Habitat degradation can increase zoonotic disease risks by altering infection dynamics in wildlife and increasing wildlife–human interactions. Bats are an important taxonomic group to consider these effects, because they harbour many relevant zoonotic viruses and have species- and context-dependent responses to degradation that could affect zoonotic virus dynamics. Yet our understanding of the associations between habitat degradation and bat virus prevalence and seroprevalence are limited to a small number of studies, which often differ in the bats or viruses sampled, the study region, and methodology. To develop a broad understanding of the associations between bat viruses and habitat degradation, we conducted an initial phylogenetic meta-analysis that combines published prevalence and seroprevalence (‘sero)prevalence’) with remote-sensing habitat degradation data. Our dataset includes 588 unique records of (sero)prevalence across 16 studies, 64 bat species, and five virus families. We quantified the overall strength and direction of the relationship between habitat degradation and bat virus outcomes and tested how this relationship is moderated by the time between habitat degradation and bat sampling and by ecological traits of bat hosts while controlling for phylogenetic non-independence among bat species. We found no effect of degradation on prevalence overall, although a weak effect may exist when forest loss occurs the year prior to bat sampling. In contrast, we detected a negative but weak association between degradation and seroprevalence overall that was strengthened when forest loss occurred the year prior to bat sampling. No bat traits that we investigated interacted with habitat degradation to impact virus outcomes, suggesting observed trends are independent of these traits. Biases in our initial dataset highlight opportunities for future work; prevalence was highly zero-inflated, and seroprevalence was dominated by Desmodus rotundus and rabies virus. These findings and subsequent analyses will improve our understanding of how global change affects host–pathogen dynamics.

Keywords: Chiroptera, deforestation, fragmentation, land conversion, pathogen spillover, zoonotic disease
Introduction

Habitat degradation can alter wildlife infection dynamics and increase wildlife–human interactions, both of which can increase zoonotic disease risks (Borremans et al. 2019). Associations between habitat degradation and pathogen spillover to humans and domestic animals have been observed for Ebola virus disease and vector-borne diseases, including but not limited to malaria and Lyme disease (Gottwald et al. 2013, Rulli et al. 2017). In addition to the direct effects of these diseases on human and domestic animal health, zoonotic spillover from degraded environments can result in substantial economic losses, sometimes costing the global economy billions of dollars (Cascio et al. 2011). Because habitat degradation is occurring at disproportionate rates across the globe, these negative health and economic effects are likely to be exacerbated in some regions relative to others. In particular, habitat degradation rates are among the highest in the Neotropics, due to rapid clearing for agricultural expansion (Malhi et al. 2014, Taubert et al. 2018). To predict outbreaks and mitigate the costs associated with heightened disease risks in vulnerable areas, a need thus exists to investigate associations between habitat degradation in these regions and the prevalence of zoonotic pathogens in their wildlife hosts. Such investigations will be particularly valuable when focus is placed on wildlife groups that harbour a rich diversity of known and potentially zoonotic pathogens.

Bats (order: Chiroptera) are highly abundant and diverse in the Neotropics, serving important ecological roles such as seed dispersal and plant pollination, and providing ecosystem services, such as pest consumption, that benefit human societies (Kunz et al. 2011). Bats are also important reservoirs for many zoonotic viruses. Indeed, bats harbour more virulent zoonotic viruses than birds and other mammals (Guth et al. 2022), although they do not necessarily host a greater proportion of zoonotic viruses than these other taxa (Mollenbrücke and Streicker 2020). The possible human health consequences of bat-associated viruses have been highly publicized owing to associations between bats and high-profile epidemics and pandemics, such as SARS-CoV and SARS-CoV-2 (for which bats harbor ancestral viruses; Wang et al. 2006, Boni et al. 2020). The ability of bats to host a wide array of viruses could be associated with their diverse ecological traits (Gonzalez and Banerjee 2022). For instance, many bat species are highly social, with some species roosting in groups composed of millions of individuals Tadarida brasiliensis (Kerth 2008). Some bat aggregations are comprised of multiple species, facilitating high contact and possible virus spread within and among species (Luis et al. 2015). As another example, bat species have highly variable diets, ranging from frugivory to obligate sanguivory (i.e. ‘blood feeding’) (Wilman et al. 2014). Diet can alter an individual’s pathogen exposure risk and aspects of immunity (Schneeberger et al. 2013, Ingala et al. 2019).

