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ARTICLE

Disease Ecology

Long-term exposure to an invasive fungal pathogen decreases *Eptesicus fuscus* body mass with increasing latitude

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Abstract

Invasive pathogens threaten wildlife health and biodiversity. Physiological responses of species highly susceptible to pathogen infections following invasion are well described. However, the responses of less susceptible species (relative to highly susceptible species) are not well known. Latitudinal gradients, which can influence body condition via Bergmann's rule and/or reflect the time it takes for an introduced pathogen to spread geographically, add an additional layer for how mammalian species respond to pathogen exposure. Our goal was to understand how hosts less susceptible to pathogen infections respond to long-term pathogen exposure across a broad latitudinal gradient. We examined changes in body mass throughout pathogen exposure time across the eastern United States (latitude ranging 30.5° N–44.8° N) in *Eptesicus fuscus*, a bat species classified as less susceptible to infection (relative to highly susceptible species) by the invasive fungal pathogen that causes white-nose syndrome, *Pseudogymnoascus destructans* (*Pd*). Using 30 years of spring through fall adult capture records, we created linear mixed-effects models for female and male bats to determine how mass or mass variation changed across the eastern United States from pre-*Pd* invasion years through *Pd* invasion (0–1 years with *Pd*), epidemic (2–4 years with *Pd*), and established years (5+ years with *Pd*). By *Pd* establishment, all female and male bats decreased body mass with increasing latitude across a spatial threshold at 39.6° N. Differences in bat mass north and south of the spatial threshold progressively increased over *Pd* exposure time-steps such that body mass was lower in northern latitudes compared to southern latitudes by *Pd* establishment. Results indicated that the progressive differences in *E. fuscus* body mass with latitude across the eastern United States are due to long-term pathogen exposure; however, other environmental and ecological pressures may contribute to decreases in *E. fuscus* body mass with latitude and long-term pathogen exposure. As pathogen introductions and emerging infectious diseases become

more prevalent on the landscape, it is imperative that we understand how less susceptible species directly and indirectly respond to long-term pathogen exposure in order to maintain population health in surviving species.

INTRODUCTION

Introduced and invasive species change environments and ecosystems globally (Crowl et al., 2008; Mack et al., 2000). Introduced pathogens contribute to emerging and reemerging infectious diseases that are evolutionary threats to biodiversity (Daszak et al., 2000) and induce varied inter- and intraspecific physiological responses in hosts (Moore et al., 2018; Poorten & Rosenblum, 2016). Host species highly susceptible to infection with high mortality from infection receive the most research attention upon disease emergence (Altizer et al., 2004; Lorch et al., 2016; McGuire et al., 2017; Voyles et al., 2007). Hosts less susceptible to pathogen infections with low mortality from infection (relative to highly susceptible host species) also do receive research attention, but typically only within the context of highly susceptible hosts (Cheng et al., 2021; Dhondt et al., 2013; Fischer et al., 1997; Harding et al., 2022; Pannkuk et al., 2021; Poorten & Rosenblum, 2016). Consequently, we know less about responses of less susceptible hosts, although they are also at risk. Ignoring less susceptible host responses overlooks the largest contributors to diversity following pathogen invasions, the mechanisms they deploy that make them less vulnerable to pathogen infection, and ignores potentially innovative and effective treatments for highly susceptible species with infections.

Pathogen exposure elicits energetically expensive host immune responses, so traits that represent energy responses (e.g., mass, fat, metabolism) may influence species' susceptibility to disease (Schoenle et al., 2018). Body condition (mass or fat) contributes to host susceptibility, such that susceptibility generally scales negatively with body condition (Downs et al., 2019). Host responses to infection can be negative, positive, or null (Sánchez et al., 2018). For example, when faced with a pathogen, animal species may respond by decreasing mass or fat due to additional costs of fighting infection, increasing energy expenditures to fight infection, or by maintaining mass or fat if infection does not cost additional energy or individuals are able to make up for additional energy losses (Cheng et al., 2019; Luong et al., 2017; McGuire et al., 2017; Poorten & Rosenblum, 2016).

Environmental, behavioral, and physiological factors may also add to the complexities of host responses to pathogens. For example, climatic and/or land use factors associated with pathogen reproduction, host resource availability, and/or host nutrition quality can contribute to pathogen emergence, transmission, and epidemics at varying spatial resolutions (Descloux et al., 2012; Hall, 2019). Avoidance of pathogens or parasites by hosts or management interventions by humans can contain the spatial extent of a disease outbreak (Ferguson et al., 2001; Loehle, 1995). Finally, seasonal movements associated with life history or life cycle stages can create hotspots for disease outbreaks geographically, particularly when hosts are under additional stressors like reproduction and/or migration (Bartel et al., 2011; Plowright et al., 2014). Thus, the environment, behavior, and physiology can influence spatial gradients of disease and add another layer of complexity to how individuals physiologically respond to pathogen emergence.

Mammalian species with broad geographic ranges may have greater mass in high latitudes compared to low latitudes to reduce heat loss through smaller surface areas to volume ratios in colder climates, as Bergmann's rule suggests (Bergmann, 1847). Body mass is also negatively associated with host susceptibility to pathogens, such that, as host body mass increases, host susceptibility to pathogen infection decreases due to increased immune functioning (Downs et al., 2019). If both tendencies for mass exist, we would then expect mammals to have decreased susceptibility to pathogen infections as latitude increases. However, these patterns are unlikely when heterothermic mammals (mammals that switch between regulating body temperature internally or through the environment) are vulnerable to pathogen infections. Heterothermic mammals undergo periods of suppressed immune functioning during torpor or hibernation (Prendergast et al., 2002), and if a pathogen that infects them can thrive in hibernacula, responses to infection like a loss of body mass can alter latitudinal thermoregulatory patterns.

Pseudogymnoascus destructans (*Pd*) is an invasive fungal pathogen that causes white-nose syndrome (WNS) in North American hibernating bats (Blehert et al., 2009;

Lorch et al., 2011). *Pd* was introduced from Eurasia and discovered in 2006 in New York, USA (Blehert et al., 2009; Drees et al., 2017; Leopardi et al., 2015). *Pd* exhibits optimal growth between 12 and 16°C (Verant et al., 2012), which allows *Pd* to thrive in bat hibernacula where environmental conditions are typically optimal for *Pd* growth. *Pd* infects epithelial tissues of bat wings and muzzles during winter hibernation, which increases host evaporative water loss, increases host metabolic rates, and induces a host energy imbalance and consequent starvation (McGuire et al., 2017; Meteyer et al., 2009). Extreme depletion of hibernating bat host energy from *Pd* infection has led to local extinctions of highly susceptible bat species, devastating populations of North American temperate bats (Frick et al., 2015).

