

RESEARCH ARTICLE SUMMARY

WILDLIFE DISEASE

Divergent impacts of warming weather on wildlife disease risk across climates

Jeremy M. Cohen*, Erin L. Sauer, Olivia Santiago†, Samuel Spencer†, Jason R. Rohr

INTRODUCTION: Infectious disease outbreaks among wildlife have surged in recent decades alongside global climate change. However, the circumstances under which climate change is most likely to promote or inhibit infectious disease remain unknown for several reasons. First, researchers know little about how climate change will alter disease risk across hosts and parasites with diverse life history traits (e.g., host thermal biology, habitat, and parasite transmission mode). Second, not all parasites will be affected by climate change, but it remains unclear how the relative risk of disease caused by bacteria, viruses, fungi, and helminths is changing. Third, impacts of temperature abnormalities and variability, rather than increasing mean temperatures alone, remain largely unexplored. Finally, it is not clear which regions of the globe may become more amenable to disease and which may become less suitable.

RATIONALE: Recently, the thermal mismatch hypothesis has emerged to predict how infection risk is affected by temperature across climate zones in an amphibian-disease system. This hypothesis suggests that hosts adapted to cooler and warmer climates should be at greatest risk of infection under abnormally warm and cool conditions, respectively, because smaller-bodied parasites are more likely to maintain performance over a wider range of temperatures than larger-bodied hosts but are limited by extreme conditions. However, thermal mismatches may not affect diverse hosts and parasites equally because wildlife host and parasite traits can greatly influence disease outcomes. For example, thermal mismatches might exert an especially strong influence over disease outcomes in ectothermic hosts because their immune responses are highly temperature-dependent.

To address this challenge, we examined how disease risk was affected by temperature for diverse wildlife hosts and parasites that vary in ecologically important traits across a world-wide climatic gradient. We amassed a global, spatiotemporal dataset describing parasite prevalence across 7346 wildlife populations and 2021 host-parasite combinations. Further, we compiled long-term climate records at each location and short-term weather records during each survey. Our modeling approach investigated how relationships between parasite prevalence and weather depend on local climate and host and parasite traits. Finally, we projected broad-scale changes in disease risk based on thermal mismatches and ensemble climate change model predictions.

RESULTS: We found that on average, hosts from cool and warm climates experienced increased disease risk at abnormally warm and cool temperatures, respectively, as predicted by the thermal mismatch hypothesis. This effect was greatest among hosts that are ectothermic and nonmigratory and among systems in which the parasite is directly transmitted (without vectors or intermediate hosts). However, the thermal mismatch effect was similar in terrestrial and freshwater systems. Projections based on climate change models indicate that ectothermic wildlife hosts from temperate and tropical zones may experience sharp increases and moderate reductions in disease risk, respectively, though the magnitude of these changes depends on parasite taxa. Prevalence of helminth parasites increased most in temperate zones, whereas fungal parasite prevalence decreased most in tropical zones.

CONCLUSION: Cold-adapted hosts may experience increasing disease risk during abnormally warm periods. Meanwhile, the risk to warm-adapted hosts may increase during cool periods and mildly decrease during warm periods. Further, these effects are dependent on the identity and traits of the parasite and the host. Our results highlight the complexity of the influences of climate change on diverse host-parasite dynamics, whereas our broad-scale predictions suggest contrasting impacts of climate change across climate zones and diverse parasites. As climate change accelerates, hosts adapted to cooler or milder climates may suffer increasing risk of infectious disease outbreaks, whereas those adapted to warmer climates could see mild reductions in infectious disease risk. ■

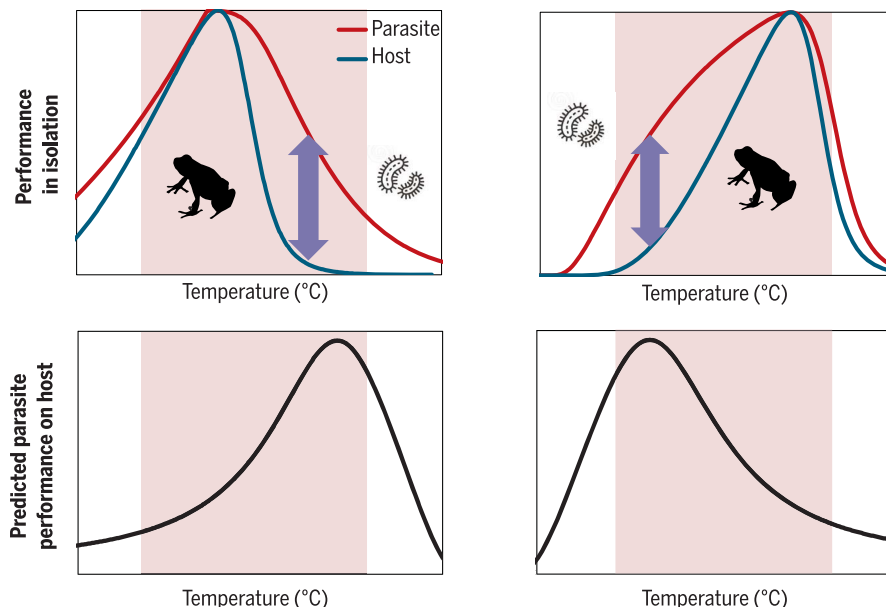
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The thermal mismatch hypothesis. Predicted patterns of thermal host and parasite performance in isolation (top, left and right) versus patterns of host-parasite interactions (bottom, left and right). Because smaller organisms generally have broader thermal performance curves in isolation than larger organisms, peak parasite growth on hosts is likely at temperatures at which host performance is poor (arrows in top left and top right; curves in bottom left and bottom right). Cold-adapted hosts (left, top and bottom) and warm-adapted hosts (right, top and bottom) should thus experience maximal parasite growth at relatively warm and cool temperatures, respectively. Shaded areas span intermediate temperatures over which relationships between temperature and parasite performance on host are likely to be approximately linear.