Bats also have species- and context-dependent responses to habitat degradation that could affect zoonotic virus dynamics (Brändel et al. 2020). Indeed, the success of bats in degraded forests often depends on a number of bat traits, including diet (Carballo-Morales et al. 2021), wing morphology and body size (Farneda et al. 2015). However, because studies are typically conducted in specific regions, or with a limited number of bat species or viruses, we lack a general understanding of how habitat degradation is affecting the dynamics of Neotropical bat viruses. Prior work has established that Neotropical bats can harbour viruses from families most relevant to zoonotic risk: the Coronaviridae (Anthony et al. 2013), Hantaviridae (Sabino-Santos et al. 2015), Flaviviridae (de Thoisy et al. 2009), Paramyxoviridae (de Souza et al. 2021), and Filoviridae (Calderón et al. 2019b). Serological evidence also suggests possible circulation of Filoviridae (Schulz et al. 2020). Our limited understanding of how habitat degradation affects these viruses could hamper our ability to forecast spillover risks and thus have important implications for bat conservation, human health and economies.

In this study, we conduct an initial meta-analysis to investigate how habitat degradation affects the prevalence and seroprevalence (hereafter ‘(sero)prevalence’ when referring to both), of Neotropical bat viruses, focusing specifically on viruses in the Coronaviridae, Hantaviridae, Flaviviridae, Paramyxoviridae, Filoviridae and Rhabdoviridae families given their known risks to human health. We also assess the relationship between habitat degradation and (sero)prevalence at different time periods following habitat degradation, because we expect these outcomes will shift temporally. We expect both prevalence and seroprevalence will be higher in regions with greater degrees of habitat degradation, as has sometimes been observed for other hosts and parasites (e.g. primate gastrointestinal parasites: Mbora and McPeek 2009; avian malaria: Fecchio et al. 2021). However, we also expect these dynamics will be affected by the time between habitat degradation and sampling; for instance, because seroprevalence may represent both active and recovered infections, high seroprevalence should persist over long periods following habitat degradation, whereas prevalence should decline over time as individuals recover from infection and acquire immunity. To address these questions, we consider measures of degradation with anthropogenic stressors specifically included as well as a broader measure of degradation that only considers forest cover loss. Indeed, although the mechanisms underlying habitat degradation can be highly variable (Scanes 2018), and can have differing effects on wildlife and host–parasite dynamics (Johnstone et al. 2014, Perrin et al. 2023), extrapolating broad-scale patterns from these highly diverse processes using meta-analysis will provide critical insight into which regions to prioritize for mitigating spillover risks and for bat conservation.

Finally, because bat ecology could also affect infection outcomes in response to habitat degradation, we also ask how relationships between habitat degradation and (sero) prevalence could be moderated by five ecologically relevant bat traits: wing aspect ratio, primary diet, maximum colony size, roost duration, and echolocation traits. We expect that each bat trait could affect the relationship between habitat degradation and (sero)prevalence. For example, bat species
that roost in ephemeral structures (e.g., leaves) are more accustomed to switching roosts and are tolerant (to some extent) of roost loss (Silvis et al. 2015), whereas other bat species that rely on more-permanent roosts show decreased colony sizes after roost loss (Borkin et al. 2011). If habitat degradation damages roosting structures, and assuming density-dependent transmission, we could expect increased (sero)prevalence for species that do not use ephemeral roosts, owing to increased mortality or emigration. As additional examples, foraging-associated traits (e.g., diet, echolocation, wing aspect ratio) can affect how bats respond to habitat degradation or their pathogen exposure risks and could thus alter the relationship between habitat degradation and (sero)prevalence. For instance, bats with shared diets could face more similar exposure routes or elevated risks to particular pathogens. Phytophagous bats, for example, could be at increased risk of acquiring pathogens that transmit via saliva, owing to remnant saliva that can be left over by other bats consuming the same plant material (as has been a proposed transmission mechanism of Nipah virus; Kuzmin et al. 2011). Additionally, echolocation traits could be associated with how certain species or groups of species respond to degradation, as these traits often reflect bats that live under similar ecological conditions (Denzinger and Schnitzler 2013). Finally, wing aspect ratio could be highly important for how animals respond to degradation, such as choosing whether to disperse or remain in degraded environments (for instance, wing aspect ratio is highly associated with dispersal distance and dispersal is affected by forest degradation in birds: Van Houtan et al. 2007, Claramunt 2021).

