (9390/9676), and 99.5% assessed for *Ribeiroia ondatrae* (9076/9126). We ran linear models for each parasite species that assessed the effect of the lab estimate (predictor) on mean infection (response) and evaluated summary statistics for the relationship (*P*-value and R^2). We did not control for variation in exposure across the sites (as in Johnson et al. 2024) because our highest information metric, dose-integrated competence, is designed to encompass natural variation in exposure. With this metric, we could then ask whether embedding variable exposure in a lab proxy approximates the variable exposure hosts experience in the field.

Does commonness underlie community assembly?

We estimated each species' commonness as an outcome of its spatial occupancy (how broadly a species occurs within the sampled pond habitats) and temporal reliability (how regularly a species is observed within a pond over time). Our estimates were derived from eleven years of amphibian data published in Johnson et al. (2024), for which the densities of larval amphibians were assessed annually using a series of dipnets deployed around each pond's perimeter. We converted published amphibian densities to presence/absence values for each pond-year combination. To quantify spatial occupancy, we computed the proportion of sampled ponds in which a species occurred within each year, then averaged the values across years. Because some species' ranges did not fully overlap with the study region (i.e., some species are never observed from ponds in certain counties or areas comprising the study region), we excluded ponds beyond the species' range from our denominator. To quantify temporal reliability, we first restricted the data to ponds in which a species occurred at least once over the entire study period. From these ponds, we then computed the proportion of years the species was present in each pond and averaged the values across ponds. We used the product of the two values (spatial occupancy and temporal reliability, which both scale between 0 and 1) as our estimate of spatiotemporal commonness, which conveys the joint likelihood of occurrence in space and time.

The amphibian communities in our study system have a well-established nested structure, which made it feasible to estimate their assembly order with a space-for-time substitution (Johnson et al. 2013). In brief, we evaluated how species' occurrences mapped onto community richness, following the premise that some species may dominate low-richness ponds across the landscape (and should be most likely to persist following disassembly), while others may occur rarely and only in high-richness ponds (and should be most likely to be lost during disassembly). By quantifying the proportion of ponds of a given richness level that a species occurs within, we could efficiently extract assembly order. We evaluated the correspondence between spatiotemporal commonness and assembly order with a simple Pearson's product-moment correlation. While our quantification of assembly produces an estimate of the order in which species are likely to occur across natural richness gradients, we note that our metric is time-independent; it combines information from both assembly and disassembly processes (both are occurring naturally to generate the compositions we observe) without specifying temporal directionality. Whether our metric for assembly reflects temporal assembly order (addition of species over time) and is the inverse of disassembly order (removal of species over time) remains a gap in this system.

Is there evidence for life history strategy shaping competence and commonness?

Building on our quantification of competence and commonness, we assembled life history data for the five amphibian species using reports from the literature (Johnson et al. 2012; Oliveira et al. 2017). Four life history characteristics that span the amphibian developmental trajectory had associated values published for all of the species: egg size (ovum diameter in mm), larval period (days to metamorphosis), adult body size (maximum adult length in mm; snout to vent for Anurans and total for Caudata), and lifespan (maximum age in years).

For each life history trait, we ran a general linear mixed model with the life history characteristic as the predictor variable and species competence as the response variable. Competence values for all host-parasite interactions were included in the analyses because we were interested in how a species' general competence (among multiple infection types) corresponded with its life history. Because multiple values were present for each amphibian (one competence value for each unique host-parasite interaction), we included amphibian species as a random effect in the model. We arcsin-transformed the competence values because they were proportional, and log-transformed larval period due to the breadth of values and their high right skew (i.e., most amphibians had larval periods less than 200 days, with the exception of American bullfrogs, who take multiple years [>500 days] to reach maturity). American bullfrogs were a clear outlier for their larval period, and also represent the only amphibian in our study that is non-native. Given that competence of a host-parasite interaction is shaped by the evolutionary history of that interaction, non-native species may have competence values that deviate from expectations. We therefore ran our life history—competence analyses with non-native bullfrogs included and excluded to see how they conformed to patterns among native species.

We ran similar general linear models between the four life history characteristics (predictors) and each amphibian species' spatiotemporal commonness (response). As with competence, spatiotemporal commonness was arcsin-transformed because the values span 0 to 1. If life history shapes both competence and commonness, life history could mediate an indirect (and important) connection between competence and assembly order. This connection is a central tenet of diversity-disease theory, and we tested it with a small and simple model. For each parasite, we ran a Pearson's product-moment correlation between amphibian assembly order and competence.

Results

How well are field infections explained by species-level competence estimates?