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Divergent impacts of warming weather on wildlife disease risk across climates

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Disease outbreaks among wildlife have surged in recent decades alongside climate change, although it remains unclear how climate change alters disease dynamics across different geographic regions. We amassed a global, spatiotemporal dataset describing parasite prevalence across 7346 wildlife populations and 2021 host-parasite combinations, compiling local weather and climate records at each location. We found that hosts from cool and warm climates experienced increased disease risk at abnormally warm and cool temperatures, respectively, as predicted by the thermal mismatch hypothesis. This effect was greatest in ectothermic hosts and similar in terrestrial and freshwater systems. Projections based on climate change models indicate that ectothermic wildlife hosts from temperate and tropical zones may experience sharp increases and moderate reductions in disease risk, respectively, though the magnitude of these changes depends on parasite identity.

In recent years, ecological communities have experienced increases in mean environmental temperatures and weather variability (1), as well as simultaneous increases in outbreaks of emerging infectious diseases (2, 3). However, complex links between climate change and infectious disease risk in wildlife remain difficult to untangle for several reasons (4–6). First, despite positive relationships between warmer temperatures and disease in many host-parasite systems [e.g., (7, 8)], warming could plausibly reduce risk in many cases [e.g., if the parasite performs poorly under warmer conditions (6)]. Second, few studies have explored how disease risk is affected by temperature abnormalities, even though increasing temperature variability is a hallmark of climate change [however, see (9, 10)]. Third, although host or parasite traits often influence disease outcomes (11), it is difficult to predict how disease risk is shifting across hosts and parasites with diverse life history traits (4, 5).

The thermal mismatch hypothesis has recently emerged to explain how abnormal temperatures alter infection risk in an amphibian-disease system (12–14). This hypothesis suggests that hosts adapted to cooler and warmer climates should be at greatest infection risk under abnormally warm and cool conditions (thermal mismatches), respectively (see summary figure). The hypothesis assumes that all organisms are physiologically adapted to their local climate but that smaller-bodied parasites generally

have broader thermal tolerances than larger-bodied hosts, meaning that the parasites can maintain performance over a wider range of temperatures [perhaps because they acclimate or adapt to new conditions faster (15)]. Sometimes, parasites may even directly reduce the thermal breadths of their hosts (10). Thus, host infection risk is hypothesized to peak at temperatures at which host performance is low but parasite performance remains high. Further, all organisms are expected to be limited by extremes that exceed their critical thermal minima or maxima (15). Therefore, infection risk is expected to be maximized during unusually cool conditions in warm environments and warm conditions in cool environments. Although thermal performance curves are inherently nonlinear, the hypothesis predicts that, under intermediate conditions where hosts occur at threshold densities needed for transmission (16), infection risk can be effectively modeled as a linear relationship with temperature. Importantly, the hypothesis is robust to violations of the aforementioned assumptions (fig. S1). The thermal mismatch hypothesis could offer a tool for understanding the impacts of climate change and disease across regions because it suggests that under abnormally warm conditions, hosts from cooler climates should experience higher disease risk, whereas hosts from warmer climates may experience no change or a reduction in risk.

The thermal mismatch hypothesis has been broadly supported on the basis of continental and global-scale analyses of survey records of the fungal pathogen *Batrachochytrium dendrobatidis* across 394 amphibian host species and 1396 populations (12–14). Additionally, experimental infections revealed that hosts from warm climates experienced the greatest *B. dendrobatidis* infection loads and mortality

under cool conditions, and vice versa (13), even when amphibians were able to thermoregulate (17), and a meta-analysis indicated that host mortality risk in the lab also increased under thermal mismatches (18). However, this hypothesis has only been shown to affect disease risk in amphibians infected with *B. dendrobatidis*, a system with an ectothermic host and ectoparasite that might be especially sensitive to environmental conditions. Several wildlife host and parasite traits influence disease outcomes, including host thermal biology, habitat, parasite taxa, and transmission mode (12). For example, thermal mismatches might exert a stronger influence over disease outcomes in ectothermic hosts than endothermic hosts because the body temperatures and immune responses of ectotherms are more dependent on environmental temperature (19). Thus, it remains unclear how temperature abnormalities influence the risk of disease outbreaks across diverse host-parasite systems from disparate climates.

Modeling changing infectious disease risk

Our primary goal was to assess how thermal mismatches, or short-term weather fluctuations, affect shifts in disease risk under long-term climate change across diverse host-parasite systems. To accomplish this, we compiled a population-level spatiotemporal parasite prevalence dataset from wildlife surveys reported in the literature. We limited our dataset to short-term surveys of wild animals, reported from precise geographic locations (see the Materials and methods). Our dataset contained 7346 population-level survey records from 355 studies on seven continents and represented 309 parasite lineages, 1381 host species from 52 taxonomic orders, and 2021 host-parasite combinations (figs. S2 and S3). The dataset contained a diverse assemblage of host taxa (31% birds, 30% amphibians, 22% fish, 9% mammals, 7% insects, and 1% reptiles) and parasite taxa (31% protozoa, 28% fungi, 23% viruses, 11% helminths, 6% bacteria, and 1% arthropods) from terrestrial (62%) and freshwater (38%) systems. We further collected the dates and locations of all surveys and compiled (i) local weather data provided by the Climate Research Unit (20) to estimate the temperature and precipitation during the month(s) of each survey (hereafter, “weather”) and (ii) local long-term climate data (1970–2000 mean temperatures, hereafter, “climate”) provided by Worldclim (21).

We fit five binomial mixed-effects models to examine how interactions between climate, weather, and various traits or features (host thermal biology, host habitat preference, host migratory distance, parasite taxa, and parasite transmission complexity) influenced parasite prevalence in hosts, which served as an indicator of disease risk. Thermal mismatches were

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represented as statistical interactions between climate and weather variables (hereafter, “thermal mismatch interaction”), whereas three-way interactions evaluated how traits or taxa influenced the strength of thermal mismatch effects (hereafter, “trait-dependent thermal mismatch interactions”). We then generated model predictions at the 10th and 90th percentiles ($\sim 5^\circ$ and $\sim 22^\circ\text{C}$) of 30-year mean temperature, representative of cold and warm climates, respectively. Given our hypothesis, we expected to find negative thermal mismatch interactions, suggesting that infection risk among hosts from cooler climates increased at warm temperatures, and vice versa. Each model controlled for monthly precipitation and the four other traits or features as fixed effects and included study and host taxa as random effects. Our models assume linear relationships between temperature and parasite prevalence covering the intermediate portions of the temperature spectrum, as predicted by the thermal mismatch hypothesis (see Materials and methods). Survey data were not spatially autocorrelated, and thus we did not control for autocorrelation (fig. S4).

