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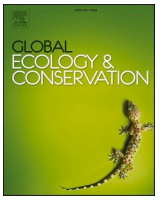

Original research article

Reproductive habitat mismatch influences chytrid infection dynamics in a tropical amphibian community☆

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ABSTRACT

Batrachochytrium dendrobatidis (*Bd*) has been decimating amphibian populations globally; previous work indicates that infection risk increases with moisture and thermal mismatch from a host's optimum. We hypothesized that, in addition to these abiotic influences, mismatch of hosts from their reproductive habitat heightens infection risk via exposure and/or susceptibility mechanisms. We evaluated this "reproductive habitat mismatch hypothesis" by quantifying the interplay of host breeding mode, habitat, and rainfall on *Bd* infection dynamics using two years of frog survey data—including swab data for 3427 captures representing 44 species—from Brazil's Atlantic Forest. We modeled infection prevalence, infection intensity, and the number of frogs captured as a function of rainfall, reproductive mode (aquatic or terrestrial), and habitat (aquatic or terrestrial) using hierarchical models. High rainfall was associated with increases in infection prevalence and infection intensity; however, these increases were particularly apparent for species in habitats that were mismatched from the species' reproductive habitat. Tropical regions experiencing increases in precipitation will likely see higher *Bd* risk, and our results indicate that such increases in rainfall will be particularly problematic for species that are forced to move from their reproductive habitats by factors such as habitat loss or thermal stress.

☆ Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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1. Introduction

Climate change is altering precipitation patterns such that droughts and abnormally wet periods are increasing in frequency and severity in many regions around the world (Dai, 2013; Trenberth et al., 2014). While such shifts are occurring globally, tropical regions—which may experience limited seasonal variation in temperature but extreme seasonal variation in precipitation—are experiencing especially dramatic shifts in the volume, intensity, and timing of precipitation (Neelin et al., 2006; Feng et al., 2013). Altered precipitation patterns influence the physiology, behavior, and distribution of organisms (Albright et al., 2010; Scheffers et al., 2016; Maxwell et al., 2019), potentially leading to altered species interactions and infectious disease dynamics within communities (Gallana et al., 2013; Stevenson et al., 2015; Carlson et al., 2022; Gilbert et al., 2022). Thus, wildlife communities in tropical biomes are increasingly facing the synergistic stressors of altered precipitation patterns and shifting disease dynamics (Hof et al., 2011; Côté et al., 2016; Cohen et al., 2019).

Amphibians are profoundly affected by precipitation given their reliance on moisture for basic physiological processes like respiration and reproduction. Populations around the globe have been collapsing due to chytridiomycosis caused by the amphibian chytrid fungus *Batrachochytrium dendrobatidis*, or *Bd* (Lips et al., 2006; Scheele et al., 2019; Luedtke et al., 2023). *Bd* demonstrates a high degree of host generalism; it has been detected in > 500 amphibian species and on all continents where amphibians occur, highlighting a need to synthesize knowledge of *Bd*'s effects across species while also understanding among-species idiosyncrasies (Scheele et al., 2019; Olson et al., 2013). Moreover, *Bd* is a waterborne fungus with infection dynamics that are strongly influenced by environmental variables such as temperature and especially moisture, since the motile zoospores (one of the life stages of *Bd*) perish if desiccated (Johnson and Speare, 2005). Thus, understanding risk factors for *Bd*-related population declines, general patterns of disease dynamics at community scales, and how those dynamics may be changed by altered precipitation patterns will be key to successful amphibian conservation efforts. A better understanding of these dynamics will be particularly important for tropical regions, which are amphibian biodiversity hotspots and often contain species that have not been assessed for susceptibility to *Bd*, including undescribed species (Catenazzi et al., 2011, 2012).

Moisture and temperature influence *Bd* infection patterns because microclimatic conditions impact the mobility and persistence of zoospores as well as the growth and reproduction of zoosporangia (Johnson and Speare, 2005). Since zoospores desiccate in dry environments, high precipitation and moisture are generally associated with increased infection prevalence because zoospores can persist and move through the environment for longer periods of time. This trend is apparent over broad geographies, such that wetter regions show higher *Bd* infection prevalence than dry regions (Liu et al., 2013; Cohen et al., 2016), and locally, such that aquatic habitats pose higher infection risk than nearby terrestrial areas (Brem and Lips, 2008). Furthermore, these trends are apparent seasonally such that *Bd* prevalence tends to be higher in wet seasons compared to dry seasons in many locations (Kriger and Hero, 2007; Longo et al., 2010). *Bd* can grow in a broad range of temperatures (4–25 °C; Kilpatrick et al., 2010), but the greatest susceptibilities for a given host species tend to occur when temperatures deviate from the host species' thermal optimum ("thermal mismatch hypothesis"; Cohen et al., 2017, Cohen et al., 2020). Thus, the general expectation is that *Bd* infection prevalence and intensity should be higher under wetter conditions and when temperatures deviate from the hosts' thermal optimum, but among-species variation and context dependence is likely (Tobler and Schmidt, 2010; Ellison et al., 2015; West et al., 2020).

In addition to greater *Bd* risk as temperatures deviate from a hosts' optimum, it is also possible that hosts are more susceptible to *Bd*—or more sensitive to thermal and/or hygric conditions—when they occur outside their reproductive habitat, an idea we henceforth refer to as the "reproductive habitat mismatch hypothesis" (Fig. 1; but see Leach et al., 2016, Huang et al., 2021). We use "reproductive