We assessed how well three laboratory-based estimates of a species' capacity to support infection aligned with natural levels of infection observed in the field (averaged among sites across the landscape). Our lab-based estimates spanned low- to high-information, and their nested structure allowed a comparison of which pieces of epidemiologically relevant information led to highest performance. The highest information metric, dose-integrated competence, best explained infection patterns (Fig. 1). Dose-integrated competence was positively, significantly ($P < 0.05$), and tightly ($R^2 > 0.80$) associated with mean infection levels for three of the four parasites (Table 1). Conversely, the low and moderate information metrics, initial susceptibility and dose-integrated susceptibility, were associated with infection for only one (*Alaria marcinae*) of the four parasites and did not themselves differ in performance (Table 1). Dose-integrated competence incorporates variation in exposure by combining dose-dependent susceptibility and dose-dependent mortality (Stewart Merrill et al. 2022). Its high performance, relative the other metrics, suggests that pre-transmission mortality meaningfully shapes infections in the field and that average levels of infection from the field (across all sites and levels of exposure) can closely match competence if the competence metric itself contains variation in exposure. Mean infection levels for *Cephalogonimus* sp. were not associated with any of the laboratory-based estimates (all $P > 0.5$; Table 1). Notably, chorus frogs had substantially higher levels of infection than their dose-integrated competence estimates might suggest (Fig. 1B). This disparity might point to additional drivers of infection in the field, such as host behavior or parasite choice, that extend beyond the transmission potential of the chorus frog-*Cephalogonimus* sp. interaction.

Does commonness underlie community assembly?

The five focal amphibians varied in their spatial occupancy and temporal reliability, both of which were positively associated (Fig. 2). Chorus frogs and California newts (assembly orders 1 and 2, respectively; Table 2) occurred in the majority of sampled ponds (high spatial occupancy) and were observed regularly over time (high temporal reliability). On the opposite end of the spectrum were the less common species, rough-skinned newts and American bullfrogs (assembly orders 4 and 5, respectively; Table 2), which tended to occur in fewer than 50% of ponds, with lower temporal

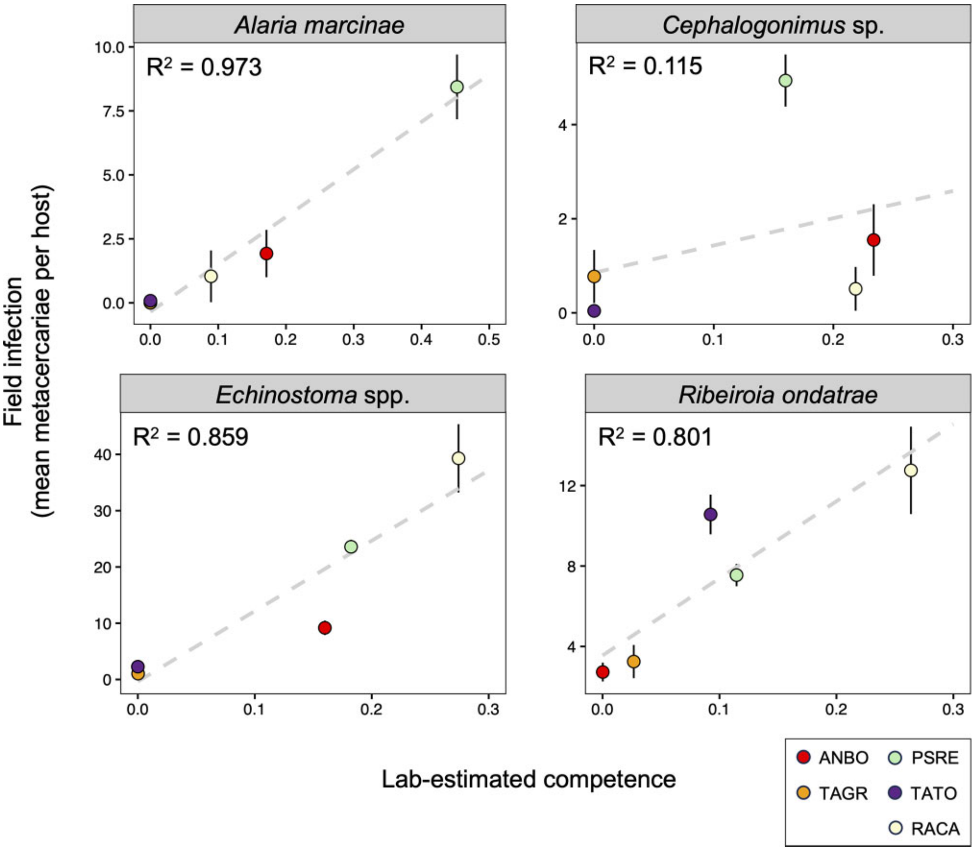

Fig. 1 *Field infections are well-explained by the competence of a given host-parasite interaction*. For each parasite taxon, we evaluated the relationship between dose-integrated competence measured in the lab and natural levels of infection observed in the field. Field infections for each host species were averaged over multiple years and multiple sites with known variation in levels of exposure, and our competence measures incorporated a range of exposure doses designed to capture this natural variation. We found remarkable correspondence between competence and infection for three of the four parasites ($R^2 > 0.8$) suggesting that the competence of a given host-parasite interaction can strongly shape infection outcomes. Deviation from this pattern, as observed for *Cephalogonimus* sp., might indicate the presence of additional epidemiological forces that can overwhelm competence (e.g., parasite choice). Amphibian code names presented in the legend are as follows: ANBO (*Anaxyrus boreas*, or western toad); PSRE (*Pseudacris regilla*, or Pacific chorus frog); RACA (*Rana catesebeiana*, or American bullfrog); TAGR (*Taricha granulosa*, or rough-skinned newt); TATO (*Taricha torosa*, or California newt).