Relationships between climate, weather, and disease

All models (tables S2 to S6) produced a significant, negative two-way interaction between climate and weather; thus, thermal mismatches broadly influenced parasite prevalence in our dataset of diverse host-parasite interactions (thermal mismatch interaction: climate $\times$ weather; model coefficient (β) = -0.003 , $p < 0.0001$). Impacts of thermal mismatches on parasite prevalence were highly dependent on host and parasite traits. Model comparisons demonstrated that, whereas thermal mismatch interactions always improved models, the greatest model improvements in Akaike information criterion (AIC), Nagelkerke’s pseudo- R^2 , and chi-square values were observed with trait-dependent thermal mismatch interactions (except habitat; table S1).

As predicted, partial residual (PR) plots revealed that ectothermic hosts from relatively cool or warm climates experienced the greatest parasite prevalence when temperatures were unusually warm or cool, respectively (trait-dependent thermal mismatch interaction-thermal biology; $p < 0.0001$; Fig. 1, A and B, and table S2). However, endotherms experienced the greatest parasite prevalence during cold weather. This could be an effect of cold-induced physiological changes in endotherms that can be immunosuppressive (22) or increasing transmission rates of airborne pathogens in cool, less humid air (23). Further, we expected that the effects of thermal mismatches on parasite prevalence may be less detectable in long-distance migrant hosts because these hosts experience greater variation in climate and have more flexibility to avoid adverse weather. Indeed,

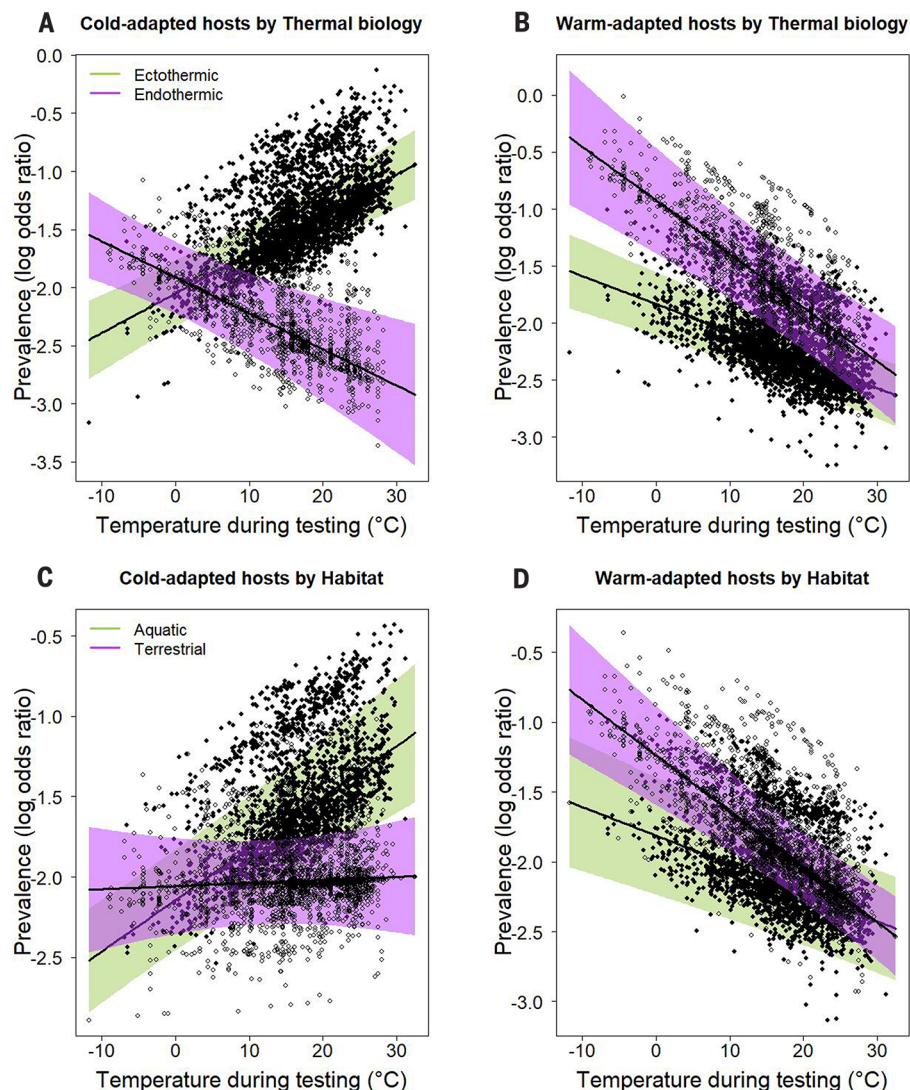


Fig. 1. Thermal mismatch effects on parasite prevalence depend on host thermal biology but not habitat. (A to D) Partial residual plots from binomial mixed-effects models display the significant three-way interactions among long-term climate, weather, and either host thermal biology [(A) and (B)] or habitat [(C) and (D)] that affect parasite prevalence (as log-odds ratios). Points represent host populations, and shading shows 95% confidence bands; green bands and solid points represent ectothermic and aquatic hosts, whereas purple bands and open points represent endothermic and terrestrial hosts. Cold-adapted (prediction at 10th percentile climate of $\sim 5^\circ\text{C}$) hosts are represented in (A) and (C), and warm-adapted (prediction at 90th percentile climate of $\sim 22^\circ\text{C}$) hosts are represented in (B) and (D). The models suggest that ectothermic and endothermic hosts from cooler climates typically experience higher and lower prevalence under warm conditions, respectively (A). Meanwhile, all warm-adapted hosts experience high prevalence when conditions are cool (B). Cold-adapted aquatic hosts experience greater parasite prevalence at warm temperatures than terrestrial hosts (C), though all warm-adapted hosts experience greater prevalence at cool temperatures (D), as predicted by the thermal mismatch hypothesis.

