Received: 5 January 2021 | Revised: 15 April 2021 | Accepted: 24 May 2021
DOI: 10.1111/geb.13347

RESEARCH ARTICLE

Global Ecology and Biogeography A Journal of Macroecology
WILEY

Why do parasites exhibit reverse latitudinal diversity gradients? Testing the roles of host diversity, habitat and climate

Pieter Johnson | **Sarah E. Haas**

Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado, USA

Correspondence
Pieter Johnson, Ecology and Evolutionary Biology, Ramaley N122, CB334, University of Colorado, Boulder, CO 80305, USA.
Email: pieter.johnson@colorado.edu

Present address
Sarah E. Haas, Texas Parks & Wildlife Department, Inland Fisheries Division, Austin, Texas, USA

Funding information
National Institutes of Health, Grant/Award Number: R01GM109499; U.S. Fish and Wildlife Service; National Science Foundation, Grant/Award Number: DEB-0841758, DEB-1149308 and DEB-1754171; David and Lucile Packard Foundation

Editor: Gregory Jordan

Abstract

Aim: The latitudinal diversity gradient (LDG), in which species richness decreases from the equator towards the poles, is among the most fundamental distributional patterns in ecology. Despite the expectation that the diversity of parasites tracks that of their hosts, available evidence suggests that many parasites exhibit reverse latitudinal gradients or no pattern, yet the rarity of large-scale datasets on host–parasite interactions calls into question the robustness of such trends. Here, we collected parasitological data from a host group of conservation importance, lentic-breeding amphibians, to characterize the form and direction of relationships among latitude, parasite richness and parasite load.

Location: The contiguous USA.

Time period: 2000–2014.

Major taxa studied: Lentic-breeding frogs and toads and their helminth parasites.

Methods: We collected information on parasite richness and infection load for 846 amphibian populations representing 31 species. We combined these data with environmental and biological data to test for LDGs and potential mechanisms.

Results: Both parasite richness and parasite abundance increased across 20° of latitude (i.e., a reverse LDG). For parasite richness, this pattern was explained, in part, by latitudinal increases in wetland area, land-cover diversity and the richness of waterbirds, which function as definitive hosts for many amphibian parasites. Host body size also correlated positively with latitude and helminth richness, potentially reflecting increased habitat availability, greater host longevity or a persistent phylogenetic signal. Parasite abundance associated positively with wetland area and land-cover diversity, but negatively with amphibian taxonomic richness. Longitude exhibited nonlinear relationships with parasite abundance and richness, which we suggest stem from large-scale variation in host availability (e.g., migratory bird flyways).

Main conclusions: With growing interest in the distribution of parasites and pathogens, these results highlight the importance of inverse latitudinal gradients while emphasizing the explanatory influence of host body size, habitat availability and host diversity.

KEYWORDS
amphibian decline, energy–richness hypothesis, host diversity, infectious disease, latitudinal diversity gradient, macroecology, migratory bird flyways, parasite species richness, seasonality, trematode

1 | INTRODUCTION

The latitudinal gradient in species diversity is among the most foundational patterns in macroecology. Across numerous animal and plant taxa in both terrestrial and aquatic ecosystems, species richness is often greatest in the tropics and progressively declines with distance from the equator (Fine, 2015; Willig et al., 2003). Many factors are likely to contribute to the latitudinal diversity gradient (LDG), including variation in energy input (i.e., light, temperature and evapotranspiration), habitat availability and heterogeneity, productivity, evolutionary history, disturbance regime and climate (Currie et al., 2004; Fine, 2015; Mittelbach et al., 2007). Among parasite species, however, considerably less is known about how richness and abundance vary over larger geographical scales (Poulin, 2014). For pathogens of some well-studied host taxa, the "classical" pattern of increasing richness toward low latitudes has been reported (e.g., Harris & Dunn, 2010; Poulin & Morand, 2004; Rohde, 1999). For instance, after compiling data on 332 human pathogens (bacteria, viruses, fungi, protozoa and helminths), Guernier et al. (2004) found that pathogen richness was greater in tropical compared with temperate areas, even after accounting for socio-demographic, physical and environmental covariates. Intriguingly, however, parasites of other taxa exhibit no relationship with latitude or "reverse" LDGs, for which species richness *increases* from tropical latitudes to more temperate regions (Dallas et al., 2018; Harris & Dunn, 2010; Kamiya et al., 2014b; Preisser, 2019; Torchin et al., 2015). Reverse LDGs have been reported from trematode infections in snails, helminth parasites of fishes, fleas on rodents and parasites of carnivores (e.g., Choudhury & Dick, 2000; Krasnov et al., 2004; Lindenfors et al., 2007; Torchin et al., 2015). Given the relative rarity of research on parasite diversity, whether reverse LDGs are more common among parasites or vary with habitat and host type remains conjectural.

Reverse latitudinal gradients in parasites are surprising because the distribution and diversity of parasites are expected to track those of their hosts (e.g., Poulin, 2014). The "diversity begets diversity" hypothesis postulates that a key determinant of parasite richness is the diversity of host species (Hechinger & Lafferty, 2005; Johnson et al., 2016; Kamiya et al., 2014a). As an extension of ecological theory, the heterogeneity of habitats (in this case, hosts) promotes diversity by enhancing niche opportunities (Dunn et al., 2010; Hechinger & Lafferty, 2005; Johnson et al., 2016; Kamiya et al., 2014a). For instance, Thieltges et al. (2011) found that the diversity of definitive (vertebrate) hosts was a positive predictor of trematode diversity in European fish at the continental scale, and a meta-analysis by Kamiya et al. (2014b) detected positive associations between host and parasite richness across metazoan and protozoan parasites of animals. Particularly for parasites that have multiple hosts, the magnitude of such influences is likely to depend on the type of host (e.g., vector, alternative host, intermediate vs. definitive host), the spatial scale and the time period considered (Lindenfors et al., 2007; Wood & Johnson, 2016).

Considerably less is known about latitudinal gradients in species abundance values (or densities), particularly for parasites. Parasite abundance could track overall trends in productivity, temperature or host body size (e.g., Gillman et al., 2015; Poulin, 2014). A priori, we might expect parasite abundance to mirror patterns in parasite richness. The species–energy or "more individuals" hypothesis for latitudinal diversity gradients aims to connect patterns of richness and abundance by postulating that, at lower latitudes where productivity is higher, larger population sizes help to buffer species against stochastic extinction, thereby promoting species richness (Hutchinson, 1959). Correspondingly, net primary productivity (NPP) tends to be greater at low latitudes, where more sun exposure and water availability promote photosynthesis (Gillman et al., 2015). The predictions stemming from this hypothesis are that (1) the total density of individuals should correlate positively with measures of potential or actual productivity over broad geographical areas, and (2) density and species richness ought to covary. A review by Currie et al. (2004) contended that, although density correlated broadly with richness for some taxa, these trends were inadequate to account for the direction and magnitude of LDGs. Although less is known about how these patterns extend to parasites, the one parasite-related example featured by Currie et al. (2004) revealed a positive relationship between parasite species richness and the number of individual parasites per fish host (both $\log_{10}$-transformed), for which the slope was consistent with previous theory (see also Rohde, 1999). Dunn et al. (2010) also reported that the diversity of human pathogens among countries correlated positively with overall prevalence for 22 pathogens that contribute to global mortality. Such observations suggest that parasite richness and abundance ought to exhibit positive covariance. It is important to emphasize, however, both that parasite abundance is often highly skewed (overdispersed) within host populations, which can make it challenging to quantify accurately, and that the average number of parasites per host (infection load) is not equivalent to the measures of organism density per unit area commonly used for free-living taxa (see Lagrue et al., 2015).