Table 1 Compared to lower-information competence metrics, dose-integrated competence best predicts natural infection patterns in the field.

	Initial susceptibility		**Dose-integrated susceptibility**		**Dose-integrated competence**	
Parasite	*P*	R^2	*P*	R^2	*P*	R^2
Alaria marcinae	**0.005**	**0.950**	**0.008**	**0.933**	**0.002**	**0.973**
Cephalogonimus sp.	0.653	0.076	0.599	0.103	0.576	0.115
Echinostoma spp.	0.636	0.084	0.172	0.515	**0.023**	**0.859**
Ribeiroia ondatrae	0.756	0.037	0.931	0.003	**0.040**	**0.801**

This high-information metric (combining host susceptibility to infection and pre-transmission mortality from infection across a range of realistic doses) generally outperformed the lower-information metrics, initial susceptibility and dose-integrated susceptibility. Evidence for relative performance is indicated by the *P* and R^2 values (bolded to denote significance) for general linear models assessing each metric's correspondence with field infection data.

reliability. Western toads (assembly order 3) were the intermediate of the five species, although fell closer in spatiotemporal rarity to American bullfrogs and rough-skinned newts. For each species, we provide spatiotemporal trends (including abundance) from a subset of ponds as an example of the broader patterns (Fig. 2a–e). Ultimately, we detected a strong correlation between spatiotemporal commonness and assembly or-