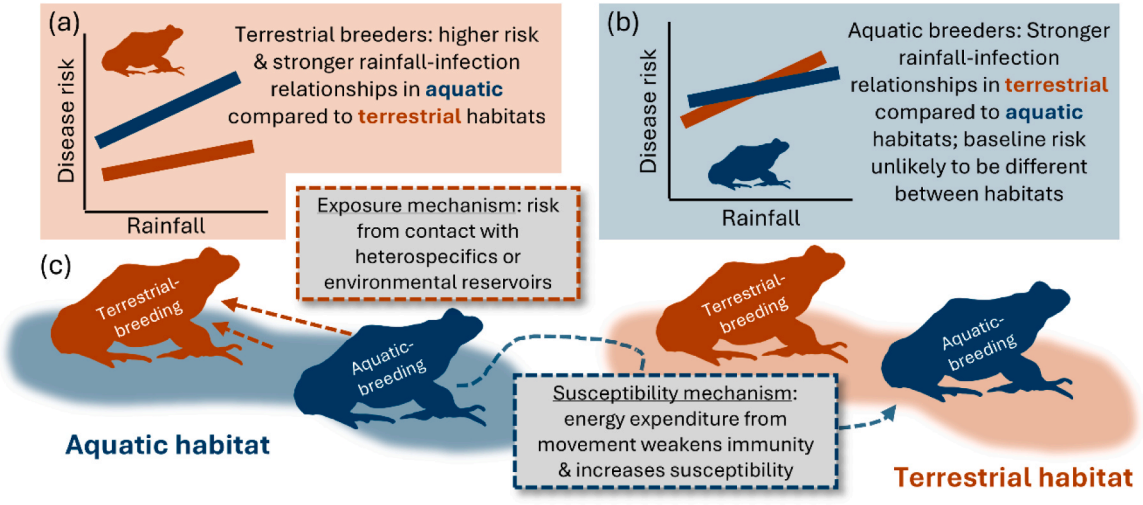

Fig. 1. (a-b) The reproductive habitat mismatch hypothesis suggests that hosts are more susceptible to infection and environmental conditions that mediate infection when they occur away from their reproductive habitats. (c) Brief description of the possible mechanisms underpinning the reproductive habitat mismatch hypothesis.

habitat" to refer to whether a species reproduces in aquatic or terrestrial environments, which is a simplification of the highly diversified reproductive modes and habitat preferences of tropical amphibians (Supplemental Information; Haddad and Prado, 2005). The reproductive habitat mismatch hypothesis may operate through exposure and susceptibility mechanisms, which are not mutually exclusive (Sweeny and Albery, 2022), and focuses on the interplay of species reproductive mode (aquatic versus terrestrial; we also use "breeding mode" as a synonym), rainfall, and habitat. Regarding exposure mechanisms, species that move to new or different habitats may experience changes in pathogen exposure, perhaps by coming into contact with other host species or environmental reservoirs they typically would not encounter (Harman and Kim, 2024; Dougherty et al., 2018). Regarding susceptibility mechanisms, the act of moving to a different habitat may incur large energy expenditures which weaken a host's immunity or acquired resistance (Neuman-Lee et al., 2015; Brown et al., 2015; Wu and Seebacher, 2022). For terrestrial-breeding frogs, we predict higher infection prevalence and loads—and stronger infection–rainfall relationships—in aquatic habitats compared to terrestrial habitats (Fig. 1a), likely from increased environmental *Bd* exposure and/or spillover from aquatic-breeding amphibian species, which may show higher rates of *Bd* prevalence through longer-term exposure (Longo et al., 2010; Smith et al., 2009; Mesquita et al., 2017; Becker et al., 2019; Moura-Campos et al., 2021). For aquatic-breeding species, we expect that under most conditions, infection prevalence and load will *not* be higher in terrestrial habitats (since *Bd* zoospores desiccate in dry conditions) compared to aquatic habitats, except under periods of high rainfall (Fig. 1b). The combination of weakened immunity (from energy expenditures associated with movement) and rainfall (facilitating survival of zoospores) may allow *Bd* infections in aquatic-breeding species to spike under these circumstances, resulting in stronger infection–rainfall relationships in terrestrial habitats compared to aquatic habitats for these species (Fig. 1).

Our objective is to evaluate the reproductive habitat mismatch hypothesis by exploring how interactions among breeding mode, habitat, and precipitation relate to *Bd* infection prevalence and intensity in a hyper-diverse tropical amphibian community. As described above, the reproductive habitat mismatch hypothesis predicts higher infection prevalence and intensity (and stronger infection–rainfall relationships) for a species when it occurs in habitats mismatched with its breeding mode, but the fact that aquatic habitats may act as environmental reservoirs for *Bd* means that this mismatch is likely asymmetrical and more apparent for terrestrial-breeding species (Fig. 1). Apart from the predictions of the reproductive habitat mismatch hypothesis, we predict generally higher *Bd* prevalence in aquatic-breeding species (compared to terrestrial breeders) because these species are exposed to *Bd* for larger portions of their life cycles (Smith et al., 2009). However, we predict higher infection loads for terrestrial-breeding species because these species may be more naïve and have fewer tolerance mechanisms to prevent the buildup of zoospores compared to aquatic-breeding species (Grogan et al., 2023). Our final objective was to assess whether species shift their habitat use depending on precipitation conditions, especially whether terrestrial-breeding species are more likely to appear in aquatic habitats during drier conditions. We address these objectives with two years of *Bd* and demographic data from a diverse anuran community (44 species) sampled from aquatic and terrestrial habitats in the Atlantic Forest of southeastern Brazil.

2. Methods

2.1. Field sampling

We conducted visual encounter surveys for adult frogs in Parque Estadual da Serra do Mar–Núcleo Santa Virgínia in Brazil's Atlantic Forest from January 2020 to January 2023. We sampled elevations from 901 to 1012 m on the Serra do Mar plateau; dominant land cover consists of moist tropical montane forest. The park harbors over 50 amphibian species, including both terrestrial- and aquatic-breeding frogs (Haddad et al., 2013). We classified aquatic-breeding species as those with an aquatic larval stage developing in water (regardless of whether the water body was lentic versus lotic, or ephemeral versus permanent; Haddad and Prado, 2005). We classified terrestrial-breeding species as those with direct development or with indirect development of endotrophic larvae that are associated with terrestrial environments (i.e., *Adenomera*). Our field sites do not harbor direct-developing species that breed in aquatic environments like Amazonian *Pipa* or a few species of Neotropical stream-associated *Craugastor*. We established 10 sites and surveyed both an aquatic (stream) transect and a terrestrial transect within each (i.e., for 20 core transects). Nearest-neighbor distances between sites were 1.6 ± 2.3 km (mean $\pm$ standard deviation); the area of the minimum convex polygon containing all sites was 19.1 km^2. Within sites, terrestrial transects paralleled aquatic transects but followed nearby hill crests (within at least 50 m of the aquatic transect). Each transect was 100 m long. The aquatic transects were centered on the middle of the stream and stretched 1 m up either bank. The terrestrial transects were surveyed out to 1 m on both sides of the centerline. We conducted sampling on three consecutive dates every two months for 12 of the 20 core transects; due to constraints on personnel and supplies (including disruptions from the COVID-19 pandemic), we visited the remaining 8 core transects on one date every two months. In addition, we sampled five auxiliary aquatic transects (ponds) and one auxiliary terrestrial transect, which we visited as logistics allowed. Thus, there were a total of 26 transects (11 terrestrial, 15 aquatic).