A persistent challenge in integrating parasite diversity research is the disconnect between many ecological studies of infection in host individuals or populations versus biogeographical investigations across host species or geographical provinces. Large-scale studies of parasite diversity frequently compile results from numerous smaller-scale surveys to assess how richness varies with host species traits, phylogeny and distributional ranges (Kamiya et al., 2014a, 2014b; Krasnov et al., 2004; Torchin et al., 2015). Although effective at synthesizing and comparing patterns among host species, disparities in the specific methods used or taxa included tend to limit opportunities to evaluate richness trends among host populations or understand the underlying mechanistic drivers. Correspondingly, ecological research into local patterns of infection within individual hosts or host populations limit the potential for macroecological assessments across gradients such as latitude. This discrepancy in biological scale underscores the need for additional parasitological data at the population scale, yet collected across larger spatial extents to test for LDGs and explore underlying drivers (e.g., Poulin, 2014; Preisser, 2019; Schemske et al., 2009).

Interactions between helminth parasites (cestodes, trematodes, nematodes and acanthocephalans) and lentic-breeding amphibians offer an interesting system in which to explore patterns of parasite diversity and abundance. Many of these parasites have complex life cycles involving multiple host species, for which amphibians can function as intermediate or definitive hosts (e.g., Koprivnikar et al., 2012). Helminth parasites of recently metamorphosed amphibians primarily reflect infections acquired during aquatic larval development (there is no direct parasite replication within these hosts), which are often dominated by digenetic trematodes (see Johnson et al., 2016). Digenetic trematodes have multi-host life cycles involving sequential transmission from a molluscan first intermediate host (often a snail), a vertebrate or invertebrate second intermediate host and a vertebrate definitive host (Esch et al., 2001). Larval amphibians become infected by free-swimming infectious stages released by freshwater snails; the infection is then transmitted to a definitive host (often a bird) after the frog is eaten. The resultant infection load determines host pathology, for which high intensities of some parasites can cause substantial morbidity and mortality (Johnson et al., 2013; Wilber et al., 2020). Ongoing declines and extinctions in amphibians underscore the importance of understanding the distribution and abundance of their infectious parasites (Collins et al., 2009).

Here, we quantified parasite richness and abundance from 846 amphibian populations across the conterminous United States. Focusing on helminth parasites in recently metamorphosed anurans, we first evaluated how parasite richness and abundance varied across 20° of latitude. Building from community ecology theory and previous research on parasites, we subsequently tested how observed latitudinal gradients were related to hypothesized drivers associated with resource availability, resource heterogeneity and colonization opportunities. Specifically, we focused on explanatory variables related to the host population (host species identity and host body size), host community diversity (the richness of intermediate and definitive hosts), habitat availability (wetland area and land-cover diversity), productivity (evapotranspiration) and climate (annual temperature and precipitation). We also assessed how parasite richness and abundance covaried with longitude owing to its potential influence on large-scale variation in host availability (e.g., migratory bird flyways). We relied on a generalized linear mixed modelling approach to help account for the hierarchically nested structure of the data while preserving response variables in their native distributions. These findings help to fill important knowledge gaps by: (1) directly assessing parasite richness in host populations across a large geographical extent (and latitudinal range); (2) incorporating measurements of both parasite richness and parasite abundance; and (3) evaluating a range of hypothesized predictors in driving reverse latitudinal gradients. Such findings have the potential to help catalyse a more integrated understanding of macroecological distributional patterns across both free-living and parasitic organisms, which remain fundamentally important for conservation (Rohde, 1999; Stephens et al., 2016).

2 | MATERIALS AND METHODS

2.1 | Study system

Between 2000 and 2014, we surveyed parasite communities from amphibian populations at 448 sites across the conterminous United States. Study sites included a wide range of lentic aquatic habitats (lakes, ponds, wetlands, etc.) sampled as part of long-term research projects, haphazard collections and a collaborative effort to survey US National Wildlife Refuges (Haas et al., 2017; Reeves et al., 2013; Figure 1). Only recently metamorphosed anurans or late-stage larvae with ≥ 10 examined hosts of a given species were included to help ensure that individuals developed in the same aquatic habitat. Previous work has found that a sample of 10 hosts is adequate for estimating local parasite species richness in metamorphic amphibians (Johnson & Hoverman, 2012), and we also compared observed parasite richness with estimated parasite richness (chao2) using the "fossil" R package (see Assessment of parasite diversity and abundance in Data S1).

Each amphibian host was measured (snout–vent length) and examined post mortem to quantify macroparasitic infections in the organs, body cavity, skin, muscles and mesentery (Hartson et al., 2011; Wilber et al., 2020). We focused on helminth parasites, including trematodes (flatworms), nematodes (roundworms), cestodes (tapeworms) and acanthocephalans (spiny-headed worms). Given that amphibians can function as intermediate or definitive hosts depending on the parasite, our examinations yielded a combination of larval stages and adults. Parasites were identified to the lowest taxonomic unit using morphological traits (see Assessment of parasite diversity and abundance in Data S1). In light of widespread cryptic diversity in helminth parasites, our values of parasite richness are almost certainly underestimated.

2.2 | Model covariates

Building from previous research on biodiversity gradients, we incorporated covariates that captured variation in resource availability, resource heterogeneity, climate and dispersal opportunities. We used geographical range data on amphibians, mammals and waterbirds to calculate host species richness covariates (for additional information, see Host diversity and density information in Data S1). We calculated the number of species for each group at sampling sites by overlaying species geographical range maps (rasters with a cell size of 1 km^2) and summing the number of species across raster cells (Figure S1-S3). Spatial data for water-associated anurans (we excluded fully terrestrial species and all salamander taxa because these taxa were not represented in the parasite dataset) and mammals were obtained from the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2015). Spatial data for waterbird richness were obtained from BirdLife International (2015). Given that many waterbirds are migratory, we initially created two richness variables: resident geographical distributions and breeding