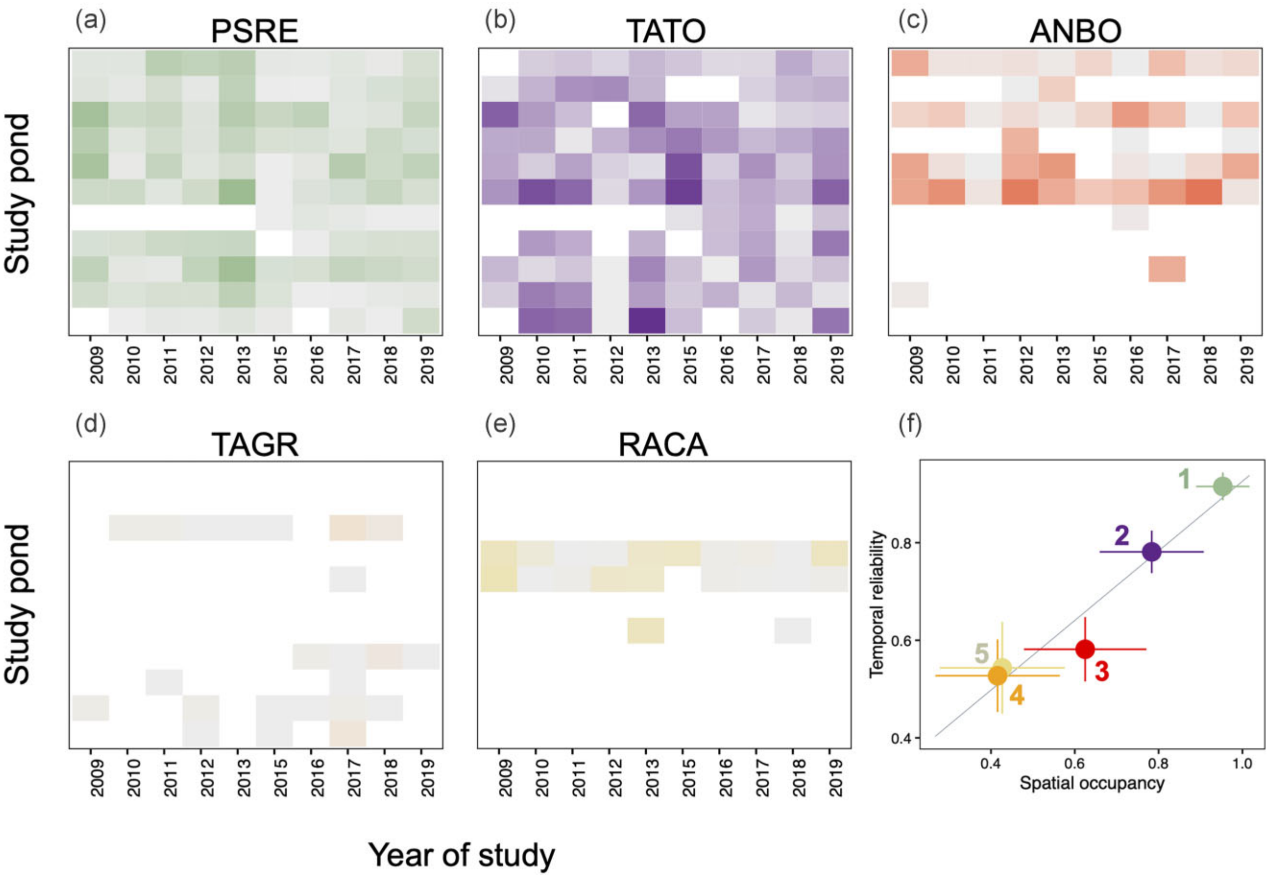

Fig. 2 *Basic demographic patterns of amphibians are closely linked with their community assembly order*. To capture fundamental differences in the demography of amphibians, we quantified their spatial occupancy (how widespread they are within suitable habitat) and temporal reliability (how consistently they occur within suitable habitat over time). Panels (a) through (e) are examples of these features for our five focal amphibians using data from a subset of ponds ($n = 11$) for which we had continuous, long-term sampling (10 years). In these panels, year of study (spanning 2009 to 2019, with the exception of 2014 where a drought and fully dried ponds limited sampling) is on the x-axis, and each row on the y-axis represents a single pond. An amphibian species' presence is indicated by filled cells, with increasing cell saturation representing increasing density of the species. Average spatial occupancy and temporal reliability across a broader set of sites and years is plotted in panel (f). These two properties are correlated, and their joint likelihood (product) directly corresponds with assembly order (assembly order estimates provided in Table 2; and indicated with inlaid numbers).

der ($r = 0.95$; $P = 0.015$; Fig. 2f), such that the most common species are also the first to assemble. This result points to the predictability of community assembly in our system and its ties to basic demographic and macroecological patterns.

Is there evidence for life history strategy shaping competence and commonness?

We found evidence that competence, but not commonness, follows classic predictions regarding the influence of life history. Competence declined with egg size (est $= -0.431$, std.err $= 0.107$, z $= -4.016$, $P < 0.001$) and lifespan (est $= -0.026$, std.err $= 0.010$, z $= -2.524$, $P = 0.012$), and declined marginally with adult body size (est $= -0.002$, std.err $= 0.001$, z $= -1.793$, $P = 0.073$). Collectively, these patterns suggest that amphibians with faster pace of life tend to be more competent. We observed no effect of larval period on competence (est $= 0.069$, std.err $= 0.217$, z $= 0.319$, $P = 0.750$), although this null result was driven by American bullfrogs, which had long larval periods relative the other species. Removal of American bullfrogs from our analyses resulted in a decline in competence with larval period (est $= -0.789$; $P = 0.006$) and increased statistical significance in the decline in competence with adult body size (est $= -0.19$; $P < 0.001$), but did not change the qualitative results of the other analyses (egg size [est $= -0.392$, $P < 0.001$]; lifespan [est $= -0.024$, $P = 0.009$]). In contrast with competence, commonness exhibited no significant associations with any of the life history characteristics (all $P > 0.1$; Supplementary Table S1). An illustrative example is that California newts are

Table 2 Assembly order from occupancy-richness associations.

Richness	PSRE	TATO	ANBO	TAGR	RACA
1	0.69	0.13	0.04	0	0.14
≤ 2	0.85	0.53	0.13	0.06	0.09
≤ 3	0.91	0.72	0.28	0.24	0.11
≤ 4	0.92	0.76	0.35	0.26	0.16
≤ 5	0.92	0.76	0.36	0.26	0.17
Order	1	2	3	4	5

We estimated each amphibian's assembly order by determining the proportion of ponds they occurred in for progressing levels of species richness. For instance, of those ponds with only one species present (richness = 1), the majority (69%) had chorus frogs (PSRE) present, indicating that chorus frogs are the dominant taxon in single-species communities. Extending to ponds that contain 2 or fewer species (richness ≤ 2), chorus frogs remain dominant (85%) with California newts (TATO) as the next-most dominant addition (occurring in 53% of ponds with 2 or fewer species). The stepwise addition of species as diversity increases allows a straightforward determination of assembly order. Rows in the table represent species richness levels, columns indicate amphibian species, and cells denote the proportion of communities a species occurs in. Shading helps illustrate how dominance of each species over increasing richness levels yields the assembly orders indicated in the final row. Amphibian code names are as follows: ANBO (*Anaxyrus boreas*, or western toad); PSRE (*Pseudacris regilla*, or Pacific chorus frog); RACA (*Rana catesebeiana*, or American bullfrog); TAGR (*Taricha granulosa*, or rough-skinned newt); and TATO (*Taricha torosa*, or California newt).

exceptionally common despite their relatively slower pace of life characteristics.