Because the anuran community contains both diurnal and nocturnal species, we conducted surveys during the day and at night to sample the highest anuran diversity possible. We sampled four transects per date; one diurnal, and then the same one again at night plus four other nocturnal-only transects. This resulted in 14 transects with nocturnal and diurnal surveys, 11 transects with only nocturnal surveys, and 1 transect with only diurnal surveys. Two observers surveyed transects for approximately 75 minutes per visit. The observers walked the transects slowly, listening for vocalizations and looking for frogs in the leaf litter, overhanging vegetation, and water. The observers—wearing disposable nitrile gloves—captured adult frogs by hand, rinsed them in distilled water, and swabbed them with a sterile rayon swab (Medical Wire & Equipment 113) using standard protocols (Hyatt et al., 2007). Swabs were stored on ice in sterile 1.5 mL tubes until they were transported to a freezer and stored at -20 °C. We capped the number of swabs collected per species per transect per visit to ten to prioritize procurement of data across multiple species.

2.2. Laboratory work: qPCR

We used GMax Mini Genomic DNA Kits (IBI Scientific) to extract *Bd* DNA from swabs using the standard protocol but extended the incubation period after addition of proteinase K to ~12 hours. Sample extraction date was randomized to minimize biases based on sample collection date, and we included an extraction control (sterile deionized water) with each set of samples. The final elution volume was 100 μL.

Our qPCR assay used *Bd*-specific primers (Boyle et al., 2004) and plasmid *Bd* standards (Pisces Molecular, CO) diluted from 2.6×10^6 to 2.6×10^0 *Bd* ITS rRNA gene copies to quantify *Bd* loads of skin swabs. We also included TaqMan Exogenous Internal Positive Control reagents (IPCs) to validate the qPCR reaction; in the rare cases (0.35 % of samples) for which IPCs did not amplify, we reran samples (Hyatt et al., 2007). Each 25 μL reaction consisted of 12.5 μL TaqMan™ Fast Advanced Master Mix (ThermoFisher Scientific), 1.13 μL of 20 μM ITS1–3 primer (ThermoFisher Scientific), 1.13 μL of 20 μM 5.8S Chytr primer (ThermoFisher Scientific), 1.20 μL of μM Chytr MGB2 probe (ThermoFisher Scientific), 1 μL of 4x BSA (Invitrogen), 0.83 μL of 10x Exo-IPC probe mix (ThermoFisher Scientific), 0.17 μL of Exo-IPC DNA (ThermoFisher Scientific), 2.05 μL of UltraPure water, and 5 μL of template DNA or *Bd* standard. The reactions were run using a QuantStudio™ 3 with the following program settings: 50ºC for 2 min, 95ºC for 10 min, then 50 cycles of 95ºC for 15 sec and 62ºC for 1 min. We included a negative control well (UltraPure water) and a 7-fold dilution series of our plasmid *Bd* standards in each qPCR run. We ran samples in singlicate; while qPCR amplification can be stochastic at low template quantities, we made the decision to prioritize analyzing swabs from as many captures as possible over conducting multiple qPCR runs per swab, which would limit our ability to sample as extensively (Kriger et al., 2006; Ebentier et al., 2013). We calculated whole-swab *Bd* load (*Bd* zoospore ITS gene copies) by multiplying detected *Bd* DNA copies by 20 to account for the proportion of the full extraction that was aliquoted for qPCR, and natural-log transformed these values prior to analysis. We reran any samples for which the IPC did not amplify (0.35 % of samples), and if they failed to amplify a second time, we diluted the samples 1:10 with nuclease-free water and reran them (we accounted for this dilution factor when calculating whole-swab *Bd* load). We did not detect *Bd* DNA on any extraction or PCR negative controls.

2.3. Rainfall data

We downloaded daily rainfall data from the São Luiz do Paraitinga weather station, located ~20 km (12.4 miles) from the study area. Daily rainfall represents accumulation (mm) between 7 am of the previous day and 7 am of the day considered, as measured with a rain gauge. Since *Bd* zoospores take roughly one week to mature into zoosporangia (Woodhams et al., 2008), we expected rainfall to exhibit a lagged effect such that cumulative rainfall over the previous week to several weeks (rather than daily rainfall) would correlate with infection prevalence and intensity. To validate this expectation and guide selection of temporal scales over which to assess the influence of rainfall on infection dynamics, we computed Pearson's correlation between infection data (both binarized infection presence data, as well as infection intensity for infected individuals) and cumulative rainfall over the previous 0–366 days, by intervals of two days (Figure S1). For infection presence, the correlation with cumulative rainfall rapidly increased within two weeks before reaching a peak at 8.8 weeks (Figure S1); for infection intensity, correlations were weaker but spiked more quickly, reaching a peak for cumulative rainfall over the previous six days (Figure S1). Therefore, we proceeded by evaluating two temporal scales: cumulative rainfall over (1) the previous week to characterize short-term hygric conditions and (2) the previous 10 weeks to characterize longer-term, seasonal hygric conditions.

2.4. Data analysis

We fit generalized linear mixed-effects models to evaluate the effects of rainfall, habitat, and host breeding mode on infection prevalence, infection intensity, and the number of frogs captured. We evaluated separate models for infection prevalence, infection intensity, and the number of frogs captured, but all models shared a covariate and random-effects structure (Eq. 2). A simulation revealed that our approach with separate regressions provided unbiased inference for infection prevalence and infection intensity while avoiding interpretation challenges associated with hurdle-gamma models (which estimate the probability of an observation being a zero—or probability of a non-infection—hampering interpretability; Figure S2; Supporting Information). We also evaluated models that accounted for phylogenetic non-independence (i.e., closely related species are more likely to show similar infection patterns relative to distantly related species) and found similar results to the models presented in the main text (Figure S3-S4; Supporting Information), and thus elected to retain the models presented in the main text because models with species random effects nested within family showed identifiability issues and phylogenetic generalized linear models could not be applied to the full dataset since a number of our species are not represented in the latest frog phylogeny (Portik et al., 2023).