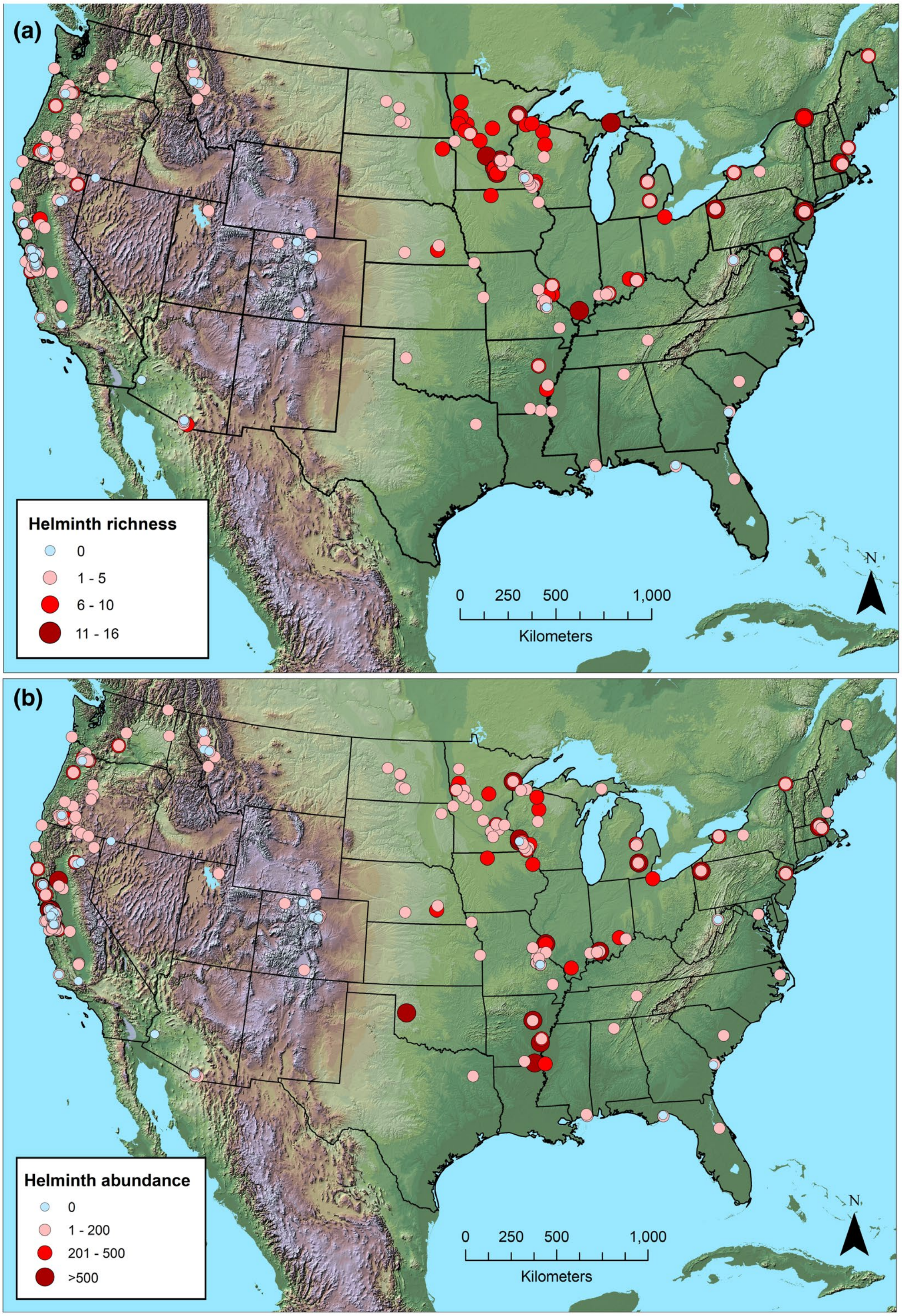

FIGURE 1 Geographical distribution of (a) amphibian parasite richness and (b) parasite abundance across 448 sites in the USA. For each sampled amphibian population, the size and colour of the circle reflect either the total number of helminth taxa encountered (in a) or the average number of helminths per host (in b). Populations with no detected parasites are indicated with small blue circles [Colour figure can be viewed at wileyonlinelibrary.com]

season distributions (for additional details, see Host diversity and density information in Data S1). We ultimately used breeding bird richness in subsequent analyses based on its stronger correlation with helminth richness. Waterfowl abundance values were derived using county-level records of hunter-harvested bird bands (ducks and geese) and weighted by county area (USFWS, 2015).

For environmental land-use variables, we created a 1 km radius around each site and determined the proportion of land area classified as wetland, forested or developed (see Land cover information in Data S1). We also generated a measure of land-cover diversity as the total number of land-cover categories included within the buffer. We expected both the types of land cover and the heterogeneity in land-cover forms surrounding a site to influence the diversity and/or abundance of potential host taxa. Contemporary bioclimatic variables were obtained from the WorldClim database (https://www.worldclim.org/data/index.html) and converted to a spatial resolution of 1 km using Geographic information system. We selected annual precipitation (BIO12) and annual mean temperature (BIO1). We also examined seasonal variability in temperature and precipitation (BIO4 and BIO15), but these variables were highly collinear and exhibited weaker univariate relationships with the parasite response terms; hence, they were omitted. As a measure of potential net primary productivity, actual evapotranspiration (AET) data were obtained from an ESRI imagery layer (see Land cover information in Data S1).

2.3 | Statistical analysis

We used generalized additive and linear mixed effects models (GAMMs and GLMMs) to evaluate the influence of predictor variables on parasite richness and abundance. GAMMs/GLMMs have the advantage of preserving the "native" distributions of response variables rather than assuming or attempting to transform data to normality and are robust to unbalanced study designs in which data collection is variable across species or regions (Bolker et al., 2009; Zuur et al., 2009). To accommodate non-independence among collections in space and time, we included random intercept terms for wetland identity, sampling year and host species in all models. We included host species identity as a random effect, rather than incorporating an explicit phylogenetic model, because our goal was to make comparisons among host populations distributed in space rather than among host species. To further assess the influence of a phylogenetic signal, we (1) explored whether the addition of a random intercept term for amphibian family improved model fit, and (2) used Pagel's λ to evaluate whether response variables covaried with phylogenetic relationships among host species (averaged by host species; following Pressier, 2019; for full description, see Phylogenetic analyses in Data S1). We modelled parasite richness per host population using a Poisson distribution. For parasite abundance, we focused on the sum of individual parasites per frog modelled using a negative binomial distribution with zero inflation and an offset term for the number of hosts examined. Given that total parasite abundance might covary with latitude because of changes in richness values, we also analysed the relationship between latitude and the abundance of parasite species individually (see Model building and diagnostics in Data S1). Models were built using the lme4, gamm4 and glmmTMB packages in R (Bates et al., 2014; Magnusson et al., 2017; R Core Team, 2019).

To test for gradients in parasite richness and abundance, we (1) first used GAMMs to analyse whether latitude or longitude exhibited linear or nonlinear associations with the response variables, and (2) subsequently used GLMMs to investigate which linear combinations of predictor variables influenced the observed relationships. Owing to strong correlations between latitude/longitude and several predictor variables, these latter, more mechanistically driven models did not also include latitude or longitude explicitly (Figure S4). We used GLMMs (rather than GAMMs) for this analysis because we did not have any a priori theoretical justification to expect nonlinear relationships between the predictors and responses. We initially built a global model with all non-collinear predictors (see Table 1), including variables related to the surrounding environment (land cover classified as wetland, forested or developed, in addition to land-cover diversity), productivity (actual evapotranspiration), amphibian host characteristics (average body size and anuran richness), attributes of definitive hosts (waterbird richness and mammal richness) and climate (annual precipitation and annual temperature). Given that waterbird richness and annual average temperature were collinear ($r = -.86$), we built a second global model with temperature instead of waterbird richness. All variables were scaled, centred and transformed where appropriate before inclusion (see Model building and diagnostics in Data S1).

After building global models, we used likelihood-ratio tests to remove the least influential terms until arriving at a simplified model for which further term removal led to a worse fit to the data ($p < .1$). This final model was assessed to evaluate the fit to the data (marginal and conditional R^2), variance inflation and overdispersion. Spatial autocorrelation in the residuals was examined using Moran's *I* and spline correlograms (for details, see Model building and diagnostics in Data S1). Finally, to assess whether we had captured variables associated with latitude adequately, we tested whether residuals from the reduced model exhibited a significant relationship with latitude (linear) or longitude (nonlinear) using a generalized additive model.

3 | RESULTS

3.1 | Overview

Between 2000 and 2014, we sampled 11,879 amphibians from 846 populations distributed across 448 water bodies and 41 US states (Figure 1). A total of 31 amphibian species (representing nine families) and 23 parasite taxa were observed (16 digenetic trematodes, four nematodes, one cestode, one monogenean and one acanthocephalan; see Supporting Information Table S1; Figure S5). Parasite taxonomic richness per host population ranged from zero to 16 (mean ±1 *SE* = 3.29 ± 0.08), with 92% of populations supporting at least one parasite taxon. Based on the species accumulation curves, observed parasite taxonomic richness correlated strongly with estimated parasite richness ($r = .92$; Figure 2a). Omitting the 14 populations in which a parasite taxon was observed in a single host (i.e., "singleton" records), this correlation increased to .96. We therefore used observed parasite richness as our response variable to maintain the data as discrete integers. Based on an analysis of Pagel's λ, we

TABLE 1 Model results from analysis evaluating potential predictors underlying observed latitudinal gradients in parasite richness and abundance

	Parasite richness			Parasite abundance		
Predictor	**Scaled coefficient**	***z*-value**	***p***	**Scaled coefficient**	***z*-value**	***p***
Wetland area	0.103 ± 0.03	4.19	.0001	–	–	–
Forest area	–	–	–	–	–	–
Development area	–	–	–	–	–	–
Land-cover diversity	0.101 ± 0.03	3.78	.0005	0.295 ± 0.09	3.29	.0005
Actual evapotranspiration	0.083 ± 0.03	2.85	.005	–	–	–
Host body size	0.168 ± 0.03	5.61	.00001	–	–	–
Anuran richness	–	–	–	-0.30 ± 0.13	−2.24	.05
Waterbird richness	0.08 ± 0.04	2.29	.02	NA	NA	NA
Waterbird abundance	–	–	–	0.157 ± 0.09	1.84	.06
Mammal richness	–	–	–	–	–	–
Precipitation	–	–	–	–	–	–
Temperature	NA	NA	NA	-0.252 ± 0.12	−2.14	.05

Note: For each of the response variables (richness or abundance), we began with a global model that included all potential predictor terms and used likelihood ratio tests to identify the final model. For each term retained in the final model, we present the scaled coefficient value, the *z*-statistic and the *p*-value from generalized linear mixed effects models. Given that waterbird richness and annual precipitation were highly collinear, these terms were not included in the same model.