Bats surviving winter *Pd* infections have physiological responses that may impact life history stages outside of hibernation. *Pd* infections in winter increase energy expenditures in spring as bats fight infection upon arousal from hibernation (Fuller et al., 2020; Meierhofer et al., 2018). At the same time that bats arouse from hibernation, bats begin to migrate to summer grounds, and females become pregnant (Wimsatt, 1944). With arousal from hibernation, migration, and initiation of reproduction occurring at once, available energy for host immune functioning is limited. Therefore, additive energy depletions within bats that survive hibernation with *Pd* infections likely have consequences that carry over into all seasons.

Despite estimated population declines of up to 50% from WNS (Cheng et al., 2021; Simonis et al., 2020; Turner et al., 2011), *Eptesicus fuscus* are classified as a less susceptible host species that may have some degree of resistance to *Pd* infection, which allows them to persist in greater numbers than highly susceptible host species with population losses exceeding 90% (Cheng et al., 2021; Frank et al., 2014; Moore et al., 2018). *E. fuscus* are a large-bodied temperate bat species, so shifts to traits that represent energy responses may go unnoticed because their ability to survive *Pd* invasion is predicted to be due, in part, to their greater body mass relative to other bat species (Haase et al., 2021). However, *E. fuscus* continue to have annual *Pd* infections each winter, setting up seasonal shifts in body mass due to additive energy expenditures needed to mount immune responses to fight *Pd* infections during winter hibernation and spring emergence (Field et al., 2015; McGuire et al., 2017; Meierhofer et al., 2018). Here, we quantify changes to *E. fuscus* body mass as a first step to understanding their persistence on the landscape despite chronic *Pd* exposure. We use long-term datasets to understand how *E. fuscus* body mass changed under long-term pathogen pressures, how variation in responses contributed to that change, and how these changes occurred across a broad spatial scale. We quantified shifts in *E. fuscus* body mass before and after *Pd* introduction across the eastern United States using 30 years of capture data. We hypothesized that average mass and mass variation would decrease over *Pd* exposure time, with declines in mass and mass variation increasing with latitude. Our results illuminate how species less susceptible to pathogen infection are subject to morphological changes under pathogen pressures over exposure time and across a large spatial gradient, which can indicate physiological changes within less susceptible host species over time.

METHODS

Data collection

We collated 40,414 *E. fuscus* capture records collected between March and October 1990–2020 from wildlife agencies and researchers in Georgia, Illinois, Indiana, Kentucky, Mississippi, New York, North Carolina, Ohio, Pennsylvania, Tennessee, and Virginia. These capture records represented individual *E. fuscus* capture but not mark and recapture; therefore, specific individuals were not tracked. We extracted records that included date of capture, capture site name, sex (male/female), reproductive status (females only: nonreproductive/pregnant/lactating/postlactating), age (adult/juvenile), and mass (in grams) at time of capture. We removed records not meeting these minimal requirements from the dataset, and 30,496 individual capture records remained. Site descriptions were substituted for unnamed sites. If no site description was reported, we further assigned an individual site name based on state and county of capture. Finally, if site names were labeled by capture nets (e.g., "Site 1 Net A" and "Site 1 Net B"), we pooled nets under the single site name (e.g., "Site 1 Net A" and "Site 1 Net B" both become "Site 1"). Due to the potential of exposing the location of sensitive species, sites were masked for all analyses by labeling each site name by state and a unique identifier. For example, "Site 1" in Ohio became "OH_01."

We subset data for adult *E. fuscus* captures only. Data were further cleaned to remove inconsistencies in the capture records. For example, if an *E. fuscus* was marked as a pregnant male, it was eliminated from the dataset. The resulting *E. fuscus* capture dataset used here represented 24,129 adults: females ($n = 14{,}162$) and males ($n = 9967$; Figure 1; Appendix S1: Figure S1).

To evaluate *E. fuscus* across the landscape, we incorporated county of capture into the dataset. If county was provided by data contributors, we used the reported county of capture. If latitude and longitude of capture
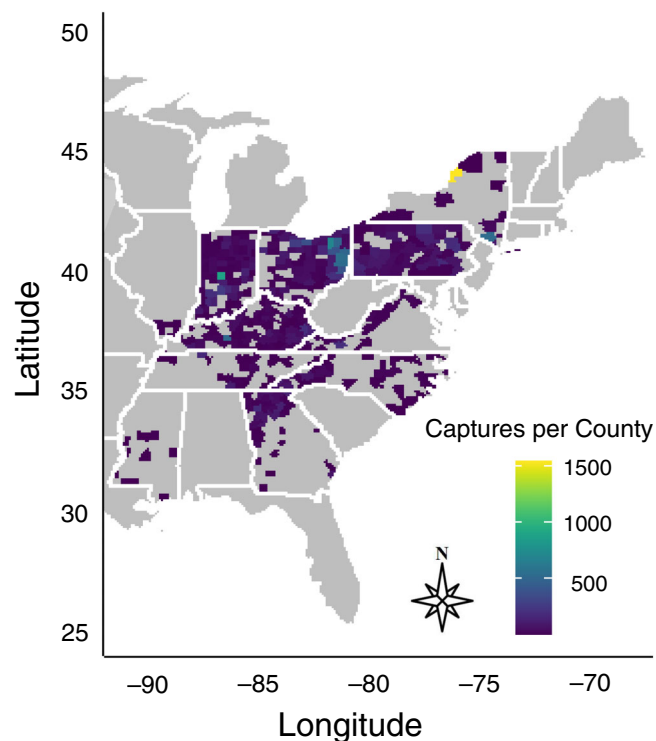
FIGURE 1 Adult (females $n = 14{,}162$; males $n = 9967$) *Eptesicus fuscus* capture counts per county from March through October from 1990 to 2020 in this eastern US dataset, ranging in latitude from 30.5° N to 44.8° N (approximately 1581 km from the northernmost to the southernmost county centroid point). Gray shading represents areas where data were either not collected or not contributed.

were provided, we linked this spatial point to the county of capture using the sp, maps, and maptools packages in the statistical environment R version 4.0.5 (Bivand et al., 2013; Bivand & Lewin-Koh, 2021; Original S code by Richard A. Becker and Allan R. Wilks. R version by Ray Brownrigg. Enhancements by Thomas P. Minka and Alex Deckmyn, 2018; Pebesma & Bivand, 2005; R Core Team, 2021). Once county was identified for each entry, we determined the county centroid point using the housingData package (Hafen, 2016), with the resulting dataset spanning from 30.5° N to 44.8° N (approximately 1581 km from the northernmost to the southernmost county centroid point). The year of *Pd* introduction was determined as the earliest year of confirmed or suspected *Pd* occurrence using data provided by the US Geological Survey for *Pd* surveillance in the form of a map application at whitenosesyndrome. org (White Nose Syndrome Response Team, 2022). To standardize *Pd* introduction across capture datasets in different states, we set year of confirmed or suspected *Pd* occurrence in each state as the baseline ("0"), so the number of *Pd* exposure years spanning from before introduction were negative integers and those after introduction were

positive integers. From these data, time-steps were created to represent groupings for disease status at the time of capture (sensu Langwig, Voyles, et al., 2015): pre-*Pd* invasion (<0 years), *Pd* invasion (0–1 years), *Pd* epidemic (2–4 years), and *Pd* established (5+ years). We used these time-steps to remain consistent with pathogen invasion time groupings used within the North American bat/*Pd* system (Cheng et al., 2021).