We found no evidence that life history mediates a connection between host competence for infection and host commonness within communities. Our analysis investigating a potential indirect association between competence and assembly order was simple (Pearson's correlation), as was the result. We observed no correlation between these properties for any of the four parasites (all $P > 0.2$), and the lack of association was often stark (Fig. 3). Hitherto, we had observed relationships between competence and pace of life. However, the amphibian demographic patterns that underlie assembly order did not correspond with life history characteristics, reducing the possibility of an indirect association.

A post-hoc analysis: reconciling the competence-assembly disassociation with evidence of dilution

Prior work in this system has observed general declines in the average competence of amphibian communities with increasing levels of species richness (Johnson et al. 2013; Johnson et al. 2024). Indeed, this relationship is thought to underlie disease dilution. So how can we reconcile that established pattern with the lack of an association between each species' assembly order and its competence?

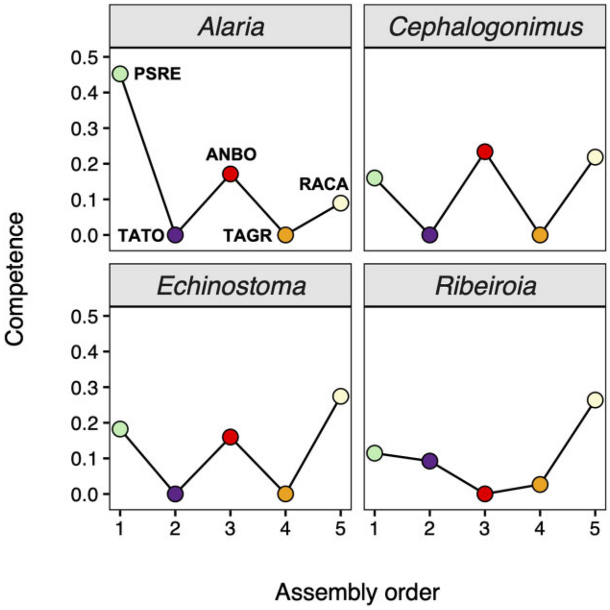

Fig. 3 *Competence is not associated with community assembly order.* While community competence (competence averaged among the species comprising a community) often declines with diversity, we found a striking lack of evidence for the idea that species' competence values (y-axis) decrease with assembly order (x-axis). In other words, increasing richness did not progressively add lower-competence species. Competence values are provided for each parasite species (indicated in panel labels), with each point denoting an amphibian host. Amphibian points are labeled in the first panel (for the parasite *Alaria*) and remain consistent in their assembly order across panels. Amphibian code names are as follows: ANBO: *Anaxyrus boreas*, or Western toad; PSRE: *Pseudacris regilla*, or Pacific chorus frog; RACA: *Rana catesebeiana*, or American bullfrog; TAGR: *Taricha granulosa*, or rough-skinned newt; TATO: *Taricha torosa*, or California newt.

Investigating the relationship between each amphibian's assembly order and its competence (Fig. 3), it is clear that chorus frogs (PSRE), which dominate single-species communities, tend to have relatively high levels of competence for all four parasites. Conversely, California newts (TATO), which join chorus frogs in two species communities, have much lower (and at times zero) competence for three of the four parasites. Consequently, a community consisting of both chorus frogs and California newts (richness = 2) will always have lower mean competence than a community of just chorus frogs (richness = 1). Extending this example to higher richness levels, we note that whenever a new species is added to a community (increasing richness by one), as long as the competence value of the newly added species is lower than the mean competence of the prior richness composition, then the mean competence of the community will decline. Indeed, we see just this effect. Lower-richness communities tend to have higher mean competence than higher-richness communities