NA = the term was not part of the final model.

did not detect a significant phylogenetic signal in the relationship with parasite richness or average load (see Phylogenetic analyses in Data S1), and inclusion of amphibian host family as a random intercept term did not improve the model fit relative to host species identity alone [change in the Akaike Information Criterion (ΔAIC) = 0.1].

3.2 | Parasite taxonomic richness

Across the 20° of sampled latitude, parasite richness increased linearly from an average of 1.62 at 30° to 6.17 at 48.8° (a reverse latitudinal gradient; Poisson GAMM: regression coefficient $[\beta]_{\mathrm{latitude}} = 0.155 \pm 0.032$, $p < .0001$; $R^2 = .21$; Figure 3a). Longitude also exhibited a nonlinear relationship with richness (estimated degrees of freedom [e.d.f.] = 4.98, $\chi^2 = 20.1$, $p = .001$), with peak values in the western and central USA (see Supporting Information Figure S6a). Among the included random intercept terms, host species identity had the largest variance (0.093) relative to collection location (0.072) and sample year (0.039). Incorporating predictor variables that represented surrounding land cover, climate, resource availability and host attributes, the best-fitting model included positive effects for wetland area ($\beta_{\mathrm{wetland}} = 0.103 \pm 0.025$, $p < .0001$), land-use diversity ($\beta_{\mathrm{land\_div}} = 0.101 \pm 0.027$, $p < .0005$), AET ($\beta_{\mathrm{AET}} = 0.083 \pm 0.03$, $p < .005$), waterbird richness ($\beta_{\mathrm{bird\_rich}} = 0.08 \pm 0.035$, $p = .02$) and host body size ($\beta_{\mathrm{size}} = 0.168 \pm 0.03$, $p < .00001$; conditional R2 [R^{2c}] = .42; marginal R2[R^{2m}] = .21; Table 1; Figure 4a). Likewise, the best-fitting model when annual temperature was included (instead of waterbird richness) identified the same predictor terms, with a negative coefficient for temperature instead of waterbird richness ($\beta_{\mathrm{temp}} = -0.089 \pm 0.033$, $p < .01$; $R^{2c} = .42$; $R^{2m} = .21$). Diagnostic analyses of these reduced models revealed no evidence of overdispersion ($p = 1.0$) or collinearity (all variance inflation factors < 1.3). Neither Moran's *I* nor the spline correlogram indicated obvious signs of spatial autocorrelation (Moran's $I = -0.00128$, $p = .8$). Finally, there was no significant influence of latitude on residuals from the best-fitting models (GAM: $\beta_{\mathrm{latitude}} = 0.0524 \pm 0.029$, $p = .08$; $R^2 = .03$), suggesting that the incorporated covariates (or unmeasured variables that were correlated with them) accounted for much of the parasite LDG. However, longitude continued to exhibit a nonlinear relationship with the richness residuals (e.d.f. = 8.39, $F = 3.7$, $p < .001$).

3.3 | Parasite abundance

Parasite load ranged from zero to 15,837 (mean ±1 *SE* = 97.1 ± 19.3). After removal of an outlier population in which frogs supported > 10,000 larval tapeworms per host, the mean decreased to 79 ± 6.6 (range: 0–2,710). Parasite abundance ($\log_{10}$+1-transformed) correlated positively with parasite richness ($r = .55$; $n = 846$) (Figure 2b); removal of 63 populations in which no hosts were infected reduced the association between richness and abundance only slightly ($r = .46$; $n = 783$). Larval trematodes (metacercariae and mesocercariae) accounted for 82.2% of observed helminth infections.

Total parasite abundance increased linearly with latitude (Negative Binomial GAMM: $\beta_{\mathrm{latitude}} = 0.391 \pm 0.085$, $p < .0001$; Figure 3b) and covaried nonlinearly with longitude (e.d.f. = 3.63, $\chi^2 = 19.7$, $p = .001$; Supporting Information Figure S6b). If we instead analysed average parasite load by species (using the long data format

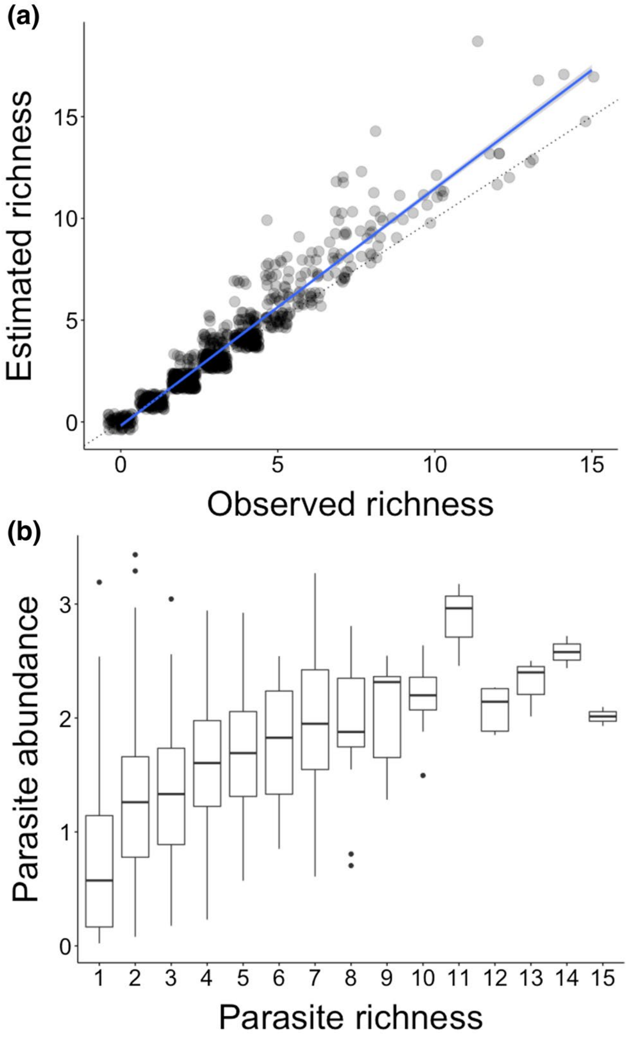

FIGURE 2 Correlational relationships between observed parasite richness and (a) chao2 estimated richness or (b) average parasite abundance ($\log_{10}$-transformed). For (a), the dashed line indicates the 1:1 relationship between observed and estimated richness, and the continuous blue line represents the best linear fit, with the 95% confidence interval indicated in grey shading (after removal of 15 "singleton" host populations). Points are jittered to enhance visibility [Colour figure can be viewed at wileyonlinelibrary.com]