Statistical analyses

We completed statistical analyses in R and data visualizations using the package ggplot2 (R Core Team, 2021; Wickham, 2009). To quantify changes in body mass with increasing *Pd* exposure time, we used a two-step approach (Appendix S1: Figure S2). First, we created linear mixed-effects models using the function lmer from the package lme4 (Bates et al., 2015). Separate linear mixed-effects models were created for male or female bats for mass as a function of an interaction between *Pd* exposure time-steps and county centroid latitude. For adult female models, we included reproductive status at the time of capture into the interaction term. We used capture site as a random effect in all linear mixed-effects models to account for differences in researcher site visits year-to-year and nightly capture effort. We also weighted each model by the number of samples in each *Pd* exposure time-step to account for increases and decreases in annual capture effort throughout different regions of the eastern United States following *Pd* introduction (U.S. Fish and Wildlife Service, 2020). Linear model assumptions were checked using the plot_model function in the sjPlot package in R, and assumptions were met for both female and male models (Lüdecke, 2021; R Core Team, 2021). We used a Type III ANOVA with Satterthwaite's method using the function anova in base R (R Core Team, 2021) to determine a relationship between the interaction terms and mass. To determine how *Pd* exposure time-steps (and reproductive status for females) drove significant changes to mass across the landscape, we calculated the slopes for mass across latitude for each time-step and reproductive status (females only) using the emtrends function in the emmeans package (Lenth, 2021).

Second, analyses for mass identified an average latitudinal point at 39.6° N where changes occurred over time for males and females. This point where the interaction occurred ranged from 37.2° N to 42.1° N depending on reproductive status (females only) and *Pd* exposure time-step. To quantify differences across this spatial threshold, we created secondary linear mixed-effects models similar to initial models but replaced county

centroid latitude with a newly created variable for categories north/south of the full model spatial threshold average at 39.6° N (Appendix S1: Figure S2A). Therefore, secondary linear mixed-effects models were created for mass as a function of an interaction between *Pd* exposure time-steps and latitudinal category. Female models also included their reproductive status at the time of capture into the interaction term. These secondary models were weighted by the number of *E. fuscus* captures within each latitudinal category. Linear model assumptions were checked and met using the plot_model function in the sjPlot package in R (Lüdecke, 2021; R Core Team, 2021). We used a Type III ANOVA with Satterthwaite's method with the function anova in base R (R Core Team, 2021) to determine differences in body mass as explained by an interaction between *Pd* exposure time-steps and latitudinal category (north/south) with a random effect for capture site. We again included reproductive status in female models to better understand how chronic *Pd* exposure may affect mass throughout reproduction. When interactions between *Pd* exposure time-step, latitudinal category, and reproductive status (females only) were significant, we restricted post hoc analyses to biologically relevant pairwise contrasts using the emmeans and pairs functions in the emmeans package (Lenth, 2021). For example, we limited contrasts to determine significant differences between bat mass from northern and southern populations within a given reproductive status and/or *Pd* time-step or to determine significant differences within a given reproductive status across *Pd* time-steps and/or latitudinal categories. Finally, differences in northern and southern masses were determined by extracting mass differences and their standard errors from post hoc analyses and performing two-tailed *t* tests on normal distributions between individual *Pd* exposure time-steps.

To quantify changes to variation in *E. fuscus* body mass across space and *Pd* exposure time-steps, we used a hierarchical method (Appendix S1: Figure S2B). We first created male or female linear mixed-effects models using the function lmer from the package lme4 (Bates et al., 2015). The models were created for mass and each sex (male/female) as functions of only random effects (no fixed effects) for capture year, month, and site. Using only random effects allowed us to account for natural year-to-year variation, fluctuations in body mass caused by reproduction and natural history from March through October, and variation in survey effort at capture sites. We then extracted residuals from these models and used them as a proxy for mass variation as the response variable in secondary linear models to determine spatiotemporal changes from pathogen invasion. Using the function lm in base R (R Core Team, 2021), we subjected mass variation (mass residuals from the first model) to an interaction of *Pd* exposure time-steps and a

latitudinal category for north/south of the spatial threshold (Appendix S1: Figure S2). In female models, we also incorporated reproductive status into the interaction term. For these secondary variation models, we used a Type I ANOVA to determine differences in mass variation north/south of the spatial threshold over time using the anova function in base R (R Core Team, 2021). We calculated post hoc pairwise contrasts using the emmeans and pairs functions in the emmeans package (Lenth, 2021) in the same way as average body mass comparisons.

RESULTS

Changes in female mass over space and time

We identified a spatial threshold at 39.6° N where an interaction of *Pd* exposure time-steps and reproductive status occurred ($F_{9,2646} = 4.010$, $p = 0.0342$, $R^2 = 0.71$; Appendix S1: Figure S3A and Table S1). Nonreproductive female mass did not have a significant slope (stable) with latitude in pre-invasion ($n = 364$; average slope [upper, lower 95% CL]; 0.0467 [−0.1476, 0.2409]) and invasion ($n = 346$; −0.0994 [−0.2039, 0.0050]) years, but decreased with latitude in epidemic ($n = 599$; −0.1206 [−0.1973, −0.0439]) and establishment years ($n = 619$; −0.2487 [−0.2171, −0.0466]; Appendix S1: Figure S3A). Pregnant bat mass was stable in pre-invasion ($n = 298$; 0.1996 [−0.0387, 0.4379]), invasion ($n = 341$; 0.0230 [−0.1463, 0.1923]), and epidemic years ($n = 745$; −0.0319 [−0.1200, 0.0562]), but decreased with latitude in establishment years ($n = 701$; −0.2810 [−0.4026, −0.1595]; Appendix S1: Figure S3A). Lactating bat mass was stable with latitude in pre-invasion ($n = 564$; 0.0605 [−0.1115, 0.2326]) and invasion years ($n = 983$; −0.0285 [−0.1186, 0.0617]), but decreased with latitude in epidemic ($n = 1677$; −0.1426 [−0.2064, −0.0787]) and establishment years ($n = 1820$; −0.2451 [−0.3269, −0.1633]; Appendix S1: Figure S3A). Postlactating bat mass was stable in pre-invasion ($n = 614$; 0.1203 [−0.0543, 0.2949]) and invasion years ($n = 1154$; −0.0493 [−0.1259, 0.0273]), but decreased with latitude in epidemic ($n = 1864$; −0.1820 [−0.2471, −0.1169]) and establishment years ($n = 1473$; −0.1319 [−0.2171, −0.0466]; Appendix S1: Figure S3A).