PR plots revealed that this was the case (trait-dependent thermal mismatch interaction-migratory distance; $p < 0.0001$; fig. S5, A and B, and table S3), although we caution that long-distance migrant hosts experience conditions over the annual cycle that often differ from the climate of the survey location.

We expected that terrestrial hosts experience greater parasite prevalence under thermal mis-

matches than aquatic hosts because environmental temperatures are typically less variable in water than in air, despite exceptions [e.g., perched wetlands (24)]. Surprisingly, all hosts experienced similarly high parasite prevalence after thermal mismatches (trait-dependent thermal mismatch interaction-habitat; $p = 0.24$; Fig. 1, C and D, and table S4), though terrestrial hosts were not as likely to experience high

parasite prevalence under warm temperatures in cold climates [possibly because aquatic hosts have evolved narrower thermal breadths (15)]. Finally, we observed increased parasite prevalence after thermal mismatches in host-parasite interactions with a directly transmitted parasite (trait-dependent thermal mismatch interaction-transmission mode; $p < 0.0001$; fig. S5, C and D, and table S6) rather than an indirectly transmitted parasite (relying on intermediate hosts or vectors; fig. S5, C and D), possibly because of the inherent complications present in these systems that might impede detection of temperature effects. For example, indirectly transmitted parasites may benefit from behavioral thermoregulation of intermediate hosts at high temperatures, which can provide shelter and thus mitigate the effects of unusually warm weather conditions in cold-adapted parasites.

Although we expected to see thermal mismatch effects across parasite taxa—including bacteria, viruses, fungi, and helminths—we predicted that the strength of effects in cool or warm climates depends on taxon. For example, fungal parasites might have a particularly strong advantage when infecting warm-adapted hosts at cold temperatures because many fungi perform best at cool or intermediate temperatures (25), whereas the opposite might be true for parasites that often grow well under warm temperatures, such as helminths (26). Indeed, the impacts of thermal mismatches on parasite prevalence were highly dependent on parasite taxa (Fig. 2 and table S5). Fungal prevalence exhibited the strongest thermal mismatch effect, increasing sharply under cold abnormalities in warm climates but more gradually under warm abnormalities in cool climates (Fig. 2). By contrast, helminth prevalence was positively related to temperature across climates, though this relationship was much stronger in cool climates (Fig. 2), suggesting that warming may benefit helminths more than other parasites. Several previous studies have found positive associations between helminth transmission and temperature [e.g., (26)], and helminth success in hosts is closely tied to host food consumption (27), which may be limited in abnormally cool conditions.

Bacterial prevalence decreased moderately under cool temperatures in warm climates but only slightly under warm temperatures in cool climates (Fig. 2). Finally, viral parasite prevalence increased under warm temperatures in cool climates but not cool temperatures in warm climates, though we advise caution in interpreting this result because viral infections progress quickly and thus hosts may be likely to clear infections or suffer mortality in time frames shorter than the monthly resolution of our weather data. These results were largely robust to reductions in model complexity (table S7) or shifts in the relative proportion of host taxa (figs. S6 to S8 and table S8).

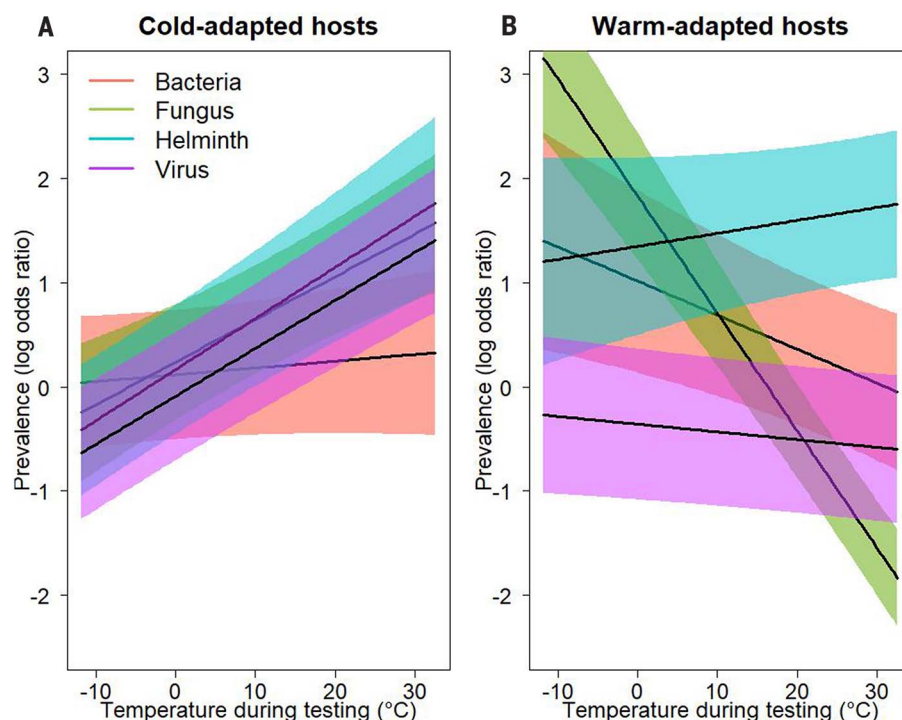


Fig. 2. Variation in thermal mismatch patterns among parasite taxa. (A and B) Partial residual plots from a binomial mixed-effects model display the significant three-way interactions among long-term climate, weather, and parasite taxa. Shading shows associated 95% confidence bands for four parasite taxa: bacteria (red), fungi (green), helminths (blue), or viruses (purple). Cold-adapted (prediction at 10th percentile climate of $\sim 5^{\circ}\text{C}$) hosts are represented in (A), and warm-adapted (prediction at 90th percentile climate of $\sim 22^{\circ}\text{C}$) hosts are represented in (B). The models suggest that hosts from cooler climates typically experience a higher prevalence of fungal, helminth, and viral parasites under warm conditions, whereas those from warmer climates experience a higher prevalence of fungal and bacterial parasites when conditions are cool.