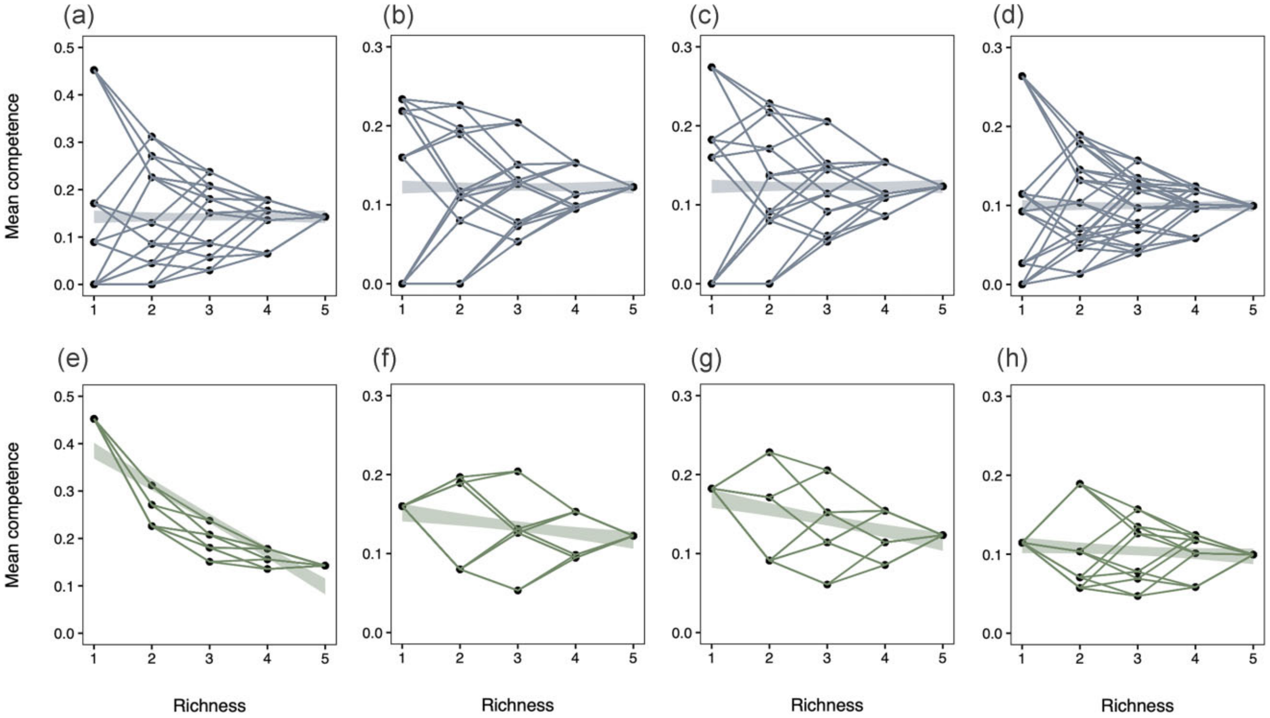

Fig. 4 *The commonness and relatively high competence of chorus frogs may drive negative relationships between species richness and community competence.* We simulated all possible permutations of community assembly order and resulting relationships between species richness and community competence (mean competence across species in a community) for the four parasites (a/e: *Alaria marcinae*; b/f: *Cephalogonimus* sp.; c/g: *Echinostoma* sp.; d/h: *Ribeiroia ondatrae*). For all possible permutations and assembly pathways (panels a through d), increases in community competence with richness are balanced against decreases in community competence with richness (as expected). However, for those permutations and pathways where chorus frogs are the first to assemble (panels e through h), community competence exhibits a general decline with species richness, regardless of the assembly order of the other community members. We note that the slope of the decline varies based on the competence of chorus frogs relative to other species, declining most steeply when chorus frogs have substantially higher values (e.g., *Alaria marcinae* in panel e).

because chorus frogs anchor the intercept at an initially high value (Supplementary Fig. S1). This observation led us to a post-hoc hypothesis. Perhaps assembly order is not the critical factor driving negative relationships between diversity and community competence; rather, this relationship may be driven by a particular species. Given the commonness and high competence of chorus frogs, we asked whether chorus frogs generate the negative relationship between amphibian species richness and mean community competence.

To address this question, we simulated all possible community compositions of the five host species across the five richness levels (120 possible compositions), and for each composition, we calculated average competence. These variable species compositions provided multiple pathways through which richness could shape mean competence. We first evaluated the relationship between richness and mean competence for this complete set of pathways (Fig. 4a–4d; representing all community compositions), then evaluated this relationship for only those pathways where chorus frogs are the first to assemble (Fig. 4e–4h). The comparison of the two sets of simulations allowed us to evaluate whether chorus frog competence is sufficiently high that the addition of new species always results in declines in mean competence, regardless of assembly order.

We found good support for our post-hoc hypothesis. When considering all possible pathways between richness and competence, we observed an expected flat relationship (Fig. 4a–d). In cases where chorus frogs are the first to assemble, the pathways between richness and competence demonstrated an overall negative (albeit not always linear) pattern (Fig. 4e–h). The slope of the chorus-frog-driven relationship varied by parasite, highlighting the importance of this species' competence (relative the other members of the community) for shaping richness-competence relationships. Ultimately, these results tell us that there can be multiple pathways to dilution. Average competence of a community can generally decline with richness as long as a highly competent host is the first to assemble.

Discussion

By combining a high-resolution infection dataset with measures of competence and life history characteristics from five amphibians, we evaluated three assumptions embedded in the criteria for parasite dilution: (1) competence governs infection patterns across the landscape; (2) host species vary predictably in their community assembly patterns; and (3) life history mediates a negative association between assembly order and competence. We found strong support for the first two criteria. For the majority of host-parasite interactions, amphibian infection patterns were tightly aligned with expectations stemming from laboratory measures of competence. As our measure of transmission potential accounted for more ecologically relevant factors (host susceptibility, parasite dose, and pre-transmission mortality), its predictive power increased. Amphibian hosts also possessed assembly orders that corresponded closely with their spatial and temporal distributions, suggesting that commonness across the landscape underlies commonness in communities. While we observed the expected associations between life history characteristics and competence (where "faster" pace-of-life amphibians tended to have higher competence), there was no such association between life history and spatiotemporal commonness. This decoupling led to no relationship between competence and community assembly. While one of the species with the fastest pace of life, Pacific chorus frogs, was the most common, the relationship between competence and assembly broke down with California newts, who had among the lowest competence values for 3 of the 4 parasites but were only second to assemble. By simulating all possible permutations of assembly, we found that average competence of a community could still decline with richness as long as the most common host (first to assemble) is of relatively high competence. Our results therefore relax the third assumption; when anchored by a widespread amplifier, community patterns of competence can possess multiple pathways to parasite dilution.