When splitting latitude into categories north/south of the spatial threshold, female mass was lower in northern latitudes compared to southern latitudes by *Pd* establishment for nonreproductive, pregnant, lactating, and postlactating bats ($F_{9,2646} = 2.185$, $p = 0.0201$, $R^2 = 0.53$; Figure 2; Appendix S1: Table S1). Nonreproductive, lactating, and postlactating bat mass was not different from north to south in pre-invasion years (post hoc Tukey's
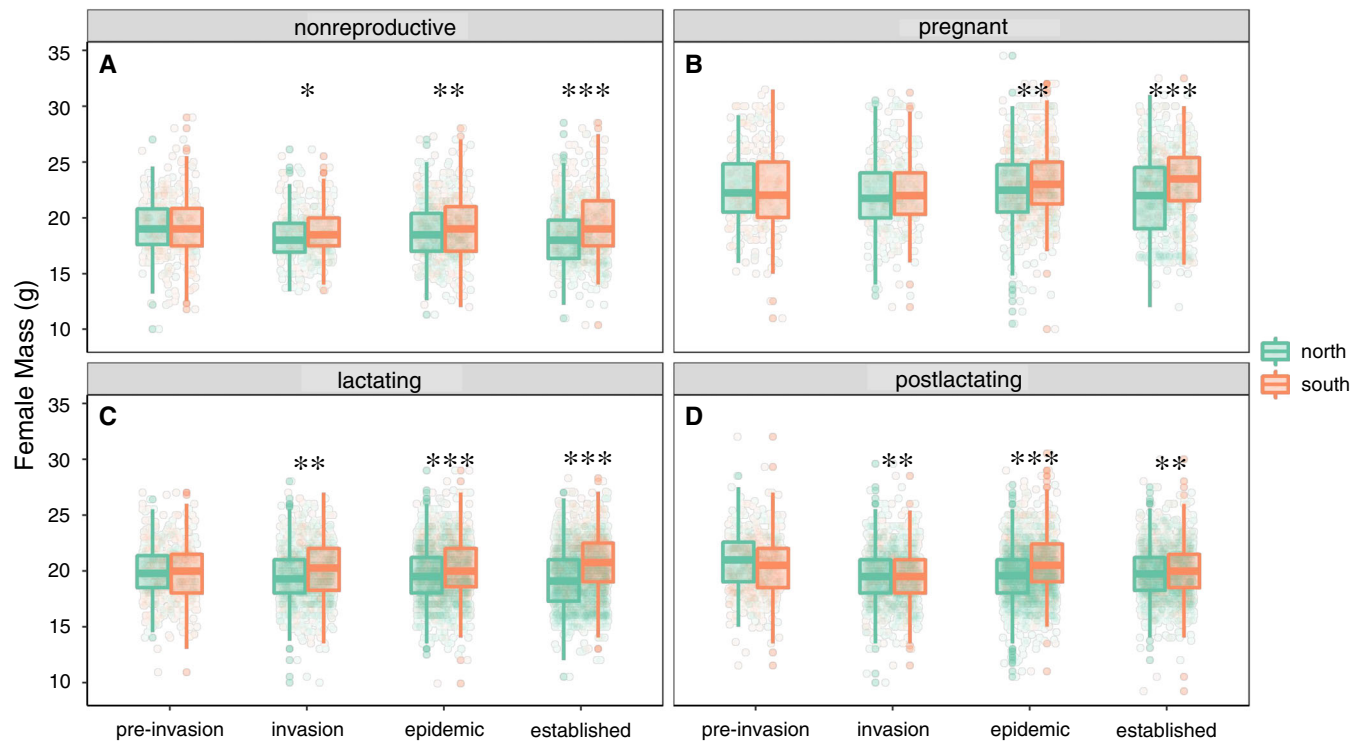
FIGURE 2 Female mass is less in northern latitudes compared to southern latitudes by *Pseudogymnoascus destructans* establishment for nonreproductive (A), pregnant (B), lactating (C), and postlactating (D) *Eptesicus fuscus* ($F_{9,2646} = 2.185$, $p = 0.0201$, $R^2 = 0.53$). Values were weighted in the linear mixed-effects model by sample sizes north ($n = 9411$) or south ($n = 4751$) of the spatial threshold at 39.6° N. Circles represent raw data. Boxes represent 50% of raw data, and thick lines within each box represent median mass. Upper and lower whiskers are an additional 25% of data each. Asterisks within the figure represent post hoc differences with a Tukey's adjustment between northern and southern female bat mass. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

adjusted p for north/south comparison; nonreproductive pre-invasion: $p = 0.3155$; lactating pre-invasion: $p = 0.0783$; postlactating pre-invasion: $p = 0.8036$), but was lower in the north compared to the south in invasion, epidemic, and establishment years (nonreproductive invasion: $p = 0.0204$; nonreproductive epidemic: $p = 0.0003$; nonreproductive established: $p < 0.0001$; lactating invasion: $p = 0.0029$; lactating epidemic: $p < 0.0001$; lactating established: $p < 0.0001$; postlactating invasion: $p = 0.0060$; postlactating epidemic: $p < 0.0001$; postlactating established: $p = 0.0059$; Figure 2A,C,D). Pregnant bat mass was not different from north to south in pre-invasion and invasion years (pregnant pre-invasion: $p = 0.2655$; pregnant invasion: $p = 0.7878$) but was less in the north than the south in epidemic and established years (pregnant epidemic: $p = 0.0021$; pregnant established: $p < 0.0001$; Figure 2B). The mass of female bats also significantly varied between northern and southern bats within each reproductive status and across *Pd* time-steps (Appendix S1: Figure S4). Nonreproductive and postlactating bat mass in the north decreased from pre-invasion to establishment years (post hoc Tukey's adjusted p for *Pd* time-step comparison; nonreproductive north: $p = 0.0067$; postlactating north: $p < 0.0001$), while

their mass in the south did not change from pre-invasion to establishment years (nonreproductive south: $p = 0.9632$; postlactating south: $p = 0.5468$; Appendix S1: Figure S4A,D). Pregnant bat mass in the north and the south did not change from pre-invasion to establishment years (pregnant north: $p = 0.9956$; pregnant south: $p = 0.0625$; Appendix S1: Figure S4B). Finally, northern lactating bat mass did not change from pre-invasion to establishment years (lactating north: $p = 0.5558$) but southern lactating bat mass increased from pre-invasion to establishment years (lactating south: $p = 0.0234$; Appendix S1: Figure S4C).