Predicting changing disease risk across the globe

Our models indicate that climate change may increase disease risk for many wildlife hosts from cooler climates, whereas wildlife from warmer climates may experience reduced disease risk. Following these models, we aimed to explore global patterns of disease risk in wildlife under climate change. We generated nearly global predictions from our model results (excluding polar areas) for how prevalence of four parasite taxa (bacteria, fungi, helminths, and viruses) will change under projected annual mean temperatures in 2070 following various greenhouse gas emission scenarios [Representative Concentration Pathways (RCPs) 2.6, 4.5, 6.0, and 8.5 by the Community Climate System Model (28); see Materials and methods]. To generate these predictions, we represented climate with long-term mean temperature and weather with projected mean temperature under a given RCP. We then divided these predictions by predictions generated under the current climate (with long-term mean temperature representing climate and weather) to standardize the change in risk relative to the present.

The resulting maps show that climate change may increase parasite prevalence sharply at high latitudes and elevations but decrease it moderately at low latitudes (Fig. 3). Predictably, the magnitude of these effects increased at greater RCPs: Changes in parasite prevalence ranged from -22 to $+66\%$ at RCP-2.6 (95% of cells warming between 0.21° and 3.57°C) but ranged from -31 to $+86\%$ at RCP-8.5 (2.11° and 7.49°C). At RCP-8.5, predictions vary by parasite taxa, although warming is expected to increase parasite prevalence at high latitudes and decrease prevalence at low latitudes across all taxa (Fig. 4). Notably, fungal parasites exhibit the greatest increases in risk at high latitudes and greatest decreases in risk at low latitudes, whereas helminths benefit most from warming overall, decreasing only slightly at low latitudes (similar to predictions generated by Carlson *et al.* (27). Across all taxa, both our models and predictions found that cold-adapted hosts generally experienced steeper increases in parasite prevalence under warm conditions than warm-adapted hosts experienced under cool conditions, suggesting that climate change-driven increases in parasite prevalence for cold-adapted hosts may

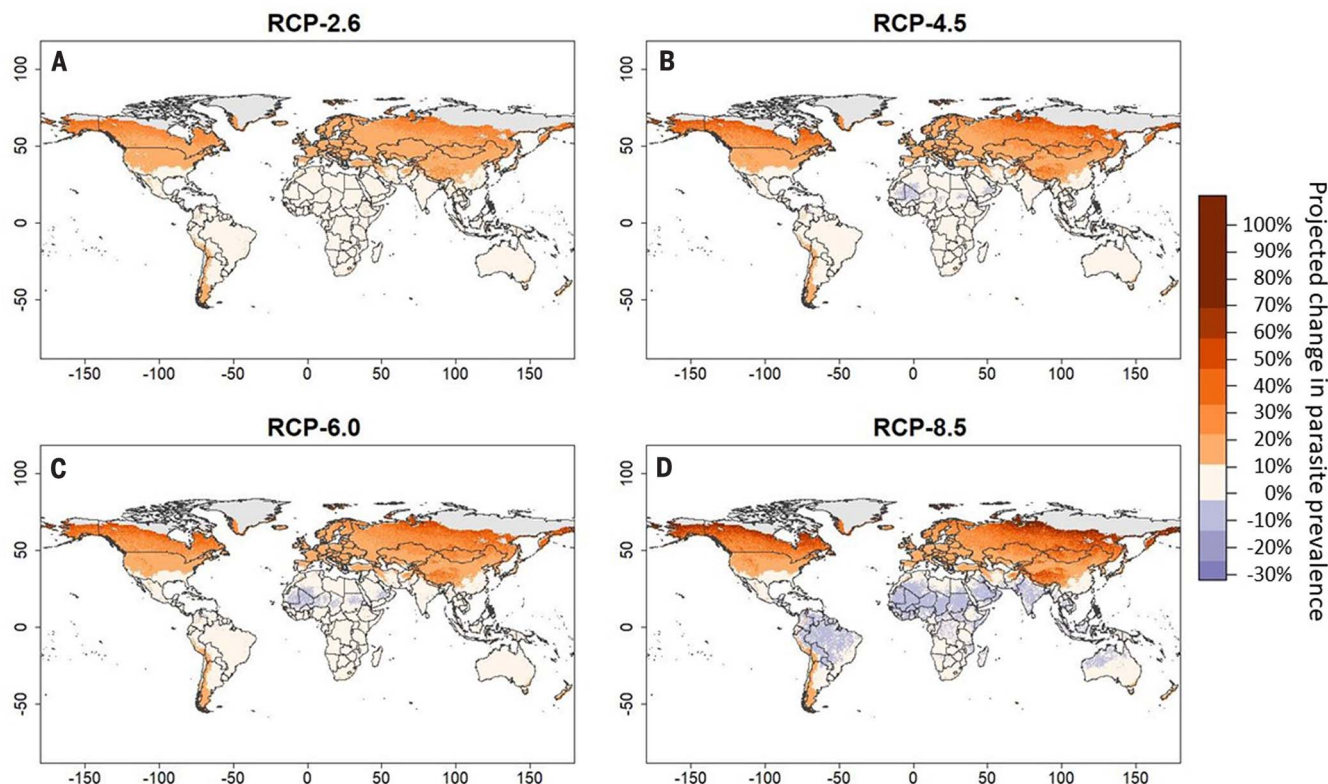


Fig. 3. Global projections of shifts in parasite prevalence under climate change. (A to D) Maps display projected change in overall parasite prevalence under four RCPs in 2070: 2.6 (A), 4.5 (B), 6.0 (C), and 8.5 (D). Parasite prevalence predictions were generated for each cell based on a binomial mixed-effects model

containing a two-way thermal mismatch interaction between long-term climate and weather. Predictions were generated for the current climate as well as for each RCP scenario, in which projected mean temperatures substituted for survey temperatures. The proportional difference between the two projections is plotted.

exceed decreases in risk for warm-adapted hosts across systems. This pattern might be explained by the shape of most thermal performance curves, which are often left-skewed with a greater per-degree change in performance at temperatures above than below an organism's thermal optimum (29) [however, see (30) for exceptions]. Boreal zones appear likely to experience the greatest increases in parasite prevalence, adding an additional stressor to a region that is projected to experience some of the most pronounced changes to its climate (28). We caution that our predictions are highly generalized and are only a general expectation for global changes in disease risk under warming, because parasite species are given equal weight in this analysis regardless of their commonness in the environment or pathogenicity. Thus, we recommend against using these maps to make predictions about any single host-parasite system but present them as only a general expectation for global changes in disease occurrence under warming.