2.4.1. Infection prevalence

For infection prevalence, the response variable was y_i, the presence (1) or absence (0) of a *Bd* infection in swabbed capture i, which we modeled with a mixed-effects logistic regression:

$$y_i \sim \text{Bernoulli}(\psi_i) \quad (1)$$

where ψ_i is the probability of infection for individual i. We modeled infection probability as a function of habitat w_i (binary; 1 = aquatic, 0 = terrestrial), species reproductive mode m_i (binary; 1 = terrestrial-breeding, 0 = aquatic-breeding), and cumulative

rainfall x_i (z-standardized). The equation for infection probability is as follows:

$$\text{logit}(\psi_i) = \beta_{1SP[i]} + \beta_{2SP[i]} w_i + \beta_3 m_i + \beta_{4SP[i]} x_i + \beta_{5SP[i]} w_i x_i + \beta_6 w_i m_i + \beta_7 x_i m_i + \beta_8 w_i x_i m_i \quad (2)$$

Note that we modeled all possible two- and three-way interactions of the three predictor variables. Notice also that the intercept β_1, the effect of habitat β_2, the linear effect of cumulative rainfall β_4, and the interaction between habitat and cumulative rainfall β_5 vary by species SP as random effects. We fit two models with cumulative rainfall calculated over 1-week and 10-week lags from the date on which the frog was swabbed.

2.4.2. Infection intensity

We separately modeled infection intensity for only the *Bd* infected individuals (i.e., *Bd* infection intensity > 0) using a mixed-effects gamma regression. The response was *Bd* infection intensity, calculated as the natural log of the number of zoospore ITS gene copies detected for infected individuals. We used the same predictor variables and random-effects structure described in Eq. 2 to model variation in the expected value for infection intensity. As with infection prevalence, we fit two *Bd* infection intensity models, with rainfall calculated over 1-week and 10-week lags from the date on which the frog was swabbed.

2.4.3. Number of frogs captured

Finally, we modeled the number of frogs captured on each transect visit using a mixed-effects zero-inflated Poisson regression. The response was the count of frogs of each species captured during each survey; this includes counts of zero for surveys for which a given species was not detected. We modeled the zero-inflation component of the model with no covariates and a random intercept by species. We modeled the expected count component of the model as a function of the same covariates and random effect structure described in Eq. 2. As with the other models, we fit two count models, with rainfall calculated over 1-week and 10-week lags from the date on which the survey was conducted.

We fit all models in a Bayesian framework with the brms package (Bürkner, 2017) through R 4.3.0 (Core Team, 2023). We used weakly informative priors, e.g., Normal(0, 1) priors for covariate coefficients and Exponential(1) priors for variance parameters (McElreath, 2020). We ran four Markov Chain Monte Carlo (MCMC) chains, each for 6000 iterations, and discarded the initial 4000 iterations as warm-up, for a total of 8000 posterior samples. We assessed model convergence by visually inspecting parameter traceplots and checking that the convergence diagnostic $\widehat{R} < 1.1$ (Brooks and Gelman, 1998). We report posterior means and 95 % credible intervals of model estimates; we also report the probabilities that fitted values differed from each other by computing the empirical cumulative distribution function for the differences in estimates' posteriors and solving for 0 (i.e., no difference).

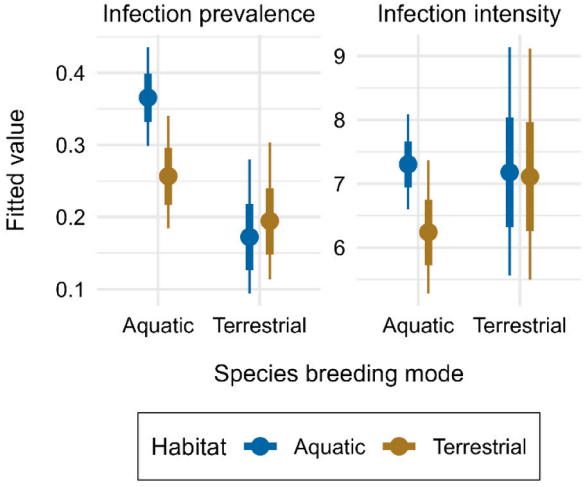

Fig. 2. Marginal effects of habitat and species reproductive mode; these estimates are from the mixed-effects logistic and gamma regressions for prevalence and intensity, respectively, with cumulative rainfall over the previous week (results from the 10-week cumulative rainfall model with rainfall were similar; Table S2). Note that infection prevalence is generally higher for aquatic-breeding species (especially in aquatic habitats) and that infection intensity is similar between aquatic- and terrestrial-breeding species, except that aquatic-breeding species have lower infection intensity in terrestrial habitats. Points are posterior means, while thick and thin bars are 68 % and 95 % credible intervals, respectively, of model predictions. The y-axis is infection probability for the left panel and the natural log of *Bd* infection intensity (zoospore ITS gene copies) for the right panel. See Table S2, which reports the mean and 95 % credible intervals for the relevant model parameters used to generate this marginal effects plot.

3. Results

3.1. Field surveys

We captured at least one frog on 501 (92.6 %) out of the 541 transect surveys completed over the course of two years. We had a total of 3859 frog captures (and obtained swab data for 3427 of these) representing 44 anuran species, of which 36 were aquatic breeders and 8 were terrestrial breeders (Table S1). Of the 1807 captures representing aquatic-breeding species, 1483 were captured in aquatic habitats and 324 were captured in terrestrial habitats. A *Bd* infection was detected in 496 (32.2 %) of the aquatic-breeding frogs swabbed; the median and maximum of observed loads were 7.2 and 16.4 ln(zoospore ITS gene copies), respectively. Of the 2052 captures representing terrestrial-breeding species, 757 were captured in aquatic habitats and 1295 were captured in terrestrial habitats. An infection was detected in 280 (14.8 %) of the terrestrial-breeding frogs swabbed; the median and maximum of observed loads were 4.9 and 18.2 ln(zoospore ITS gene copies), respectively. Across both breeding modes, the most common species was *Brachycephalus pitanga* (1657 captures; a terrestrial breeder), while the distant second-most common species was *Dendrophryniscus haddadi* (304 captures; an aquatic breeder). On the other end of the spectrum, five species were represented by a single capture, while 13 species were represented by five or fewer captures (Table S1).