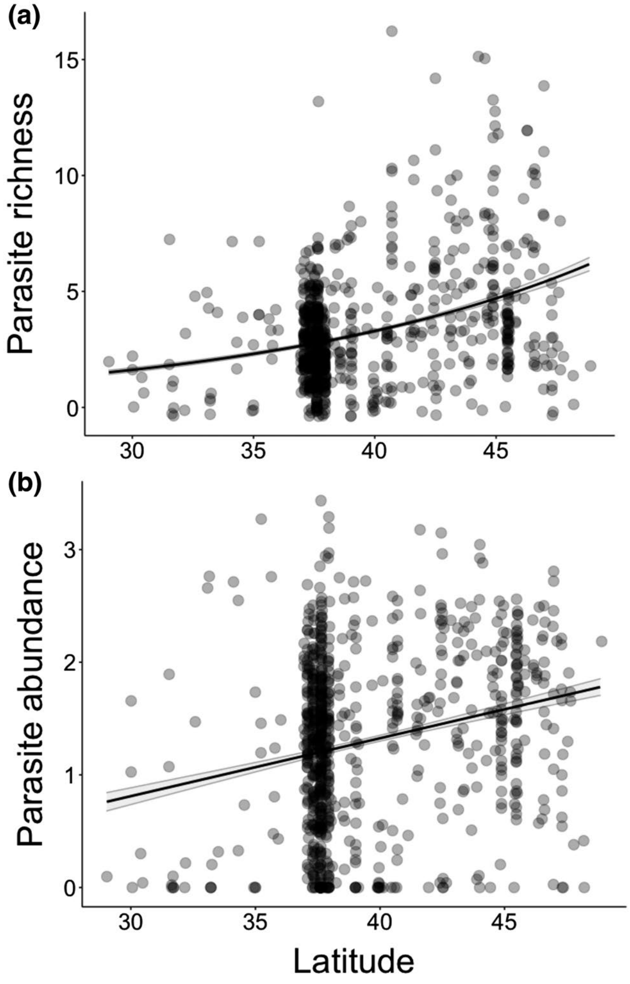

FIGURE 3 Relationship between latitude of sampled amphibian populations and (a) parasite richness or (b) average parasite load ($\log_{10}$-transformed). The best-fitting line and 95% confidence interval for (a) is derived from a Poisson generalized linear mixed effects model, whereas for (b) we plotted a linear fit of the transformed data for illustrative purposes (analyses were conducted using a zero-inflated negative binomial model). Points are jittered to enhance visibility

and including parasite species as a random effect), latitude had a similarly positive effect on parasite abundance per species (see Model building and diagnostics in Data S1), and we therefore focused on aggregated parasite abundance (summed among parasite species) in subsequent model selection. Beginning from the global GLMM with waterbird richness, our backward elimination identified positive coefficients for land diversity ($\beta_{\text{land\_div}} = 0.318 \pm 0.089$, $p < .0005$) and wetland area ($\beta_{\text{wetland}} = 0.159 \pm 0.089$, $p = .075$), with a negative influence of anuran richness ($\beta_{\text{frog\_rich}} = -0.455 \pm 0.131$, $p < .0005$; Table 1; Figure 4b). Including annual temperature rather than waterbird richness led to a final model with a positive coefficient for waterbird abundance ($\beta_{\text{bird\_abun}} = 0.157 \pm 0.085$, $p = .06$) and a negative coefficient for annual temperature ($\beta_{\text{temp}} = -0.252 \pm 0.117$, $p < .05$); the effects for land diversity ($\beta_{\text{land\_div}} = 0.295 \pm 0.089$, $p < .0005$) and anuran richness ($\beta_{\text{frog\_rich}} = -0.30 \pm 0.134$, $p < .05$) also persisted, although the influence of wetland area did not. The correlation between the observed and fitted values was 0.71 (95% CI = 0.68, 0.75). We detected no evidence of spatial autocorrelation based on the spline correlogram examining correlation in the residuals as a function of distance. Residuals from the best-fitting model of parasite abundance exhibited no significant relationships with latitude or longitude (GAM; All $p > .09$, $R^2 \approx .006$).

4 | DISCUSSION

Despite the prevalence of latitudinal diversity gradients across a wide range of free-living organisms, reported relationships between parasitic species richness and latitude are more variable (see reviews

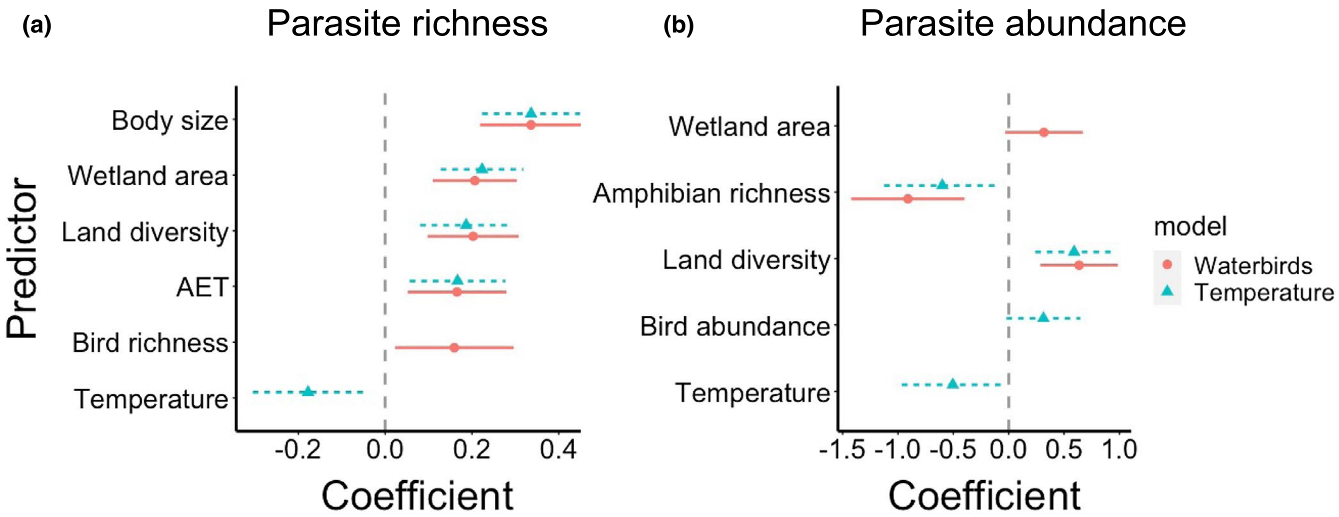

FIGURE 4 Coefficient plots from the best-fitting model for (a) parasite richness and (b) parasite abundance among sampled amphibian host populations. For each, we show the scaled coefficient values (with 95% confidence interval) for biological or environmental covariates identified as influential in predicting parasite richness or abundance, as determined from generalized linear mixed models. Only terms retained in the reduced, final model are included (based on likelihood ratio tests for backward elimination from the initial global model). Given that annual temperature and waterbird richness were highly collinear, we ran separate models for each, with coefficients from the models including temperature indicated in blue and those with waterbird richness in red [Colour figure can be viewed at wileyonlinelibrary.com]

by Pressier, 2019; Rohde, 1999). Whether this stems from the rarity of large-scale research on parasite diversity, discrepancies in the types of systems studied (e.g., terrestrial vs. aquatic) or is an emergent characteristic of host–symbiont interactions remains an open question. There are also relatively few studies of latitudinal gradients from small freshwater ecosystems, such as those favoured by amphibians. Using a standardized protocol to assess parasite abundance and richness directly in North American amphibians, the present study offers insight into population-level patterns of parasitism in a host group of conservation importance: lentic-breeding amphibians. Across 846 populations of 31 amphibian host species, we found evidence for a reverse latitudinal gradient, in which both parasite taxonomic richness and average infection load increased across a *c*. 20° increase in latitude. Our hierarchically nested statistical models highlighted influential roles for multiple variables associated with resource availability, resource heterogeneity and colonization opportunities, while accounting for non-independent observations among host species, years and locations.