Material and methods

Search protocol and data extraction

We systematically searched Web of Science, CabDirect and Pubmed using terms related to bats, disease, and our selected virus families of interest Coronaviridae, Hantaviridae, Flaviviridae, Paramyxoviridae, Rhabdoviridae and Filoviridae. Final searches were conducted by 15 September 2022 (Supporting information). We then followed a systematic protocol for study inclusion (Moher et al. 2009, O’Dea et al. 2021). Duplicates were removed among all databases and searches, which resulted in 3118 studies. We then filtered abstracts, using the ‘metagear’ ver. 0.7 package in R ver. 4.2.1 (www.r-project.org), to retain only articles that met our inclusion criteria (Lajeunesse 2016): studies of the six virus families listed above in any bat species in the Neotropics. Further, given the potential for urbanisation to affect virus outcomes independently of habitat degradation, we excluded studies where bats were sampled in such habitats based on site descriptions of the authors or our own analyses.

After screening abstracts, we reviewed retained articles (n = 127) for final inclusion. We excluded studies with samples collected using methods other than traditional field methods such as mist netting or harp trapping, to avoid biases toward clinically diseased (and thus positive) bats. We also excluded studies where samples taken from different individuals were pooled (i.e., we required (sero)prevalence to represent the proportion of positive individuals).

Forty-five studies were retained for inclusion in our meta-analysis. From each study, we systematically reviewed the references to identify additional studies missed by our literature search (Foo et al. 2021). Of 44 additional studies identified from references as relevant for inclusion, only two met our criteria and were retained, resulting in 47 studies total.

For each of our 47 studies, we required (sero)prevalence data and location information. Such data were wholly extracted from the main text or supplementary material for only two studies. We emailed authors for the other 45 studies, excluding 19 studies owing to no response, email failure, or lack of access to data. Eleven additional studies were excluded owing to 1) redundancy in datasets (n = 4); 2) lack of author contact information (n = 1); 3) categorization of all sampled sites as urban (n = 7). We, therefore, included a total of 16 studies in our meta-analysis (Carrington et al. 2008, Carvalho et al. 2011, Blackwood et al. 2013, Casagrande et al. 2014, Moreira-Soto et al. 2015, de Thoisy et al. 2016, Cabrera-Romo et al. 2016, Wray et al. 2016, Vicente-Santos et al. 2017, Calderon et al. 2019a, b, Griffiths et al. 2020, Seethal et al. 2020, Becker et al. 2021, Moreira Marrero et al. 2021, Darcissac et al. 2021).

From each study, we extracted the bat species sampled, the virus family, (sero)prevalence, sample size, and sampling information (e.g., sampling location). For bat species, we used a recent mammal-wide phylogeny (Upham et al. 2019; n = 1287 bats). We excluded records where (sero)prevalence was not resolved to species (e.g., Myotis spp.). For viruses, we extracted the genus and/or serotype. For sampling information, we extracted site names, country, and GPS coordinates, along with the month and year when sampling occurred. In some cases, coordinates were not provided, and we relied on site names or the midpoint of the specified region; if coordinates were not provided, sites were close together, and (sero) prevalence was not reported by site, we used approximate coordinates for the most central sampling location for those sites (for analyses conducted with these sites excluded, see the supporting information; results were qualitatively consistent with results presented in-text). Finally, we extracted the type of sample, virus detection method, and the primer set and target. In a few instances (n = 3), the raw dataset (i.e., data obtained from a repository or via email) did not correspond with the published data; in these cases, we relied on the published data unless the dataset provided detail at a finer resolution. Each row of the resulting data corresponds to a (sero) prevalence estimate from a single bat species, at a specific site, at a specific sampling period, for a given sample type. All abstracts were screened, and data were extracted, by the same individual.