3.2. Infection prevalence & intensity: species reproductive mode & habitat

Infection prevalence was higher for aquatic-breeding species than terrestrial-breeding species, a difference that was particularly apparent for aquatic habitats (Fig. 2). Holding rainfall at its average value, the model with rainfall over the previous week estimated infection prevalence for aquatic-breeding species to be 0.26 [95 % CI: 0.18, 0.34] for terrestrial habitats but 0.37 [95 % CI: 0.30, 0.44] for aquatic habitats (Fig. 2). For terrestrial-breeding species, infection prevalence was 0.19 [95 % CI: 0.11, 0.30] for terrestrial habitats and 0.17 [95 % CI: 0.09, 0.28] for aquatic habitats (Fig. 2). Infection prevalence for aquatic-breeding species was higher than infection prevalence for terrestrial-breeding species with 0.99 probability in aquatic habitats and 0.85 probability for terrestrial habitats (Fig. 2).

Infection intensity was lowest for aquatic-breeding species in terrestrial habitats; infection intensities for the other reproductive mode–habitat combinations were higher and of similar magnitude (Fig. 2). Holding rainfall at its average value, the model with rainfall over the previous week estimated infection intensity for aquatic-breeding species to be 6.24 [95 % CI: 5.29, 7.37] and 7.30 [95 % CI: 6.60, 8.09] zoospore ITS gene copies (ln scale) in terrestrial and aquatic habitats, respectively. Comparing between habitats for aquatic-breeding species, the infection intensity estimate for aquatic habitats was higher than the infection intensity estimate for terrestrial habitats with 0.98 probability (Fig. 2). For terrestrial-breeding species, the estimates were 7.11 [95 % CI: 5.50, 9.12] for terrestrial habitats and 7.18 [95 % CI: 5.56, 9.14] for aquatic habitats. Comparing between breeding modes, infection intensity

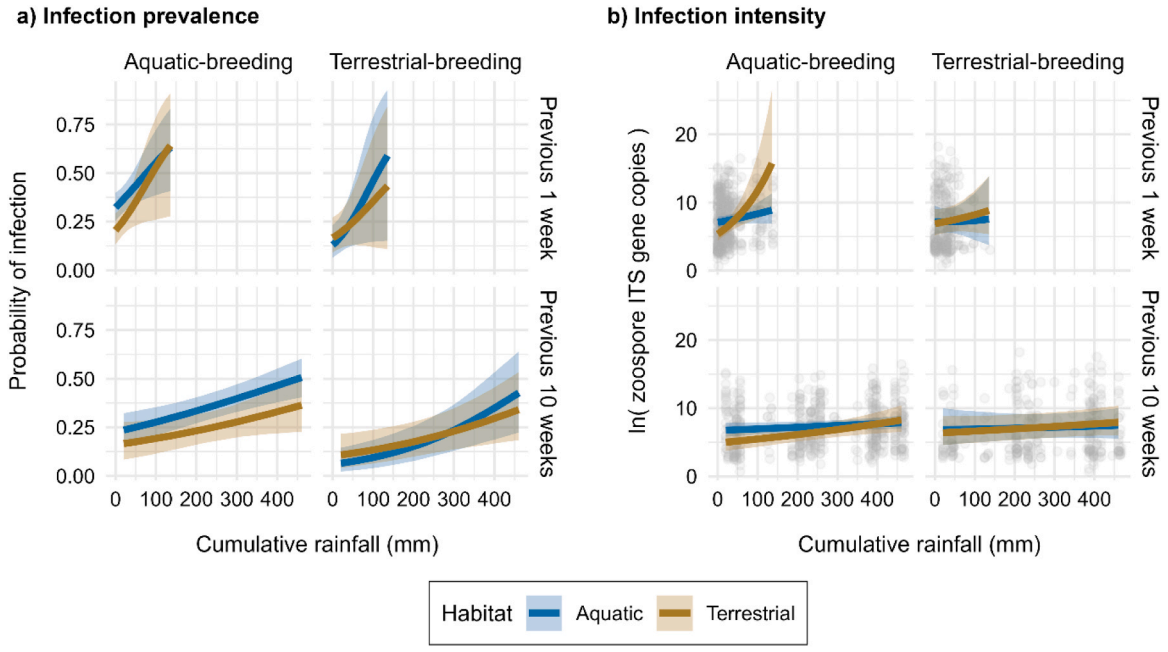

Fig. 3. Estimated community-level relationships between infection prevalence (a) and infection intensity (b) and cumulative rainfall over the preceding one (top row) or 10 (bottom row) weeks for aquatic- (left panels) and terrestrial-breeding (right panels) species for aquatic habitats (blue) and terrestrial habitats (brown). Lines are means and shaded areas are 95 % credible intervals of model predictions. Mixed-effects logistic (a) and gamma (b) regressions were used for analyses. Gray points in (b) are the observed data. See Table S2, which reports the mean and 95 % credible intervals for the relevant model parameters used to generate this marginal effects plot.

estimates were higher for terrestrial-breeding species relative to aquatic-breeding species with 0.80 probability in terrestrial habitats and 0.42 probability in aquatic habitats, respectively (Fig. 2).

3.3. Infection prevalence & intensity: rainfall

Infection prevalence increased with rainfall (Fig. 3a). The strength of this association was similar between the two models that included rain over the preceding 1 versus 10 weeks (Figure S5). The estimated linear effect of rainfall (logit scale) was 0.38 [95 % CI: 0.04, 0.74] at the 1-week scale but 0.36 [95 % CI: 0.01, 0.71] at the 10-week scale (Figure S5; Table S2). The combination of interaction terms (Figure S5) indicated that 1) infection prevalences were generally lower for terrestrial-breeding species than aquatic-breeding ones, 2) infection prevalences increased more rapidly with rainfall in terrestrial habitats for aquatic breeders, and 3) infection prevalences increased more rapidly with rainfall in aquatic habitats for terrestrial breeders (Fig. 3). This resulted in probabilities of mismatch effects of 0.74 for aquatic breeders and 0.81 for terrestrial breeders, respectively, for rainfall over the previous week (Figure S6). For rainfall over the previous 10 weeks, mismatch effects were unlikely for aquatic breeders (probability = 0.24) but were stronger relative to rainfall over the previous week for terrestrial breeders (probability = 0.90; Figure S6).