Our findings reinforce and extend a growing body of research on LDG in parasites and pathogens. Similar to the present results but unlike those commonly reported for free-living organisms, reverse latitudinal gradients have been reported in helminths of fishes (Choudhury & Dick, 2000), fleas on rodents (Krasnov et al., 2004), trematodes in estuarine snails (Torchin et al., 2015) and parasites of carnivores (Lindenfors et al., 2007) (see review by Pressier, 2019). This pattern is surprising given that parasite diversity is postulated to follow the classical diversity gradient often reported in free-living species, for which richness peaks near the tropics and declines progressively toward the poles. The second part of our analysis identified hypothesized covariates that helped to account for trends in parasite richness and abundance, but only some of these were related explicitly to latitude. In particular, the most influential covariates for helminth richness that also covaried strongly with latitude included waterbird richness, average host body size, wetland area and land-cover heterogeneity (e.g., Supporting Information Figure S4). In parallel with research on the diversity of free-living taxa, both the amount of surrounding wetland area and the diversity of intersecting land-cover types correlated positively with latitude and helminth richness. Thus, greater wetland area at higher latitudes (which might be explained, in part, by historical patterns in land use or glaciation in North America; McDonald et al., 2012) provides more habitat for larval amphibians, enhancing host density or diversity and contributing positively to parasite richness. Likewise, greater heterogeneity in the types of surrounding land cover might enhance interactions or spatial overlap among host species involved in helminth life cycles (e.g., snails, invertebrates, amphibians, birds or mammals).

Although we found no link between parasite richness and the regional diversity of amphibian or mammalian taxa, the richness of waterbirds, which are common definitive hosts and dispersal vehicles for helminths, correlated positively with amphibian parasite richness. Interestingly, this association was evident for waterbirds only during the breeding season, which correlated strongly and positively with latitude (r = .75) and longitude (r = .58), rather than for residential bird populations. This higher parasite diversity could stem from greater aggregation of bird host species during the breeding season along North American bird flyway routes or from the potential for migratory birds to acquire more diverse parasites owing to "environmental sampling" during dispersal (Gutiérrez et al., 2019; Koprivnikar & Leung, 2015; Krauss et al., 2010). This might also help to explain the nonlinear relationships between longitude and both parasite richness and abundance, for which we tended to observe peak values along the major migratory bird flyways (e.g., Pacific, Central, Mississippi and Atlantic; see Supporting Information Figure S6). Likewise, Thieltges et al. (2011) reported that the diversity of definitive (bird) hosts was a positive predictor of trematode diversity in European fish at the continental scale, and Krauss et al. (2010) found that the transmission of avian influenza is linked to the migratory movements of waterfowl. In a survey of wood ducks (which frequently feed on amphibians) along the Atlantic Flyway in the USA, Thul et al. (1985) reported that eight of 10 trematode species (with ≥ 5% overall prevalence) exhibited significantly higher abundance or prevalence values in northern (migratory) as opposed to southern (residential) populations. Thus, although host richness is often treated as a static property, migratory hosts vary seasonally in their distribution and in their parasite community.

Finally, average host body size associated positively with both helminth richness and latitude. Host body size is among the most widely supported and consistent predictors of parasite species richness, probably because larger-bodied hosts encounter more infectious stages in the environment owing to their bigger size, faster consumption rates and higher activity levels (see Kamiya et al., 2014a; Poulin & Morand, 2004). Larger-bodied hosts also offer more habitat niches and are often longer lived, allowing more opportunities for accumulation of infections and promoting phenological overlap between hosts and parasites. Amphibian body size also increased with latitude, consistent with Bergmann's rule applied to ectotherms (Vinarski, 2014), which might help to explain the reverse LDG. Although we did not collect body size or infection data on snail intermediate hosts, we and others (Morris & Boag, 2011) have noted that pulmonate snails in temperate areas are often larger and longer lived, and these factors could lead to more trematode parasites and less turnover relative to tropical areas. For example, after detecting a reverse LDG in parasite richness and infection prevalence among estuarine snails, Torchin et al. (2015) suggested that this pattern was likely the result of high-latitude snail populations exhibiting greater densities, less patchiness and lower mortality.

The additional inclusion of parasite abundance offered an opportunity to assess how parasite load varied with latitude, parasite richness and specific predictor variables. There are fewer empirical or theoretical studies detailing how organismal abundance changes with latitude, particularly for parasites. A priori, we might expect higher infection loads at lower latitudes, where productivity is greater and warmer temperatures help to promote transmission (Poulin, 2006). Instead, however, helminth burden per host correlated positively with latitude and parasite richness, with no significant connection to temperature or AET. The positive link between abundance and richness is consistent with ecological theory (e.g., species–energy hypothesis) and some previous empirical data (e.g., Currie et al., 2004; Rohde, 1999). Land-cover diversity also associated positively with helminth abundance, with weaker influences for wetland area and waterbird abundance. Given that most infections in the present study involved larval trematodes, these variables could have a direct or indirect influence on the density of trematode-infected snails or the relative availability of hosts that are suitable for transmission; for instance, if changes in land use tend to promote host types necessary for transmission (e.g., Hartson et al., 2011). We also detected consistently negative relationships between amphibian host richness and parasite abundance, consistent with a “dilution effect” in which higher host diversity inhibits transmission (Keesing et al., 2006). Increases in amphibian richness have also been shown to inhibit the success of trematode infection within amphibian hosts (e.g., Johnson et al., 2013). However, given the lack of data on snail infection and the large geographical scale at which amphibian richness was assessed, this association could reflect the influence of unmeasured variables, particularly if dilution effects are more likely to operate locally (see Cohen et al., 2016; Wood & Johnson, 2016). Surprisingly, we found no evidence for a relationship between host body size and parasite load.

Overall, inclusion of covariates related to resource availability, resource heterogeneity and dispersal accounted for much of the variance in parasite richness and abundance associated with latitude. After incorporating these variables into regression models, the influence of latitude on model residuals was weak or non-significant. This approach recognizes that latitude itself has no direct influence on parasite richness but is instead a proxy for mechanisms influencing the geographical distribution of parasite colonization, establishment and persistence. We acknowledge, however, that the correlational nature of these analyses means that observed linkages could, alternatively, reflect the influence of other, unmeasured variables. Of particular note is the absence of data on amphibian host density, which influences transmission and local extinction risk, in addition to a lack of information on the distribution and diversity of freshwater molluscs, which function as key hosts for trematode parasites (Esch et al., 2001). It is also possible that edge effects in the geographical distributions of hosts could help to explain the lower values of parasite richness and abundance. For instance, if the southern USA represented a distributional boundary for important host taxa, it could support lower densities and therefore fewer infections. Incomplete knowledge about host use by parasites in this survey coupled with data gaps regarding the distribution of certain hosts (e.g., intermediate snail hosts for trematodes) limit our ability to test this hypothesis at present.

Growing interest in disease ecology has focused on large-scale, macroecological patterns of parasites and pathogens and the degree to which they follow the same “rules” as free-living species (Guernier et al., 2004; Gutiérrez et al., 2019). Although patterns in parasites often parallel those reported classically for free-living taxa, others show intriguing differences (Lagrue et al., 2015; Stephens et al., 2016). Given that parasitism is a life-history strategy that has evolved independently across many taxa, such differences might emerge from the added scale inherent to host–symbiont relationships, rather than from phylogenetic niche conservatism. This suggests that further comparative studies and integration between research on free-living and symbiotic organisms holds potential for deeper insights into macroecology, which is a position reinforced by estimates that parasitic organisms make up a substantial yet understudied fraction of overall biodiversity (Dobson et al., 2008). Identification of the factors shaping variation in parasite diversity and abundance is therefore important both for understanding diseases of human and wildlife populations and for conservation of parasites themselves, the loss of which can lead to unexpected ecological outcomes (e.g., Wood & Johnson, 2015).