Conclusions

Here, we amassed a global spatiotemporal dataset of population-level parasite prevalence across

thousands of wildlife populations worldwide and describe how temperature abnormalities influence parasite prevalence across diverse host-parasite systems from disparate climates. We show that cold-adapted hosts may experience increasing parasite prevalence, and thus disease risk, during abnormally warm periods. Meanwhile, risk to warm-adapted hosts may increase during cool periods and mildly decrease during warm periods. Further, these effects are dependent on the identity and traits of the parasite and the host. Our results highlight the complexity of the influences of climate change on diverse host-parasite dynamics, whereas our broad-scale predictions suggest contrasting impacts of climate change across climate zones and diverse parasites. As climate change accelerates, wildlife hosts adapted to cooler or milder climates may suffer increasing risk of infectious disease outbreaks, whereas those adapted to warmer climates could see mild reductions in infectious disease risk.

Materials and methods

Overview of data selection and extraction

We aimed to acquire spatiotemporal datasets describing population-level parasite prevalence across as many host-parasite systems as possi-

ble, defining a population as a group of hosts of the same species sampled at a single location and time. Because we aimed to test interacting effects of climate (30-year baseline mean temperature) and weather (temperature at the time of sampling) on host-parasite outcomes at the specific locations of each survey, our dataset was limited to records with information about location (to a 10th of a degree) and date (to month). We further limited our dataset to surveys among animal wildlife, excluding systems with human hosts and farmed or captive animal hosts because of the various complications arising from reporting, medical treatment, and climate-controlled buildings. We excluded any data acquired through antibody tests because these data do not reflect current parasite presence. Because our predictions only hold under intermediate local temperature conditions, we excluded two data points collected during very cold weather ($<-10^{\circ}\text{C}$; our dataset had no surveys conducted above 30°C). In addition, we excluded marine systems because spatiotemporal data of equivalent resolution are not readily available. Finally, we limited our dataset to definitive hosts.

We used several strategies to gather appropriate datasets, including searching the

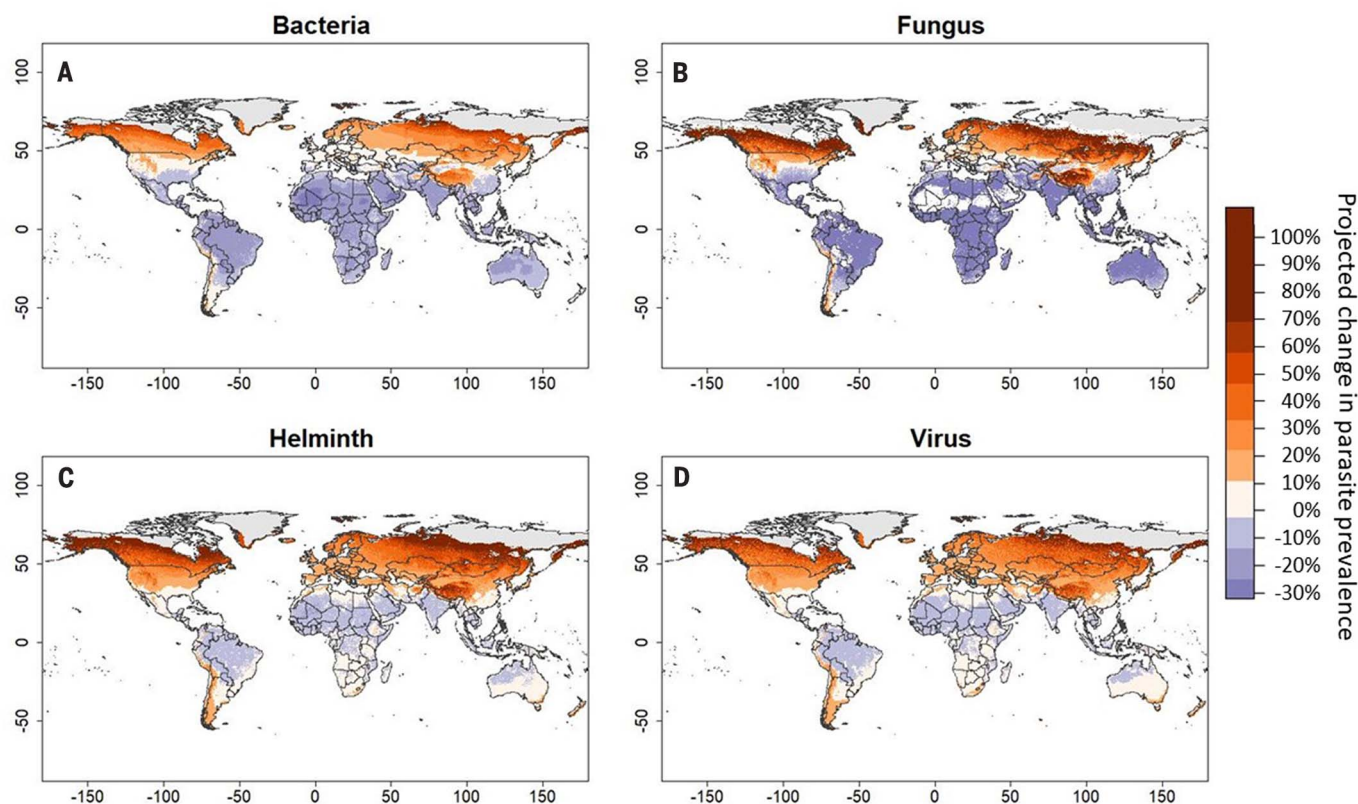


Fig. 4. Global projections of shifts in prevalence of four parasite taxa under climate change. (A to D) Maps display projected changes in parasite prevalence of four taxa—bacteria (A), fungi (B), helminths (C), and viruses (D)—in 2070 under RCP-8.5. Disease risk predictions were generated for each

cell based on a binomial mixed-effects model containing a three-way thermal mismatch interaction between long-term climate, weather, and parasite taxa. Predictions were generated for current climate as well as RCP-8.5, and the proportional difference between the two projections is plotted.