Differences in north to south bat mass from pre-invasion to establishment years increased for all female demographics (Figure 3). The difference between northern and southern female bat mass was greater in establishment years than in pre-invasion years for nonreproductive (t test p for northern and southern bat mass differences; $p = 0.0014$), pregnant ($p = 0.0150$), lactating ($p = 0.0002$), and postlactating bats ($p = 0.0334$; Figure 3). The greatest mass difference between northern and southern non-reproductive, pregnant, and lactating bats occurred in *Pd* establishment years, but postlactating bats had the greatest mass difference during epidemic years (Figure 3).
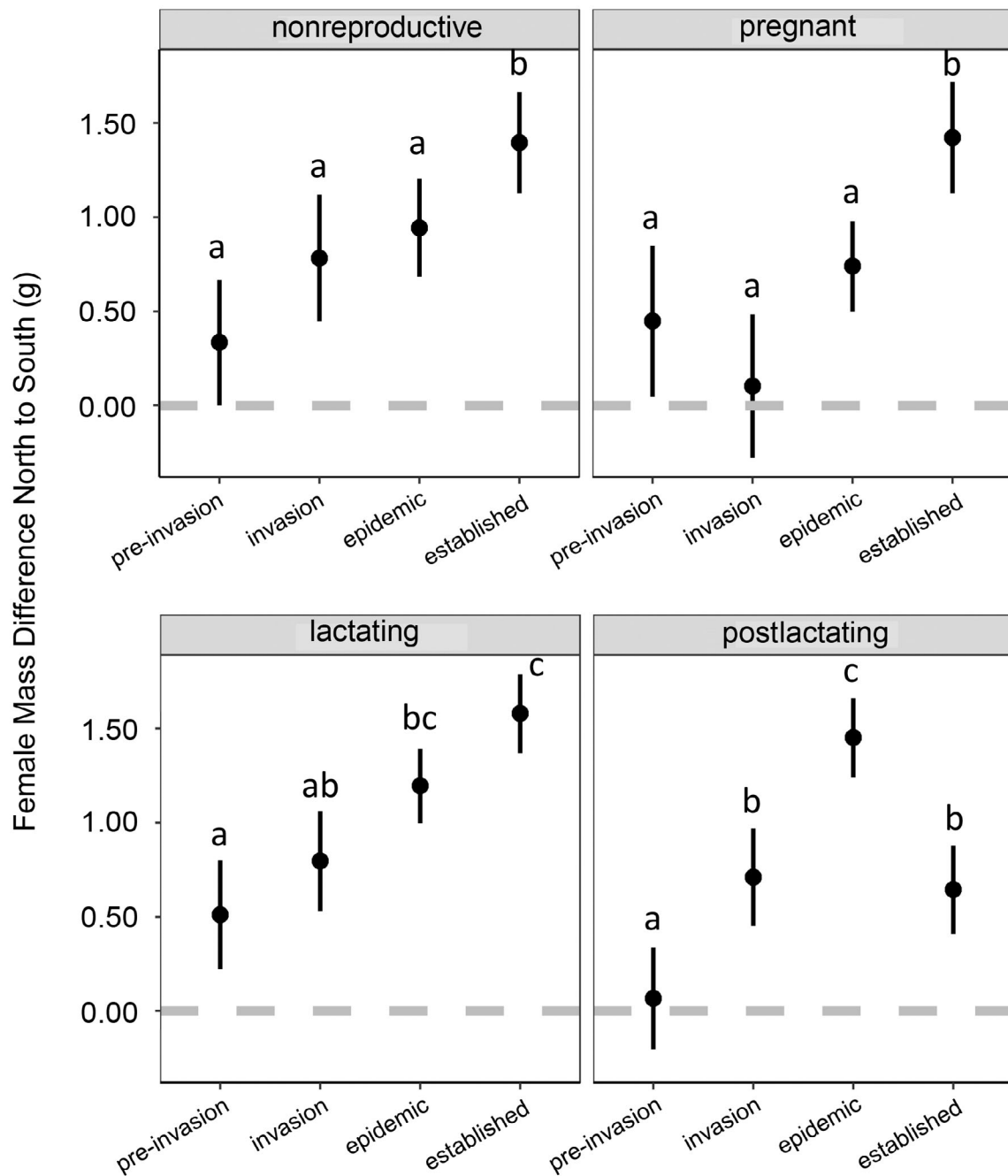
FIGURE 3   The difference in female mass from north to south increases from pre-invasion to *Pseudogymnoascus destructans* (*Pd*) established years. Points are mean differences in mass, and error bars are standard errors extracted from post hoc results for north/south comparisons across *Pd* time-steps and grouped by reproductive status. Dotted lines at "0" represent the neutral point where there is no difference in body condition from north to south. Different lowercase letters indicate significant differences based on *t* tests between individual comparisons for *Pd* exposure time-steps within groupings for reproductive status.

Changes in female mass variation over space and time

Year, month, and capture site accounted for 53% of variation in mass ($t = 29.22$, $p < 0.0001$, $R^2 = 0.53$; Appendix S1: Table S2). Mass variation also significantly differed between categories north/south of the spatial threshold with *Pd* exposure time-steps and reproductive status ($F_9 = 1.986$, $p = 0.0367$, $R^2 = 0.05$; Appendix S1: Figure S5 and Table S2). Mass variation for all female demographics was not different from north to south in pre-invasion and invasion years (post hoc Tukey's adjusted *p* for north/south comparison; nonreproductive pre-invasion: $p = 0.7466$; nonreproductive invasion:

$p = 0.3239$; pregnant pre-invasion: $p = 0.8918$; pregnant invasion: $p = 0.0606$; lactating pre-invasion: $p = 0.9401$; lactating invasion: $p = 0.9472$; postlactating pre-invasion: $p = 0.2169$; postlactating invasion: $p = 0.2070$; Appendix S1: Figure S5). In epidemic years, postlactating bat mass variation in the north was less than in the south (postlactating epidemic: $p = 0.001$), but nonreproductive, pregnant, and lactating bat mass variation was not different from north to south (nonreproductive epidemic: $p = 0.2437$; pregnant epidemic: $p = 0.1227$; lactating epidemic: $p = 0.8569$; Appendix S1: Figure S5). In Pd establishment years, nonreproductive and lactating female bats had more mass variation skewed toward values greater than the mean in the north compared to the south (nonreproductive established: $p = 0.0017$; lactating established: $p = 0.0432$), pregnant bats had less mass variation in the north compared to the south (pregnant established: $p = 0.0244$), and postlactating bat mass variation was not different from north to south (postlactating established: $p = 0.7728$; Appendix S1: Figure S5).