ACKNOWLEDGMENTS

This work would not have been possible without the generosity and dedication of the many individuals who helped to collect and process samples. For assistance with field sampling, we acknowledge J. Bowerman, J. Bettaso, L. Guderyahn, T. McDevitt-Galles, W. Moss, A. Pinkney, S. Krest and >100 US Fish and Wildlife Service (USFWS) biologists, refuge managers and volunteers. For their efforts in processing amphibian samples for parasites, we recognize D. Calhoun, K. Leslie, T. Riepe and D. Sutherland. D. Thieltges offered essential comments and advice during revision of earlier drafts of this manuscript. This work was supported by funding from the USFWS (including a postdoctoral contract to S.E.H. and P.J.), the National Science Foundation (DEB-0841758, DEB-1149308 and DEB-1754171), the US National Institutes of Health (R01GM109499) and the David and Lucile Packard Foundation.

AUTHOR CONTRIBUTIONS

P.J. and S.E.H. designed the study. S.E.H. developed and obtained spatial covariates. P.J. and S.E.H. organized data and analysed experimental results. Both authors helped to write the manuscript.

ETHICAL STATEMENT

This paper follows all the appropriate policies of the journal with respect to scientific ethics and integrity.

DATA AVAILABILITY STATEMENT

The data and metadata associated with this article are available on Dryad (https://doi.org/10.5061/dryad.bvq83bk8v).

ORCID

Pieter Johnson https://orcid.org/0000-0002-7997-5390

REFERENCES

Bates, D. M., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

BirdLife International. (2015). *BirdLife international data zone*. Version 2015. http://www.birdlife.org/

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology and Evolution*, *24*, 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Choudhury, A., & Dick, T. A. (2000). Richness and diversity of helminth communities in tropical freshwater fishes: Empirical evidence. *Journal of Biogeography*, *27*, 935–956. https://doi.org/10.1046/j.1365-2699.2000.00450.x

Cohen, J. M., Civitello, D. J., Brace, A. J., Feichtinger, E. M., Ortega, C. N., Richardson, J. C., Sauer, E. L., Liu, X., & Rohr, J. R. (2016). Spatial scale modulates the strength of ecological processes driving disease distributions. *Proceedings of the National Academy of Sciences USA*, *113*, E3359–E3364. https://doi.org/10.1073/pnas.1521657113

Collins, J. P., Crump, M. L., & Lovejoy, T. E. III. (2009). *Extinction in our times: Global amphibian decline*. Oxford University Press.

Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guegan, J.-F., Hawkins, B. A., Kaufman, D. M., Kerr, J. T., Oberdorff, T., O'Brien, E., & Turner, J. R. G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, *7*, 1121–1134. https://doi.org/10.1111/j.1461-0248.2004.00671.x

Dallas, T. A., Aguirre, A. A., Budischak, S., Carlson, C., Ezenwa, V., Han, B., Huang, S., & Stephens, P. R. (2018). Gauging support for macroecological patterns in helminth parasites. *Global Ecology and Biogeography*, *27*, 1437–1447. https://doi.org/10.1111/geb.12819

Dobson, A., Lafferty, K. D., Kuris, A. M., Hechinger, R. F., & Jetz, W. (2008). Homage to Linnaeus: How many parasites? How many hosts? *Proceedings of the National Academy of Sciences USA*, *105*, 11482–11489. https://doi.org/10.1073/pnas.0803232105

Dunn, R. R., Davies, T. J., Harris, N. C., & Gavin, M. C. (2010). Global drivers of human pathogen richness and prevalence. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 2587–2595. https://doi.org/10.1098/rspb.2010.0340

Esch, G. W., Curtis, L. A., & Barger, M. A. (2001). A perspective on the ecology of trematode communities in snails. *Parasitology*, *123*, S57–75. https://doi.org/10.1017/S0031182001007697

Fine, P. V. A. (2015). Ecological and evolutionary drivers of geographic variation in species diversity. *Annual Review of Ecology, Evolution, and Systematics*, *46*, 369–392. https://doi.org/10.1146/annurev-ecolsys-112414-054102

Gillman, L. N., Wright, S. D., Cusens, J., McBride, P. D., Malhi, Y., & Whittaker, R. J. (2015). Latitude, productivity and species richness. *Global Ecology and Biogeography*, *24*, 107–117. https://doi.org/10.1111/geb.12245

Guernier, V., Hochberg, M. E., & Guegan, J.-F. (2004). Ecology drives the worldwide distribution of human diseases. *PLoS Biology*, *2*, 740–746. https://doi.org/10.1371/journal.pbio.0020141

Gutiérrez, J. S., Piersma, T., & Thieltges, D. W. (2019). Micro- and macroparasite species richness in birds: The role of host life history and ecology. *Journal of Animal Ecology*, *88*, 1226–1239. https://doi.org/10.1111/1365-2656.12998

Haas, S. E., Reeves, M. K., Pinkney, A. E., & Johnson, P. T. J. (2017). Continental-extent patterns in amphibian malformations linked to parasites, chemical contaminants, and their interactions. *Global Change Biology*, *24*, e275–e288.

Harris, N. C., & Dunn, R. R. (2010). Using host associations to predict spatial patterns in the species richness of the parasites of North American carnivores. *Ecology Letters*, *13*, 1411–1418. https://doi.org/10.1111/j.1461-0248.2010.01527.x

Hartson, R. B., Orlofske, S. A., Melin, V. E., Dillon, R. T., & Johnson, P. T. J. (2011). Land use and wetland spatial position jointly determine amphibian parasite communities. *EcoHealth*, *8*, 485–500. https://doi.org/10.1007/s10393-011-0715-9

Hechinger, R. F., & Lafferty, K. D. (2005). Host diversity begets parasite diversity: Bird final hosts and trematodes in snail intermediate hosts. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 1059–1066.

Hutchinson, G. E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist*, *93*, 145–159. https://doi.org/10.1086/282070

IUCN. (2015). *The IUCN red list of threatened species*. Version 2015. https://www.iucn.redlist.org

Johnson, P. T. J., & Haas, S. E. (2021). *Biogeographical data on helminth richness and abundance in North American amphibian populations*. Dryad. https://doi.org/10.5061/dryad.bvq83bk8v

Johnson, P. T. J., & Hoverman, J. T. (2012). Parasite diversity and coinfection determine pathogen infection success and host fitness. *Proceedings of the National Academy of Sciences USA*, *109*, 9006–9011. https://doi.org/10.1073/pnas.1201790109

Johnson, P. T. J., Preston, D. L., Hoverman, J. T., & Richgels, K. L. D. (2013). Biodiversity reduces disease through predictable changes in host community competence. *Nature*, *494*, 230–234.

Johnson, P. T. J., Wood, C. L., Joseph, M. B., Preston, D. L., Haas, S. E., & Springer, Y. P. (2016). Habitat heterogeneity drives the host-diversity-begets-parasite-diversity relationship: Evidence from experimental and field studies. *Ecology Letters*, *19*, 752–761. https://doi.org/10.1111/ele.12609

Kamiya, T., O'Dwyer, K., Nakagawa, S., & Poulin, R. (2014a). Host diversity drives parasite diversity: Meta-analytical insights into patterns and causal mechanisms. *Ecography*, *37*, 689–697. https://doi.org/10.1111/j.1600-0587.2013.00571.x

Kamiya, T., O'Dwyer, K., Nakagawa, S., & Poulin, R. (2014b). What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biological Reviews*, *89*, 123–134. https://doi.org/10.1111/brv.12046

Keesing, F., Holt, R. D., & Ostfeld, R. S. (2006). Effects of species diversity on disease risk. *Ecology Letters*, *9*, 485–498. https://doi.org/10.1111/j.1461-0248.2006.00885.x

Koprivnikar, J., & Leung, T. L. F. (2015). Flying with diverse passengers: Greater richness of parasitic nematodes in migratory birds. *Oikos*, *124*, 399–405. https://doi.org/10.1111/oik.01799