Infection intensity increased with rainfall (Fig. 3b). As with infection prevalence, this relationship was slightly stronger for cumulative rainfall over the previous one week versus the previous 10 weeks (Figure S5). The estimated linear effect of rainfall (ln scale) was 0.11 [95 % CI: 0.02, 0.19] for the 1-week scale but 0.08 [95 % CI: −0.01, 0.17] for the 10-week scale (Figure S5; Table S2). The combination of interaction terms (Figure S5) indicated that relationships between infection intensity and rainfall were stronger in terrestrial habitats than aquatic habitats, particularly for aquatic-breeding species. This resulted in a probability of a mismatch effect for rainfall over the previous week of 0.98 for aquatic breeders but only 0.30 for terrestrial breeders (Fig. 3, Figure S6). These interactions were more apparent for the model with cumulative rainfall over the previous week compared to the previous 10 weeks (Fig. 3, Figure S5, Figure S6).

3.4. Infection prevalence & intensity: species-level results

Results for individual species paralleled the community-level results (Fig. 4). For both infection prevalence and infection intensity, a greater share of among-species variation was attributable to species-level variation in the intercept (indicating considerable among-species variation in baseline infection prevalence and intensity) than among-species variation in the coefficients for rainfall, habitat, or their interactions (Table S2). For example, for infection prevalence, the standard deviation among species-level intercepts was 0.60 [95 % CI: 0.37, 0.89], while the standard deviation among species-level rainfall coefficients was 0.26 [95 % CI: 0.02, 0.56]. The species with highest baseline infection prevalence (i.e., with rainfall held at its average value) was for *Phrynomedusa dryade* (an aquatic breeder) in aquatic habitats, estimated to be 0.62 [95 % CI: 0.43, 0.80]; the species with the lowest baseline infection prevalence was *Brachycephalus pitanga* (a terrestrial breeder), estimated to be 0.10 [95 % CI: 0.07, 0.13] in aquatic habitats and 0.12 [95 % CI: 0.10, 0.14] in terrestrial habitats. Finally, relationships between rainfall and infection metrics tended to be stronger for habitats that were

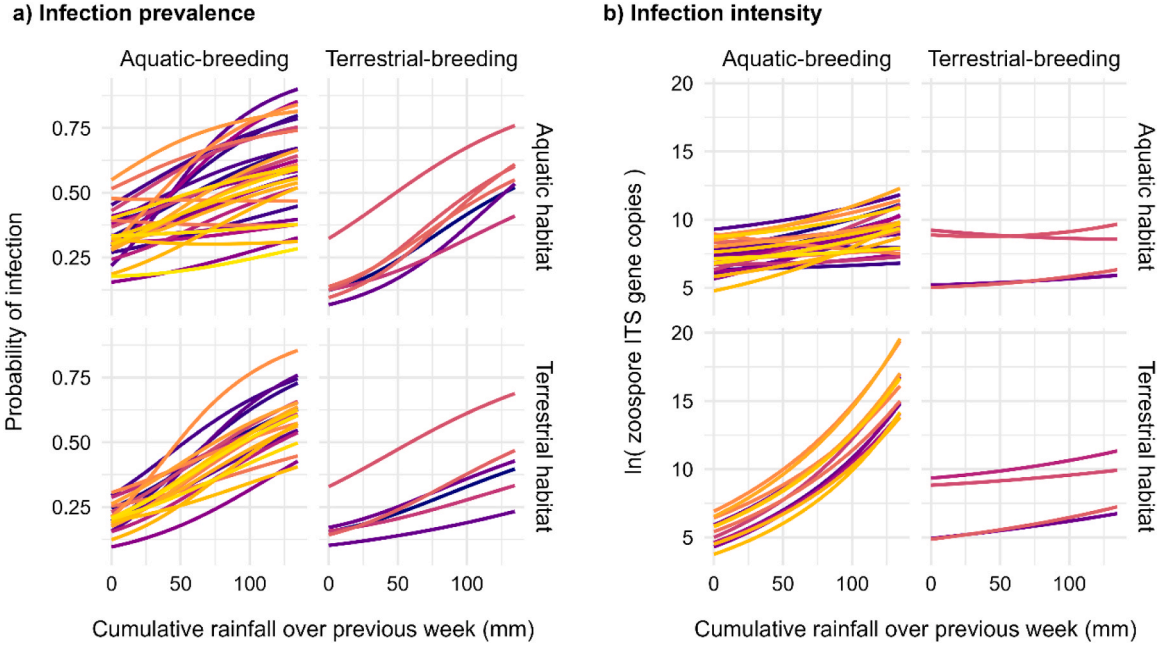

Fig. 4. Species-level relationships (each colored line represents a species) between cumulative rainfall over the previous one week and (a) infection prevalence and (b) infection intensity. Only posterior means of estimated relationships are shown for clarity.

mismatched with the species' reproductive mode, though this pattern did not emerge for infection intensity for terrestrial breeders (Fig. 5). That is, the difference in fitted values between the wettest and driest conditions was of larger magnitude in terrestrial habitats for aquatic-breeding species (17 out of 18 species for infection prevalence; 11 out of 11 species for infection intensity). This difference was of larger magnitude in aquatic habitats for terrestrial-breeding species for infection prevalence (5 out of 5 species) but not for infection intensity (0 out of 3 species; Fig. 5, Figure S7).

3.5. Number of frogs captured

Across species, the only variable that had a clear relationship with the number of captures was habitat; more captures occurred in aquatic habitats than terrestrial habitats (Figure S8). Thus, at the community level, there was not evidence of terrestrial-breeding species congregating around water bodies during drier conditions (Figure S8), although the study did not overlap with droughts or any abnormally low rainfall when compared to historical records.

At the species level, four species tended to be captured in larger numbers in aquatic habitats when there was limited rainfall over the previous week (Figure S9). In aquatic habitats, 3.0 more captures [95 % CI: 0.9, 4.6] of *Brachycephalus pitanga* (terrestrial-breeding), 1.1 more captures [95 % CI: 0.2, 1.9] of *Ischnocnema parva* (terrestrial-breeding), 2.3 more captures [95 % CI: 1.0, 3.4] of *Ololygon flavoguttata* (aquatic-breeding), and 1.6 more captures [95 % CI: 0.2, 2.6] of *Proceratophrys boiei* (aquatic-breeding) occurred under the driest conditions compared to the wettest conditions (Figure S9). At the broader temporal scale, four species were captured in larger numbers in aquatic habitats when there was less rainfall over the previous 10 weeks (Figure S9); five species were captured in smaller numbers in aquatic habitats when there was more rainfall over the previous 10 weeks (Figure S9); and one species was captured in larger numbers in terrestrial habitats when there was less rainfall over the previous 10 weeks (Figure S9). Of the species that increased in aquatic habitats during dry conditions, *Ischnocnema parva* (terrestrial-breeding), *Ololygon flavoguttata* (aquatic-breeding), and *Proceratophrys boiei* (aquatic-breeding) did so at both temporal scales, while *Rhinella icterica* (aquatic-breeding) did so only at the 10-week scale and *Brachycephalus pitanga* (terrestrial-breeding) did so only at the 1-week scale (Figure S9).