For three of the four parasites, our high-information competence estimate well explained natural patterns of infection from the field. This estimate—dose-integrated competence—incorporated two pieces of information that have the potential to critically shape natural infections (Stewart Merrill et al. 2022; Johnson et al. 2024). First, a range of experimental doses captures the variety of exposure regimes that hosts might find themselves in, as well as any non-linear sensitivity in their responses to exposure. Second, pre-transmission mortality accounts for the possibility that parasite pathology can kill heavily infected hosts, thereby constraining infection prevalence and intensity in natural systems (Wilber et al. 2020; Westphal 2024). That this high-information estimate generally outperformed lower-information metrics highlights the ecological importance of both dose-dependent responses to infection and pre-transmission mortality for shaping (and creating detection biases for) infections in the field. In practice, our result suggests that susceptibility assays that rely on a single exposure dose and short-term infection outcomes alone may not fully reflect a species' natural capacity to support infection. Interesting caveats from these trends arose for *A. marcinae* and *Cephalogonimus* sp. While dose-integrated competence was the strongest predictor of *A. marcinae* field infections, the lowest information metric (initial susceptibility) performed nearly as well. Prior experimental infections with *A. marcinae* demonstrated high host survival and minimal dose sensitivity (Stewart Merrill et al. 2022); it is therefore not surprising that the addition of this information did not meaningfully improve prediction of field infection for this less pathogenic trematode. Conversely, none of the competence estimates for *Cephalogonimus* predicted field infections, and chorus frog infections were notably higher than expected. In part, this pattern may reflect host and parasite behaviors not accounted for in laboratory-based competence estimates (e.g., Daly and Johnson 2011; Johnson et al. 2019). Infective cercariae may be more likely to select certain larvae of particular amphibian species, whereas amphibian larvae can also vary in their capacity to avoid or dislodge colonizing cercariae (Sears et al. 2015). In sum, species competence can profoundly shape parasite infections in natural systems—how we measure this property is critical for our assumptions regarding which hosts are sources versus sinks for parasites.

Across twenty host-parasite interactions, we observed strong correspondence between competence and host life history traits. Amphibians with faster pace-of-life characteristics (smaller eggs, shorter lifespans, and smaller body sizes) tended to have higher competence values than those with larger eggs, longer lives, and greater body sizes. The most prominent host on the "fast" end of the pace-of-life spectrum was the Pacific chorus frog, which has a reputation for acting as an indicator of infection (Johnson et al. 2024). On the "slow" end of the life history spectrum for native amphibian hosts was the California newt, who was non-competent for three of the four parasites and may have a strong capacity to dilute infection. These results support laboratory-based (Johnson et al. 2012; Huang et al. 2013) and observational evidence (Cappelli et al. 2020; Halliday et al. 2023) for a link between life history traits and infection, while elevating competence as a distinct property generating that link (Martin et al. 2016). This body of evidence has focused on a variety of life history traits, ranging from body size and offspring number in animals (Joseph et al. 2013; Han et al. 2015) to specific leaf area and growth rate in plants (Welsh et al. 2020; Halliday et al. 2023).

We found a complex, albeit interesting, association between duration of the amphibian larval period (i.e., time to metamorphosis) and competence. Longer amphibian developmental periods represent the "slower" end of the pace-of-life spectrum, and we expected that larval period would be negatively associated with competence. Yet, non-native bullfrogs had both the longest larval periods and exhibited the highest competence and infection levels for two of the four parasites. The relationship between larval period and competence was absent when this non-native species was included, but became negative (in line with expectations) when bullfrogs were excluded. Bullfrogs exhibit a multi-year larval period that exceeds that of the other amphibians by four to thirteen times; bullfrogs are thus an outlier in their developmental rate as much as they are in their ecological status. Competence is an outcome of host and parasite traits and is shaped by evolutionary pressures on both players and their interaction (Stewart Merrill and Johnson 2020). Whether life history predictions can be extended to host-parasite interactions that lack coevolutionary history is an important question for determining the role of non-native hosts, such as bullfrogs, in the community ecology of disease. Given their multiyear exposure to infective cercariae, bullfrogs could play important epidemiological roles in our study system, acting as reservoir hosts (maintaining larval trematodes across years), diluters (reducing transmission), or amplifiers (increasing transmission). To better understand these roles, future work must ascertain how bullfrog rates of exposure (during active trematode transmission) are balanced against rates of infection clearance (over the full larval period) to determine the net success of infective cercariae contacting this species.