Mass variation significantly differed by reproductive status, latitudinal category, and Pd time-steps (Appendix S1: Figure S6 and Table S2). Northern nonreproductive female mass variation increased toward values less than the mean from pre-invasion to establishment years (post hoc Tukey's adjusted p for Pd time-step comparison; nonreproductive north: $p = 0.0469$), while southern nonreproductive mass variation did not change from pre-invasion to establishment years (nonreproductive south: $p = 1.000$; Appendix S1: Figure S6). Northern and southern pregnant and lactating bat mass variation did not change from pre-invasion to established years (pregnant north: $p = 0.9609$; pregnant south: $p = 0.0637$; lactating north: $p = 0.9934$; lactating south: $p = 0.6339$; Appendix S1: Figure S6). Finally, northern postlactating bat mass variation decreased from pre-invasion to establishment years (postlactating north: $p = 0.0141$), while southern postlactating bat mass variation did not change from pre-invasion to establishment years (postlactating south: $p = 0.8433$; Appendix S1: Figure S6).

Changes in male mass over space and time

Just as with female mass, we identified a spatial threshold at 39.6° N where an interaction of Pd exposure time-steps occurred ($F_{3,2729} = 5.474$, $p < 0.0001$, $R^2 = 0.58$; Appendix S1: Figure S3B and Table S3). Male mass did not have a significant slope with latitude in pre-invasion ($n = 1542$; 0.0130 [−0.0752, 0.1013]) and invasion years ($n = 1813$; 0.0339 [−0.0182, 0.0860]), but decreased with increasing latitude in epidemic ($n = 3237$; −0.0690 [−0.1082, −0.0298]) and establishment years

($n = 3$, 375; −0.0839 [−0.1339, −0.0339]; Appendix S1: Figure S3B). When using a latitudinal category for north/south of the spatial threshold, male mass significantly differed from north to south depending on Pd exposure time-steps ($F_{3,2729} = 6.790$, $p = 0.0002$, $R^2 = 0.41$; Figure 4A; Appendix S1: Table S3). Male bat mass was lower in the north than the south in pre-invasion years (post hoc Tukey's adjusted p for north/south comparison; pre-invasion: $p = 0.0340$), undistinguishable from north to south during invasion years (invasion: $p = 0.6508$), but weighed less in the north compared to the south in epidemic and establishment years (epidemic: $p < 0.0001$; established: $p < 0.0001$; Figure 4A). Although northern male mass was lower than southern male mass in pre-invasion years, the difference between northern and southern mass more than doubled by Pd establishment. When grouped by latitudinal category, northern male bat mass decreased from pre-invasion to establishment years while southern male bat mass did not change from pre-invasion to establishment (post hoc Tukey's adjusted p for Pd time-step comparison; north: $p = 0.0001$; south: $p = 0.6749$; Appendix S1: Figure S7).

Differences between northern and southern male bat mass increased from pre-invasion to epidemic and Pd establishment years (Figure 4B). By Pd establishment, the difference between northern and southern male $E.\ fuscus$ body mass was greater than in pre-invasion years (t test p for northern and southern bat mass differences; $p = 0.0036$; Figure 4B). In epidemic and established years, male bats had the greatest mass differences between latitudinal categories (Figure 4B).

Changes in male mass variation over space and time

Month, year, and site described 61% of male mass variation ($t = 23.75$, $p < 0.0001$, $R^2 = 0.61$; Appendix S1: Table S4). Male mass variation significantly differed from north to south depending on Pd exposure time-steps ($F_3 = 3.006$, $p = 0.0291$, $R^2 = 0.003$; Appendix S1: Table S4). However, this secondary male mass variation model failed to converge with a y-intercept that was not statistically different from zero.

DISCUSSION

Emerging infectious disease epidemics threaten biodiversity globally (Daszak et al., 2000) and are difficult to assess, often due to lack of data prior to pathogen emergence. Furthermore, research on species less susceptible to pathogen infections (e.g., $E.\ fuscus$) is limited and/or
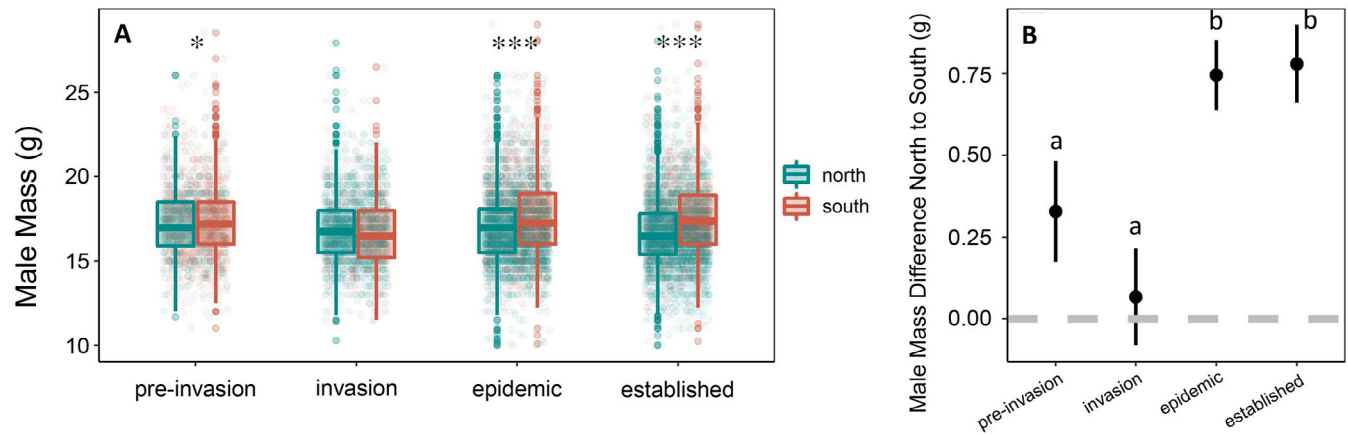
FIGURE 4 Male *Eptesicus fuscus* mass is less in northern latitudes compared to southern latitudes during *Pseudogymnoascus destructans* (*Pd*) establishment ($F_{3,2729} = 6.790$, $p = 0.0002$, $R^2 = 0.41$; A), and the north/south difference in mass increases across *Pd* exposure time-steps (B). (A) Values were weighted in the linear mixed-effects model by sample sizes north ($n = 6273$) or south ($n = 3694$) of the spatial threshold at 39.6° N. Circles represent raw data. Boxes represent 50% of raw data and thick lines within each box represent median values. Upper and lower whiskers represent an additional 25% of values. Asterisks within the figure represent post hoc differences with a Tukey's adjustment between northern and southern female bat mass. *$p < 0.05$; ***$p < 0.001$. (B) Points are mean differences in mass, and error bars are standard errors extracted from post hoc results for north/south comparisons across *Pd* time-steps. Dotted lines at "0" represent the neutral point where there is no difference in body condition from north to south. Different lowercase letters indicate significant differences based on *t* tests between individual comparisons for *Pd* exposure time-steps.