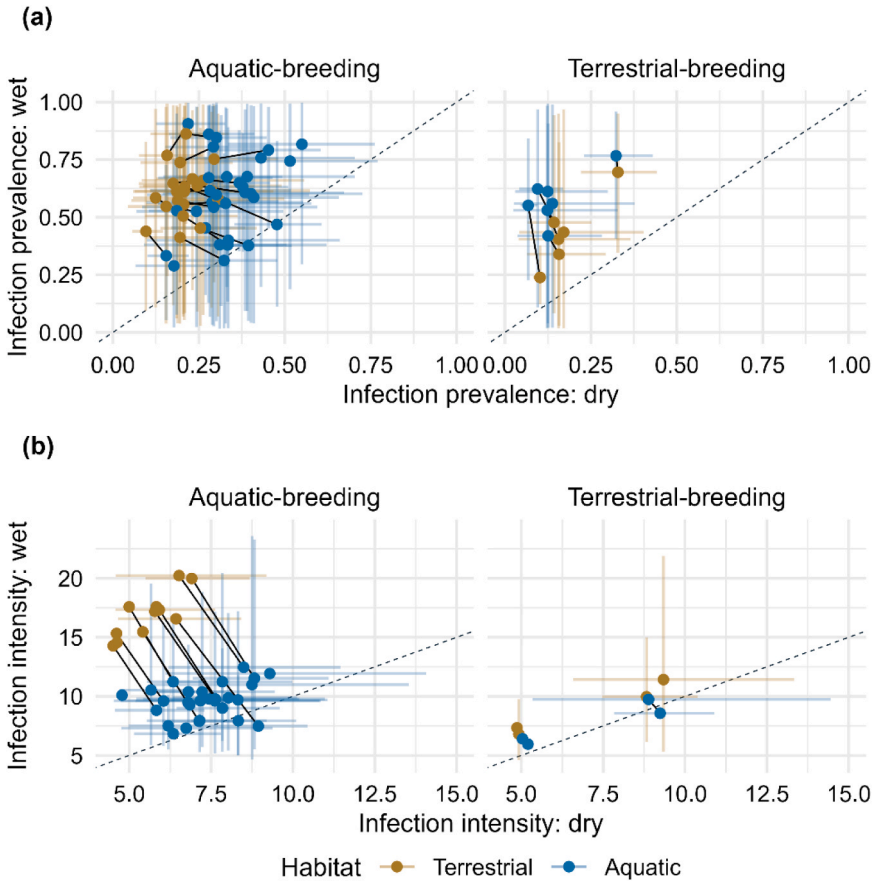

Fig. 5. Comparison of infection prevalences (a) and infection intensities (b) between the wettest (vertical axes) and driest (horizontal axes) conditions recorded during the study period. Points are posterior means of fitted values, colored translucent bars are the 95 % credible intervals, and solid black lines connect estimates for species between habitat types. The dashed line is the one-to-one line.

4. Discussion

Using a monitoring dataset for a hyper-diverse community of frogs in Brazil's Atlantic Forest, we found some support for the reproductive habitat mismatch hypothesis: species showed higher infection prevalence (both reproductive modes) and intensity (aquatic breeders only) with higher rainfall when they occurred in habitats that were mismatched with their reproductive mode (Fig. 5). However, when ignoring variation in rainfall (i.e., holding rainfall at its average value), the effect of reproductive habitat mismatch was not apparent: infection prevalence and intensity were higher in aquatic habitats for aquatic-breeding species (i.e., no mismatch), and there was no difference in infection prevalence or intensity between aquatic and terrestrial habitats for terrestrial-breeding species (Fig. 2). As we predicted, aquatic-breeding species showed higher infection prevalences than terrestrial-breeding species (Fig. 2; Brem and Lips, 2008; Lips et al., 2003; Murray and Skerratt, 2012). This pattern likely arises because aquatic-breeding species spend larger proportions of their lives in and adjacent to water bodies (i.e., the equivalent of the "lifetime aquatic index" developed by Lips et al., 2003), meaning that they face more frequent and intense exposure to waterborne *Bd*. Other work indicates that previous or frequent *Bd* exposure can lead to host resistance or tolerance (Siomko et al., 2023; McMahon et al., 2014), and though there is some evidence that our focal amphibian species show acquired resistance to previous *Bd* exposure (Becker et al., 2016), further research is needed to clarify underlying mechanisms. However, contrary to our expectations (Lambertini et al., 2021), we did not find evidence that terrestrial-breeding species showed higher infection loads than aquatic-breeding species (Fig. 2). Loads were similar for the two reproductive modes in aquatic habitats and slightly higher for terrestrial-breeding species than aquatic-breeding species in terrestrial habitats (Fig. 2). This finding may indicate that *Bd* infections in terrestrial-breeding species are less sensitive to habitat than for aquatic-breeding species, an idea that contradicts the narrative of relative naivete of terrestrial-breeding species (Smith et al., 2009; Becker et al., 2019). However, hygric context—rainfall—is clearly important in infection dynamics and adds complexity to the effects of reproductive mode and habitat (Fig. 3, Fig. 5).