Amphibian commonness over time, space, and across communities showed no associations with pace of life. The amphibian communities in our study exhibit a well-substantiated nested structure, where low-diversity communities represent reasonable subsets of higher-diversity communities (Johnson et al. 2019). This feature lends predictability to species occurrences, as well as efficiency in extracting their assembly orders (Johnson et al. 2013). As expected, we found that these assembly orders were closely related to each amphibian's commonness—the most widespread species through space and time were also the first to assemble. Thus, the demographic factors that control spatiotemporal occupancy may also shape dominance or rarity within communities (Brown 1984). When we evaluated this result in the context of dilution, regressing each species' commonness against four distinct life history characteristics, we observed null results. Moreover, some data points presented clear conflicts with predictions. For instance, California newts were exceptionally common across the landscape, but also occupied the slow end of the pace-of-life spectrum. It is therefore unlikely that the lack of associations stemmed from lack of statistical power. It is possible, however, that commonness is not the best measure of extirpation risk during environmental change and that disassembly order is not fully reflected by our assembly metric. Indeed, observations taken during an extreme drought demonstrated that California newts had among the most substantial declines in habitat occupancy (Moss et al. 2021)—a sensitivity that stands in stark contrast to their early assembly order and typical patterns of abundance. Meta-analyses are increasingly demonstrating that species losses, rather than diversity gradients per se, underlie dilution effects (Halliday et al. 2020; Mahon et al. 2024). Collectively, these and our results motivate efforts to establish robust measures of extinction vulnerability, and formalize connections (as well as disparities) between spatiotemporal patterns and temporal assembly and disassembly orders. Establishing such linkages will broaden our theoretical foundation for which community processes make dilution effects more likely.

Given inconsistent associations with life history, it was not surprising to find disjointed relationships between assembly order and competence. As richness increased progressively, the competence values of added species often vacillated from high to low in a non-linear pattern. This pattern deviates from the triad of associations between life history, competence, and assembly that are expected for dilution, and in broader evolutionary theory, contrasts with expectations regarding parasite adaptation to common hosts (Lively and Dybdahl 2000). At face value, this nonlinear relationship also appears to challenge established patterns of parasite dilution in this system (Johnson et al. 2013; Johnson et al. 2024). Through simulation, however, we reconciled this disparity. By exploring all community assembly permutations and their associated changes to competence, we observed that non-linearity in species' competence values can still produce overall declines in average community competence, as long the first species to assemble has a relatively high value. For *A. marcinae*, for example, chorus frog competence is over two times higher than that of other amphibians; when chorus frogs assemble first, community competence will always decline regardless of subsequent assembly order. This result is highly consistent with simulations from the Lyme disease system, where highly competent white-footed mice produce a strong anchoring effect on community competence (Ostfeld and LoGiudice 2003). Similarly, Johnson et al. (2019) observed that random amphibian assembly orders produced no change in infection with richness, but realistic assembly orders (where chorus frogs assemble first) resulted in negative richness-infection relationships. While we focused our simulations on the arithmetic mean of competence, we note that incorporating host relative abundance (to produce a weighted mean [Allan et al. 2009; Johnson et al. 2013]) would likely strengthen these results, given expected lower densities of added species. Hence, while a linear negative relationship between competence and assembly order increases the likelihood of dilution, such a strict association is not required for the phenomenon to occur.

Conclusion

We found empirical support for some, but not all, of the pathways to competence-based dilution in a multi-host, multi-parasite system. In foundational theory, the dilution effect proposed a triad of associations between life history, competence, and extirpation risk. The elegance of this triad stemmed from how it connected growing ideas on the life history drivers of immune defense with more classic theory on how pace of life constrains population dynamics and vulnerability. Logistical challenges in quantifying these parameters have led to a slowly developing empirical foundation for connections between all three factors, which we have aimed to build toward in our study. While we found good evidence that competence follows life history expectations and can be a strong determinant of infection patterns, how species competence values correspond with assembly order and underlying demographic patterns was somewhat idiosyncratic. Importantly, we found that average competence of the community could still decline in spite of this idiosyncrasy, given dominance of a highly competent host. Careful evaluations of the assumptions that underlie dilution criteria, as well as their relative importance for generating negative diversity-disease relationships, will clarify predictions for where and when this phenomenon is most likely. As we extend such approaches to broader assemblages of parasites, as well as more speciose host communities, we will gain valuable insight into the generality of competence-based disease dilution.

Author contributions

The project was conceptualized by TESM and PTJJ. TESM designed and ran the analyses and wrote the first draft of the manuscript, with input from PTJJ. Both authors provided revisions to subsequent drafts.

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Supplementary data

Supplementary Data available at *ICB* online.

Conflict of interest

The authors declare no conflicts of interest.

Data availability

Data and code supporting analyses will be publicly available at FigShare upon publication (doi: 10.6084/m9.figshare.29172116).

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