typically put in the context of comparisons to highly susceptible species. We focus on understanding how pathogen exposure uniquely changes less susceptible species as they become greater contributors to what remains of diversity as highly susceptible species become more rare (Cortez et al., 2017). Using a robust 30-year dataset consisting of 24,129 individual *E. fuscus*, we demonstrate that progressive *Pd* exposure caused *E. fuscus* body mass to decrease with increasing latitude, the effects of which were greater with increasing pathogen exposure time and were most pronounced at higher latitudes. Additionally, variation in body mass decreased or skewed toward values below average mass with increasing latitude and pathogen exposure time-steps. These results highlight the importance of how introduced pathogens can cause spatially driven reductions in trait diversity over time.

Anthropogenic changes in the environment that alter insect prey populations, such as climate change and insecticide use, could have played a role in altering *E. fuscus* body mass with *Pd* exposure time-steps (Wagner, 2020). Declines in available insect prey and the nutrition quality of insect prey have also been suggested to contribute to declines in other temperate bat body conditions over time without *Pd* infections (Davy et al., 2022). All female demographics and male bat body mass decreased with latitude by *Pd* establishment, and differences between northern and southern bat mass progressively increased. Decrease in body mass with latitude may reflect differences in insect availability. *E. fuscus* are

insectivores and typically prefer to eat beetles and moths even when the relative abundance of beetle and moth prey is low compared to other insect prey species (Becker et al., 2015; Menzel et al., 2020; Valdez & O'Shea, 2014; Whitaker, 1995; Wray et al., 2021). However, *E. fuscus'* preference for beetles and moths could contribute to their body mass declines with latitude since beetle, moth, and insect abundance, in general, has decreased globally (Sánchez-Bayo & Wyckhuys, 2019; Wagner et al., 2021). For example, warming winter conditions in the northeastern United States have decreased beetle abundance by 39% since the 1970s (Harris et al., 2019). These declines in available beetle and moth prey in northern latitudes are also likely due to heavy insecticide use, which contributes to global insect declines (Sánchez-Bayo & Wyckhuys, 2019). In our dataset, the threshold that delineated changes in body mass (39.6° N) runs directly through the lower extent of the Corn Belt region in the midwestern United States, which is one of the strongest contributors to terrestrial global insect declines (van Klink et al., 2020). The Corn Belt region has the largest quantities of insecticide use in the United States (Pimentel & Burgess, 2014), suggesting beetle and moth availability may be lower in the Corn Belt region compared to other regions. In addition to decreasing beetle and moth availability, ingestion of insecticides can impact *E. fuscus'* physiology. When *E. fuscus* ingests insecticides, insecticide toxicity can cause thermoregulatory irregularities and weight loss (Eidels et al., 2016),

which could contribute to bat body mass being lower in northern latitudes, where the Corn Belt region is, compared to southern latitudes by pathogen establishment. Therefore, the impacts of climate change and insecticide use could have additive effects on *E. fuscus* body mass with increasing latitude and long-term *Pd* exposure.

We expected broad latitudinal patterns for body mass to be altered by a pathogen because of increased energy expenditures associated with active and healing infections (Derting & Compton, 2003; Hawley et al., 2012; McGuire et al., 2017; Meierhofer et al., 2018). Bergmann's rule suggests that species have greater mass in higher latitudes compared to lower latitudes to reduce surface area to volume ratios, thereby decreasing heat loss in those colder climates (Bergmann, 1847). Latitudinal patterns for *E. fuscus* body mass did change across *Pd* exposure time-steps (pre-invasion, <0 years; invasion, 0–1 years; epidemic, 2–4 years; and established, 5+ years), but *E. fuscus* did not follow Bergmann's rule at any *Pd* time-step. There was no difference in body mass from north to south in pre-invasion years across *E. fuscus* reproductive statuses; however, lower body masses were found in northern latitudes compared to southern latitudes by *Pd* establishment years. Further, male *E. fuscus* weighed less in northern latitudes compared to southern latitudes in pre-invasion and establishment years, and overall, *E. fuscus* body mass opposed Bergmann's rule by *Pd* establishment for all adult bats in all reproductive stages (body mass decreasing with latitude). We also expected patterns for Bergmann's rule to be present in pre-invasion years (which was not supported) because it would maximize *E. fuscus*' ability to conserve body heat in cooler, northern climates in combination with Allen's rule (Burnett, 1983). *E. fuscus* are known to follow Allen's rule prior to *Pd* introduction, which states that the length of mammalian extremities should decrease with increasing latitude to reduce surface area to volume ratios (Allen, 1877). To provide insight into how latitudinal thermoregulatory patterns are altered with pathogen exposure, research investigating changes in extremities, such as forearm length, for *E. fuscus* is needed.

Latitudinal patterns for *E. fuscus* body mass following *Pd* introduction could be explained by changes in inter- and intraspecific competition for resources. *E. fuscus* body mass for males and females decreased with increasing latitude by *Pd* establishment years with differences between northern and southern bat mass increasing with *Pd* exposure time-steps. These effects could support a spatially driven, unstable coexistence between less susceptible and highly susceptible species. Mortality from *Pd* infections of highly susceptible hosts is greater in northern latitudes compared to southern latitudes in the eastern United States, likely due to how individual hosts and *Pd*

interact with their environment and because *Pd* has been in the northeastern United States longer (Frick et al., 2017; Hayman et al., 2016). Interspecific competition for resources (i.e., food, water, foraging habitat) with *E. fuscus* should decrease with increasing latitude since there are fewer highly susceptible hosts. Decrease in interspecific competition with latitude suggests intraspecific competition between *E. fuscus* individuals may increase with latitude throughout spring through summer months because (1) there are proportionally more *E. fuscus* individuals present in northeastern and midwestern states following *Pd* introduction (Francl et al., 2012; Pettit & O'Keefe, 2017), and (2) *E. fuscus* have strong site fidelity, especially for females during reproduction, suggesting they would still use the same foraging and roosting areas post-*Pd* (Brigham, 1991; Wilkinson & Barclay, 1997). Taken together, progressive effects of *Pd* exposure time on *E. fuscus* body mass mirrors spatial gradients of highly susceptible species mortalities. Increased intraspecific competition for resources like food, water, and foraging habitat would not benefit populations long-term because, theoretically, intraspecific competition is stronger than interspecific competition according to the Lotka–Volterra competition model (Gotelli, 2008). Although *E. fuscus* may attempt to mitigate the cost of intraspecific competition following *Pd* invasion by taking advantage of optimal foraging sites where highly susceptible *Myotis lucifugus* are still present in small numbers (Jachowski et al., 2014), pressures for intraspecific competition under *Pd* establishment may be an indirect effect of pathogen invasion, as reflected by reductions in body mass with latitude and *Pd* exposure time-steps.