Our results suggest an interplay between precipitation, habitat, and breeding mode in determining infection outcomes. First, both infection prevalence and intensity increased with recent rainfall for all reproductive modes and habitats (Fig. 3); while this result agrees with previous literature, it opposes the drought spillover hypothesis, which suggests that terrestrial-breeding species are forced to congregate in moister environments during dry conditions, leading to higher risk of infection (Moura-Campos et al., 2021). There likely were not severe enough drought conditions during the study period to trigger widespread movements of terrestrial-breeding species to refugial water bodies. This idea is supported by the fact that only a few terrestrial-breeding species increased in numbers—and only slightly—in aquatic habitats during dry conditions (Figure S9). We did, however, find some evidence that relationships between rainfall and infection prevalence and infection intensity were stronger when an individual occurred in a habitat mismatched from its reproductive habitat (infection intensity for terrestrial breeders excepted; Fig. 5, Figure S6). Thus, anurans may be especially vulnerable to increased precipitation when they are away from their reproductive habitats. This idea—which we call the reproductive habitat mismatch hypothesis—parallels the thermal mismatch hypothesis, which suggests that hosts are most vulnerable to pathogen infection under conditions that are either cooler or warmer than their optimal temperatures (Cohen et al., 2017). Indeed, thermal mismatch may be at play, since individuals likely encounter different microclimates—including temperatures—when they shift habitats (Beever et al., 2017; Kemppinen et al., 2024). Habitat mismatch—or any scenario in which a species is in a novel or mismatched environment—may lead to changes in disease outcomes through at least two routes: changes to exposure and/or susceptibility (Sweeny and Albery, 2022). Movement of naïve species to habitats which act as environmental reservoirs for a pathogen and/or contain novel species reservoirs offers an example of the former pathway. Moreover, or alternatively, such movements may be costly energetically, which may lead to divestments from tolerance mechanisms and subsequently increase susceptibility. Previous work has found high vulnerability of anurans after metamorphosis, which is an energy-intensive process and involves major physiological changes, e.g., restructuring of the immune system (Grogan et al., 2023). Both mechanisms may contribute to patterns that would support the reproductive habitat mismatch hypothesis. Finally, the fact that terrestrial-breeding species did not show evidence of a mismatch effect for infection intensity may indicate that terrestrial-breeding species are sensitive to rainfall regardless of habitat. Alternatively, the lack of a mismatch effect may be the result of limited load data for terrestrial-breeding species: we detected infections for only 5 terrestrial-breeding species, compared to 31 aquatic-breeders (Table S1).

Results for individual species generally followed community trends: infection prevalence and intensities were higher in aquatic habitats (rather than in terrestrial habitats) and during wet periods (Fig. 4). However, there was also dramatic—and unexplained—among-species variation in both infection prevalence and intensity (Fig. 4). The relatively large variation among the species-level intercepts indicates that factors other than those we modeled (rainfall, habitat, reproductive mode, and their various interactions) influence *Bd* infection dynamics for a species. What might those factors be? First, species may vary in endogenous factors such as gene expression or microbiome composition (Ellison et al., 2015; Kruger, 2020). For example, several studies have found that—counterintuitively—sustained immune responses to *Bd* infection lead to reduced host survival, and that species varied considerably in their expression of genes regulating immune response activation (Ellison et al., 2015; Savage et al., 2020). Second, species may vary in factors such as behavior or reproductive mode. For example, species may vary in avoidance behavior, i.e., avoiding contact with infected individuals (Grogan et al., 2023), or in the amount of time they spend in habitats that act as environmental reservoirs of *Bd (*Smith et al., 2009*)*. The binary reproductive mode variable we used in our analysis is a simplification of diversified reproductive modes and habitat use which influence species' exposure to *Bd* (e.g., bromeliad-breeding frogs are coded as aquatic breeders because their eggs are deposited in water—but these pools of water are often high above the ground and away from environmental reservoirs of *Bd* such as ponds (Haddad and Prado, 2005)). A supplemental analysis which included lifetime aquatic index rather than binary reproductive mode yielded parallel results: less-aquatic species showed stronger relationships between rainfall and infection prevalence in aquatic habitats, and more-aquatic species showed stronger relationships between rainfall and infection

intensity in terrestrial habitats (Supporting Information, Figure S10). Third, our decision to run qPCR reactions in singlicate to maximize the number of swabs analyzed—rather than performing multiple runs on individual swabs—could have led to under-detection of low-intensity infections (Miller et al., 2012), possibly contributing to the among-species heterogeneity estimated with our models. The constellation of potential factors that drive among-species variation in *Bd* infection dynamics adds to the challenge of understanding the risks that amphibian communities face—and implementing conservation actions to minimize those risks—as multiple forces of global change reshape the milieu in which these species experience *Bd* risk (Garner et al., 2016).

The clear associations we document between *Bd* infection risk and rainfall indicate that tropical regions experiencing increased precipitation (Mamalakis et al., 2021) should see concomitant increases in *Bd* risk (Fig. 3). However, our results also indicate that such changes will not be equal among species or habitats, highlighting the importance of species- and system-specific monitoring for conservation efforts. Moreover, our results, which partially support the reproductive habitat mismatch hypothesis, suggest that tropical amphibians may be particularly vulnerable to altered precipitation patterns when other forces of global change—such as warming temperatures, habitat alteration, or invasive species—force species to shift habitats and occur in unfamiliar settings. For example, if species shift upslope to track their thermal niches (Kusrini et al., 2017; Freeman et al., 2018; Bolitho and Newell, 2022), they may encounter novel habitats and be more vulnerable to changes in precipitation. Of course, the species that can endure—or respond—to stressors such as warming temperatures or habitat change may also be less vulnerable to *Bd* infections (Becker and Zamudio, 2011; Frishkoff et al., 2015). The particularly strong mismatch effects that we documented for aquatic-breeding species (Fig. 5, Figure S6) indicate that conservation actions such as protecting or restoring aquatic habitats to enhance connectivity for aquatic taxa facing habitat loss or climate-mediated range shifts may be especially important (Becker et al., 2023). Ultimately, in an era characterized by multiple threats—climate change, habitat loss, and disease—it is important to understand synergies, as well as dissonances, among threats, and how those threats affect both entire communities of species as well as individual species in light of among-species idiosyncrasies (Garner et al., 2016).

Ethics Statement

Field sampling permits were provided by Sisbio-Brasil #74576; Sisgen-Brasil #AC2F7B2; UA IACUC #20–05–3622; PSU IACUC #PROTO202102112; CEUA UNESP #0597–1 & #0597–2; and Fundação Florestal do Estado de São Paulo, FF/NSV #003838/2020–26.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Neil A. Gilbert reports financial support was provided by National Science Foundation. C. Guilherme Becker reports financial support was provided by National Science Foundation. Celio F. B. Haddad reports financial support was provided by State of Sao Paulo Research Foundation. Celio F. B. Haddad reports financial support was provided by Brazilian National Council for Scientific and Technological Development. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03599.

Data availability

Data are available on Dryad: https://doi.org/10.5061/dryad.69p8cz9c3. Code for analyses is available on GitLab: https://doi.org/10.5066/P13TRTVG.

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