literature (31–223), searching the internet for available datasets, assembling datasets from scratch for several host-parasite systems that are sampled frequently, and contacting various experts in disease ecology. Our internet search identified five available spatiotemporal datasets that we downloaded: (i) avian malaria data from Malawi (224), (ii) the Global Mammal Parasite Database [GMPD (225)], (iii) fish parasite data from the National Wild Fish Health Survey (NWFHS) database (<https://www2.usgs.gov/ecosystems/disease/fishdisease.html>), (iv) neotropical avian parasite data presented in Barrow *et al.* (40), and (v) honeybee data from McMahon *et al.* (135). We supplemented the Malawi and GMPD datasets with month and year of collection from the original published articles cited for each entry and excluded any entries describing captive hosts or missing geographic coordinates or for which we could not find dates. The NWFHS and Barrow *et al.* (40) databases were organized at the individual level and needed to be summarized to the population level. When summarizing individual-level data at the population level, we grouped individuals into populations based on species, identical location (geographic coordinates in decimal

degrees, rounded to two decimal places), and month.

We also manually collected spatiotemporal survey data from the literature. First, we searched Web of Science for the term “disease survey*,” yielding 1925 results from a wide variety of host-parasite systems, and extracted data from 28 papers that met our criteria. Second, we targeted several host-parasite systems for which we knew data would be available in the literature. We searched Web of Science for the term *Batrachochytrium dendrobatidis* (Bd), producing 1215 total results and extracting data from 159 papers. We also searched Web of Science for papers relating to iridoviruses, using the terms (“Frog virus 3” OR “Epizootic haematopoietic” OR “necrosis virus” OR “European sheatfish virus” OR “European catfish virus” OR “Regina ranavirus” OR “Santee-Cooper ranavirus” OR “Bohle iridovirus” OR “Red sea bream iridovirus” OR “White sturgeon iridovirus” OR “ranavirus”), obtaining 612 results and extracting data from 29 papers that reported iridovirus prevalence. Despite the focus on Bd and iridovirus, they accounted for only 21 and 5% of our dataset, respectively. We screened all papers using the *metagear* package (226) in R 3.4.2 (227) and manually

extracted relevant data. All literature searches and data collection associated with these searches took place between May 2018 and February 2019, and all data were combined into a single dataset for analysis.

When extracting data from papers and databases, we recorded host and parasite species, number of hosts sampled, host life stage, number of infected and uninfected individuals or infection prevalence (if only one was given, the other was calculated), date of sampling, and geographic coordinates. When coordinates were not given in a paper or database, we searched named sites for coordinates on Google Maps. We only included field surveys conducted over a continuous period up to a maximum of 4 months and up to a maximum area of 50 km² to ensure that weather data were local and sufficiently short term. We collected taxonomic information and standardized all classifications according to the International Union for Conservation of Nature [IUCN (228)]. Prevalence data was bimodally distributed in our dataset, with many populations having no infection or 100% infection, and this pattern was consistent across time periods (fig. S9). Surveys were most common in summer regardless of latitude, though there was some variation (fig. S10).

We classified all parasites as either bacteria, viruses, protozoa, helminths, arthropods, or fungi (hereafter referred to as “parasite taxa”) and classified them as having either direct or indirect life cycles. All hosts were classified as either ecto- or endothermic, terrestrial or aquatic, and migratory (long-distance migrants) or nonmigratory (short-distance migrants or residents). Amphibian habitat associations were classified based on Sodhi *et al.* (229). Birds were classified as terrestrial except for species in the orders Anseriformes, Charadriiformes (family Laridae only), Gaviiformes, Pelecaniformes, and Sphenisciformes (other aquatic taxa were not present in our dataset). Mammals, reptiles, and insects were assessed at the species level on the basis of the judgment of the data collectors. See below for definitions of the classifications.

Climate data

We extracted historic monthly mean temperature and total precipitation data from the University of East Anglia Climate Research Unit [CRU (20)] for the location and specific month(s) that each population was tested in the field [raster package (230)]. CRU data are the finest-scale global, historic climate data available, offered at a resolution of $0.5^{\circ} \times 0.5^{\circ}$ cells (about 50 km²) for each month dating to 1901. If sampling took place over the course of up to four consecutive months or less, and was not reported at the monthly level, then we averaged climate data across the sampling months. We did not use data collected over longer periods of time because doing so would have been inappropriate to seasonal analysis.

We collected annual mean temperature between 1970 and 2000 for each population (as a representative of mean temperature in their climate) on the basis of their locations using interpolated Worldclim rasters (21), which have been used in hundreds of previous ecological studies to represent long-term climate means. Long-term annual temperatures in the range of a species are a useful approximation of thermal tolerance (19, 231). Though the time period is somewhat arbitrary, such high-resolution historic data are not available at a global scale for other time periods. In our view, this window adequately represents the historic mean conditions in a given area to which an organism has likely adapted.