Koprivnikar, J., Marcogliese, D. J., Rohr, J. R., Orlofske, S. A., Raffel, T. R., & Johnson, P. T. J. (2012). Macroparasite infections of amphibians: What can they tell us? *EcoHealth*, *9*, 342–360. https://doi.org/10.1007/s10393-012-0785-3

Krasnov, B., Shenbrot, G., Khokhlova, I., & Degen, A. (2004). Flea species richness and parameters of host body, host geography and host "milieu". *Journal of Animal Ecology*, *73*, 1121–1128. https://doi.org/10.1111/j.0021-8790.2004.00883.x

Krauss, S., Stallknecht, D. E., Negovetich, N. J., Niles, L. J., Webby, R. J., & Webster, R. G. (2010). Coincident ruddy turnstone migration and horseshoe crab spawning creates an ecological "hot spot" for influenza viruses. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 3373–3379. https://doi.org/10.1098/rspb.2010.1090

Lagrue, C., Poulin, R., & Cohen, J. E. (2015). Parasitism alters three power laws of scaling in a metazoan community: Taylor's law, density-mass allometry, and variance-mass allometry. *Proceedings of the National Academy of Sciences USA*, *112*, 1791–1796. https://doi.org/10.1073/pnas.1422475112

Lindenfors, P., Nunn, C. L., Jones, K. E., Cunningham, A. A., Sechrest, W., & Gittleman, J. L. (2007). Parasite species richness in carnivores: Effects of host body mass, latitude, geographical range and population density. *Global Ecology and Biogeography*, *16*, 496–509. https://doi.org/10.1111/j.1466-8238.2006.00301.x

Magnusson, A., Skaug, H. J., Nielsen, A., Berg, C. W., Kristensen, K., Mächler, M., van Bentham, K., Bolker, B., & Brooks, M. E. (2017). *glmmTMB: Generalized linear mixed models using template model builder*. R package version 0.1.3. https://github.com/glmmTMB

McDonald, C. P., Rover, J. A., Stets, E. G., & Striegl, R. G. (2012). The regional abundance and size distribution of lakes and reservoirs in the United States and implications for estimates of global lake extent. *Limnology and Oceanography*, *57*, 597–606. https://doi.org/10.4319/lo.2012.57.2.0597

Mittelbach, G. G., Schemske, D. W., Cornell, H. V., Allen, A. P., Brown, J. M., Bush, M. B., Harrison, S. P., Hurlbert, A. H., Knowlton, N., Lessios, H. A., McCain, C. M., McCune, A. R., McDade, L. A., McPeek, M. A., Near, T. J., Price, T. D., Ricklefs, R. E., Roy, K., Sax, D. F., … Turelli, M. (2007). Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecology Letters*, *10*, 315–331. https://doi.org/10.1111/j.1461-0248.2007.01020.x

Morris, J. R., & Boag, D. A. (2011). On the dispersion, population structure, and life history of a basommatophoran snail, *Helisoma trivolvis*, in central Alberta. *Canadian Journal of Zoology*, *60*, 2931–2940.

Poulin, R. (2006). Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. *Parasitology*, *132*, 143–151. https://doi.org/10.1017/S0031182005008693

Poulin, R. (2014). Parasite biodiversity revisited: Frontiers and constraints. *International Journal for Parasitology*, *44*, 581–589. https://doi.org/10.1016/j.ijpara.2014.02.003

Poulin, R., & Morand, S. (2004). *Parasite biodiversity*. Smithsonian Books.

Preisser, W. (2019). Latitudinal gradients of parasite richness: A review and new insights from helminths of cricetid rodents. *Ecography*, *42*, 1315–1330. https://doi.org/10.1111/ecog.04254

R Core Team (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org/

Reeves, M. K., Medley, K. A., Pinkney, A. E., Holyoak, M., Johnson, P. T. J., & Lannoo, M. J. (2013). Localized hotspots drive continental geography of abnormal amphibians on U.S. wildlife refuges. *PLoS One*, *8*, e77467.

Rohde, K. (1999). Latitudinal gradients in species diversity and Rapoport's rule revisited: A review of recent work and what can parasites teach us about the causes of the gradients? *Ecography*, *22*, 593–613. https://doi.org/10.1111/j.1600-0587.1999.tb00509.x

Schemske, D. W., Mittelbach, G. G., Cornell, H. V., Sobel, J. M., & Roy, K. (2009). Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics*, *40*, 245–269. https://doi.org/10.1146/annurev.ecolsys.39.110707.173430

Stephens, P. R., Altizer, S., Smith, K. F., Aguirre, A. A., Brown, J. H., Budischak, S. A., Byers, J. E., Dallas, T. A., Davies, T. J., Drake, J. M., Ezenwa, V. O., Farrell, M. J., Gittleman, J. L., Han, B. A., Huang, S., Hutchinson, R. A., Johnson, P., Nunn, C. L., Onstad, D., … Poulin, R. (2016). The macroecology of infectious diseases: A new perspective on global-scale drivers of pathogen distributions and impacts. *Ecology Letters*, *19*, 1159–1171. https://doi.org/10.1111/ele.12644

Thieltges, D. W., Hof, C., Dehling, D. M., Brändle, M., Brandl, R., & Poulin, R. (2011). Host diversity and latitude drive trematode diversity patterns in the European freshwater fauna. *Global Ecology and Biogeography*, *20*, 675–682. https://doi.org/10.1111/j.1466-8238.2010.00631.x

Thul, J. E., Forrester, D. J., & Abercrombie, C. L. (1985). Ecology of parasitic helminths of wood ducks, *Aix sponsa*, in the Atlantic Flyway. *Proceedings of the Helminthological Society of Washington*, *52*, 297–310.

Torchin, M. E., Miura, O., & Hechinger, R. F. (2015). Parasite species richness and intensity of interspecific interactions increase with latitude in two wide-ranging hosts. *Ecology*, *96*, 3033–3042. https://doi.org/10.1890/15-0518.1

USFWS (2015). *US Fish and Wildlife Service migratory bird program*. https://www.fws.gov/birds/surveys-and-data/reports-and-publications/hunting-activity-and-harvest.php

Vinarski, M. V. (2014). On the applicability of Bergmann's rule to ectotherms: The state of the art. *Biology Bulletin Reviews*, *4*, 232–242. https://doi.org/10.1134/S2079086414030098

Wilber, M. Q., Briggs, C. J., & Johnson, P. T. J. (2020). Disease's hidden death toll: Using parasite aggregation patterns to quantify landscape-level host mortality in a wildlife system. *Journal of Animal Ecology*, *89*, 2876–2887. https://doi.org/10.1111/1365-2656.13343

Willig, M. R., Kaufman, D. M., & Stevens, R. D. (2003). Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 273–309. https://doi.org/10.1146/annurev.ecolsys.34.012103.144032

Wood, C. L., & Johnson, P. T. J. (2015). A world without parasites: Exploring the hidden ecology of infection. *Frontiers in Ecology and the Environment*, *13*, 425–434. https://doi.org/10.1890/140368

Wood, C. L., & Johnson, P. T. J. (2016). How does space influence the relationship between host and parasite diversity? *Journal of Parasitology*, *102*, 485–494. https://doi.org/10.1645/15-920

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media.

BIOSKETCHES

Pieter T. J. Johnson (www.johnsonlaboratory.com) is a professor at the University of Colorado whose research programme focuses on the community ecology of disease. He specializes in host–parasite interactions within aquatic ecosystems. **Sarah E. Haas** is a senior scientist at Texas Parks and Wildlife Department. Her current interests focus on freshwater fisheries management and research, including ecosystem and habitat assessment, in addition to enhancing diversity and inclusion in the fisheries profession.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

How to cite this article: Johnson, P., & Haas S. E. (2021). Why do parasites exhibit reverse latitudinal diversity gradients? Testing the roles of host diversity, habitat and climate. *Global Ecology and Biogeography*, 30, 1810–1821. https://doi.org/10.1111/geb.13347