E. fuscus may have some degree of resistance to *Pd* infection (Frank et al., 2014) and are less susceptible to infection compared to the highly susceptible host *M. lucifugus* (Moore et al., 2018). However, resistance to pathogens comes at an energetic cost. For example, it costs energy to mount immune responses (Hegemann et al., 2012), avoid pathogens or parasites (Luong et al., 2017), or even just meet increased energy demands (Voigt et al., 2010). We found males and nonreproductive and postlactating females lost mass from pre-invasion to *Pd* establishment in northern latitudes. From pre-invasion to establishment, northern males lost 3% (0.6 g) of their mass. Although northern males weighed 2% (0.4 g) less than southern males in pre-invasion years, that difference was doubled to 5% (0.8 g) by establishment years. Northern nonreproductive females lost on average 5% (0.9 g) of their body mass from pre-invasion to establishment years. Northern postlactating bats lost 5% (1 g) of their mass in the same time period. Declines in body mass in northern latitudes could be detrimental to *E. fuscus* entering hibernation, as surviving hibernation is positively correlated with body mass (Brigham, 1987). In contrast, highly

susceptible, nonresistant *M. lucifugus* surviving *Pd* invasion have opposite changes to body mass, with 1.1 g increases in mass on average (Cheng et al., 2019). Although *M. lucifugus* have lost over 90% of their populations due to *Pd* infections and WNS (Cheng et al., 2021), increases in body mass and fat in the few surviving *M. lucifugus* could potentially provide enough energy for them to make it through hibernation with *Pd* infections (Cheng et al., 2019). *E. fuscus*, on the other hand, have not had as extreme declines in winter populations (35% declines; Cheng et al., 2021); thus, a selection event for body mass or fat as seen in *M. lucifugus*, would not be as easily captured or could be ongoing as *E. fuscus* annually and possibly cumulatively cope with the energy costs of resistance (Bonneaud et al., 2003; Hawley et al., 2012; Martin et al., 2003). Therefore, although highly susceptible, nonresistant host species have widespread mortalities from initial pathogen invasion (Cheng et al., 2021), resistant *E. fuscus* may also incur detrimental consequences in dealing with energy demands of chronic pathogen exposure as time goes on.

We expected reproductive female body mass to decrease following *Pd* introduction because winter *Pd* infections increase bat energy expenditures in spring (Meierhofer et al., 2018). Prior to *Pd* invasion, female *E. fuscus* needed to consume 99% of their body mass during peak lactation in order to maintain body mass while caring for pups (Kurta et al., 1990). Therefore, in order for pregnant and lactating *E. fuscus* to maintain body mass in northern latitudes or increase body mass in southern latitudes in the face of additional energy losses from winter *Pd* exposure, bats would either need to eat more or increase torpor to conserve energy. Since *E. fuscus*' preferred food choice of beetles and moths are limited throughout spring and summer months (Menzel et al., 2020), we predict that reproductive *E. fuscus* use torpor to reduce caloric use more frequently following *Pd* invasion. Many heterothermic small mammals and birds use torpor during reproduction as a fitness trade-off between managing energy stores to care for young and delaying the growth of young, thus potentially limiting reproductive success (Calder & Booser, 2016; Geiser et al., 2005; McAllan & Geiser, 2014). *E. fuscus* specifically use torpor during pregnancy and lactation (Audet & Fenton, 1988). Additionally, *E. fuscus* have lower torpid metabolic rates at warm temperatures in the southern United States than in the northern United States (Dunbar & Brigham, 2010). Therefore, it is possible that pregnant and lactating *E. fuscus* north/south of the spatial threshold we identified here are maximizing their use of torpor during reproduction to maintain body mass in the north or increase body mass in the south over *Pd* exposure time-steps. Further research into reproductive energy expenditures is needed to determine how torpor

patterns in pregnant and lactating *E. fuscus* change following *Pd* invasion and if changes could affect future populations by limiting reproductive success.

We could not directly measure pathogen pressures on bats (i.e., fungal loads on individual bats); therefore, we used *Pd* exposure time-steps as an index of chronic pathogen exposure. Our methods for accounting for *Pd* exposure are adequate for the following two reasons: First, North American bats heal from winter *Pd* infections, and *Pd* becomes undetectable in spring months (Fuller et al., 2020; Langwig, Frick, et al., 2015). Since pathogen intensity decreases in spring months and becomes largely nonexistent, we may not detect *Pd* on individual bats even if they were swabbed for *Pd* during April through October. Second, body condition for North American bats is less likely to be related to *Pd* infection intensity but more likely to the duration of infection and/or exposure time (Cheng et al., 2019; Moore et al., 2018). Therefore, while the failure to directly measure pathogen pressure is a limitation in this dataset, *Pd* exposure time-steps are a suitable indirect metric for pathogen pressures within the *Pd* system.

CONCLUSIONS

Our work represents a crucial first step in quantifying how less susceptible host species respond to an introduced pathogen and how their body mass responds to long-term exposure to that pathogen. We also highlight how the long-term effects of pathogen exposure on less susceptible species are spatially manifested. The management implications from our findings are currently unclear. However, we suggest spatial gradient effects for mass with long-term pathogen exposure could be intertwined with changes to climate and food availability, indirect effects of losses of highly susceptible competitor host species, and host physiological responses to annually mediate pathogen infections at the same time as reproduction. More research into understanding how *E. fuscus* is directly impacted by *Pd* in combination with other ecological and environmental pressures is warranted to determine management implications that will benefit *E. fuscus* populations. As emerging pathogens become more prominent, it is likely that less susceptible host species will become greater contributors to host population dynamics as species richness decreases following pathogen invasions. Thus, making efforts to understand less susceptible host species responses to pathogens over time will support wildlife diversity in the future.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Simonis et al., 2022) are available from Dryad: https://doi.org/10.5061/dryad.ngf1vhhvv. R code (Simonis, 2023) is available from Zenodo: https://doi.org/10.5281/zenodo.7548231.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.