Statistical analyses

All analyses were conducted in R 3.4.2 (227). We fit a series of four generalized linear mixed-effects models (GLMMs) with binomial distributions to test relationships between thermal mismatches, host or parasite traits, and parasite prevalence in wildlife using the package *glmmTMB* (232). Thermal mismatches were represented in models as statistical interactions between 30-year mean temperature

(representing climate) and monthly mean temperature during sampling (representing weather) for a given host population at the location it was sampled. Because we expect that hosts adapted to warm conditions should have the greatest parasite prevalence under cool conditions and vice versa, the estimate of the coefficient of the two-way thermal mismatch interaction is hypothesized to be negative. In our five models, we tested for effects of three-way interactions (the thermal mismatch interactors and one of five host or parasite traits) on the number of infected and uninfected hosts (binomial response variable). Host or parasite traits were each categorical factors—either host thermal biology (ecto- or endotherm), host habitat type (summarized as terrestrial or aquatic based on where the host spends a majority of its time at its tested life stage), host migratory strategy (migratory or nonmigratory), parasite transmission complexity (direct or indirect; the latter representing parasites that are vector-transmitted or requiring an intermediate host), or parasite taxa (limited to virus, bacteria, fungus, protozoa, or helminth). Our goal in assessing the impacts of migration was to determine whether hosts migrating long distances were less affected by thermal mismatches, because they experience a greater range of climates than other species; thus, we considered all hosts migrating on average >200 km per year to be migratory (a category that included some birds, mammals, and fish) and others to be nonmigratory, even if they do migrate shorter distances. In the model testing for an interaction between thermal mismatch and parasite taxa, we subsetted the data to exclude insect parasitoids and protozoans because these categories were not fully crossed with our other fixed effects. We did not explicitly test for differences in relationships across host taxa because of redundancy between taxonomic group and our other traits, and we did not compare zoonotic systems with others because we lacked sufficient data in zoonotic systems.

In each model, we included the following as fixed effects: the absolute value of latitude, log-transformed total precipitation during the month(s) of sampling, and the other host or parasite traits that were not part of the three-way thermal mismatch interaction (excluding parasite transmission mode, which is highly redundant with parasite taxa). Because studies contained varying numbers of surveys, study was included as a random effect to account for nonindependence among sampling events within a study. Further, we included host taxonomic class as a random effect to ensure that outsized effects of a single taxonomic group did not sway the outcome of the models. Unfortunately, traditional phylogenetic correlation structures cannot be included in mixed models with a binomial error distribution because the

distribution is only defined by a single parameter specifying both the mean and variance, whereas correlation structures affect only variance parameters.

To evaluate the importance of the thermal mismatch and its dependence on host, parasite, and environmental traits, we compared among nested models using AIC scores, Nagelkerke's pseudo- R^2 values [MuMIn package (233)], and chi-square values. Because highly complex models with partially correlated predictor variables can sometimes produce spurious results (though this is less of a concern when analyzing large datasets), we explored fitting simplified models corresponding to each of the five primary models that did not include any host or parasite taxa or traits other than main effects of terms included in interactions but were otherwise identical. Additionally, we explored fitting models in which major host taxa (birds, mammals, amphibians, invertebrates, and fish) were equally represented by randomly subsampling 2000 rows from the original dataset for each category. All results were visualized using the *visreg* package (234).

Spatial structure of the data

Unfortunately, the size of our dataset made controlling for spatial structure computationally unfeasible (requires accounting for >56 million distance estimates per model). Instead, we generated correlograms to evaluate spatial autocorrelation (Moran's I) at a sequence of distances up to 30° from each point. To reduce the computational burden, which increases exponentially with the number of records, we randomly subsampled 1000 rows from our dataset nine times and produced correlograms for each subsample [ncf package (235)].

Climate change projections

We generated two sets of global maps, projecting future change in parasite prevalence at four RCPs (different possible greenhouse gas trajectories predicted by climate models, with RCP-2.6 representing an optimistic climate change scenario and RCP-8.5 representing a business-as-usual model) or for four parasite taxa (bacteria, fungi, helminth, and virus). The RCP maps were based on a GLMM that tests how the two-way interaction between 30-year mean temperature and temperature during surveying predicts population-level parasite prevalence [glmmTMB package (232)]. The model contained log-transformed monthly precipitation and study as a random effect, though we did not include categorical fixed effects because this would necessitate assuming categorical values of host or parasite traits while generating model predictions and our goal was to keep the predictions general (study ID was randomized when making predictions). We first generated predictions for all cells on a global map (aggregated by mean to $0.21^{\circ} \times 0.21^{\circ}$ resolution)

based on projections of 2070 annual mean temperature at four RCP scenarios (2.6, 4.5, 6.0, and 8.5) by the Community Climate System Model, version 4 [CCSM4 (28)]. For each cell, we used Bioclim 30-year mean temperature [bio1 (21)] as 30-year mean temperature and CCSM4 bio1 projections as the temperature during surveying. We then divided each of these by a “current climate” projection in which Bioclim 30-year mean temperature was used for both temperature variables. Resulting rasters show change in parasite prevalence globally and were plotted using the *raster* package (230) and color palettes from *RColorBrewer* (236).

Projections of parasite prevalence by taxa were based on a GLMM that tests the three-way interaction between both temperature terms and parasite taxa, a categorical variable with the four levels given above. Predictions were generated for current and future climate (RCP-8.5) based on 30-year temperature and temperature during sampling, respectively. All other methods were identical to those described above.

Data availability

All data and code compiled for this study are available on Github (223).

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interests: The authors declare no competing interests. **Data and materials availability:** All data and code compiled for this study are available on Github ([223](#)).

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Divergent impacts of warming weather on wildlife disease risk across climates

Jeremy M. Cohen, Erin L. Sauer, Olivia Santiago, Samuel Spencer and Jason R. Rohr

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Climate change alters disease risks

Climate change appears to be provoking changes in the patterns and intensity of infectious diseases. For example, when conditions are cool, amphibians from warm climates experience greater burdens of infection by chytrid fungus than hosts from cool regions. Cohen *et al.* undertook a global metanalysis of 383 studies to test whether this "thermal mismatch" hypothesis holds true over the gamut of host-pathogen relationships. The authors combined date and location data with a selection of host and parasite traits and weather data. In the resulting model, fungal disease risk increased sharply under cold abnormalities in warm climates, whereas bacterial disease prevalence increased sharply under warm abnormalities in cool climates. Warming is projected to benefit helminths more than other parasites, and viral infections showed less obvious relationships with climate change.

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