We next compiled information from external databases and literature searches on the five species-level ecological traits we expected could impact the relationship between the degree of habitat degradation and virus (sero)prevalence:
wing aspect ratio (Norberg and Rayner 1987), maximum colony size (Santana et al. 2011), diet (Wilman et al. 2014), roost duration (Patterson et al. 2007), and echiolocative variables (bandwidth, peak frequency, call duration; Collen 2012). For diet, bats were classified as phytophagous, insectivorous, carnivorous, or sanguivorous if more than half of their diet consisted of fruit or nectar, insects, animals, or blood, respectively. Species whose diets were not dominated by one food type were categorized as omnivores, because all species in this category consumed both plants and insects. We used classifications small or medium-large for colony size, depending on whether colonies comprise fewer than 100 individuals or over 100 individuals. We categorized colony sizes as such because data are often presented as ranges owing to population-level variation. Because the relatedness of different bat species could impact their infection responses to degradation, we used the ‘ape’ package ver. 5.4.1 to trim the previously mentioned global bat phylogeny to our species and computed a correlation matrix to include in subsequent analyses (Paradis et al. 2004).

Spatial analysis

We used three datasets to quantify habitat degradation: the Human Footprint (HF; ver. 1.9; Venter et al. 2018), Global Human Modification of Terrestrial Systems (GHMT; Kennedy et al. 2020), and Hansen Global Forest Change (HGFC; Hansen et al. 2013) datasets. Each provides different insights into the mechanisms underlying habitat degradation. The HF and GHMT datasets use anthropogenic stressor inputs, such as those encompassed by agriculture and transportation, whereas the HGFC dataset includes only forest cover change. An advantage of the HGFC dataset is that forest cover change data are available annually from 2000–2021, whereas yearly data are not available for the HF (only for 2009) or GHMT datasets (the mean and median years are 2014 and 2016, respectively). The HGFC dataset therefore allows more closely pairing habitat degradation and bat (sero)prevalence data based on sampling year. Because the mechanisms underlying habitat degradation are highly variable across the datasets, we use the term ‘habitat degradation’ when referring to the datasets broadly or discussing analyses conducted with GHMT and HF, but we specifically use ‘forest cover change’ when discussing specific analyses conducted with HGFC.

We analyzed the HF and GHMT datasets in R ver. 4.0.4 (all other analyses were conducted in R ver. 4.2.1). We first converted the raster files from Mollweide projections to the WGS84 decimal system. Within a 10 km buffer of each sampling location, we extracted the mean footprint from the HF dataset and mean land use change values from the GHMT dataset; reported home ranges suggest that this buffer size encompasses the average home range of many Neotropical bat species (e.g. Artibeus watsoni: 0.09 km², Micronycteris microtis: 0.038 km², Lonchophylla dekeyeri: 6.4 km²; Albrecht et al. 2007, Aguiar et al. 2014). We analyzed the HGFC dataset in Google Earth Engine (Gorelick et al. 2017). For comparison with the HF and GHMT datasets, we extracted the overall mean forest change value for each 10 km buffer across all years. To extract forest change more closely matched to years of bat sampling, we calculated the total mean forest change for each buffer for each year from 2001–2021; for each site, we obtained up to 21 values within 10 km, one for each year prior to when sampling occurred.

Finally, although we excluded sites or studies that explicitly sampled in urban areas, many sites could include urban areas within the 10 km buffer. To identify and exclude these sites, we used the Gridded Population of the World dataset ver. 4.11 in Earth Engine (Center For International Earth Science Information Network-CIESIN-Columbia University 2018). For each site, we extracted the maximum number of persons per square kilometer within the same 10 km buffer. Sites that included at least 300 humans km⁻² within our buffer were excluded, because this density should include both towns and cities (OECD and European Commission 2020). Human population data were available for every five years from 2000–2020; to be conservative, we excluded sites where the human population density exceeded 300 inhabitants km⁻² within five years after bats were sampled.

Statistical analyses

For downstream analyses of virus prevalence and seroprevalence we calculated Freeman–Tukey double arc sine transformed (PFT) proportions and sampling variances for the response variables. We selected this effect size because it is appropriate for proportion data and is more suitable than alternative transformations for handling boundary proportions (especially given the high extent of zero-inflation in our prevalence dataset). Effect sizes were calculated using the escalc() function in the ‘metafor’ R package ver. 3.0.2 (Viechtbauer 2010). Separately considering prevalence and seroprevalence, we first built intercept-only meta-analysis models to estimate phylogenetic signal (HF) and heterogeneity (F) in both response variables. Meta-analysis models are a special case of linear mixed models where the variances of the error terms (i.e. the sampling variances) are known (Viechtbauer 2010). For these and all subsequent models, we started by including five random effects to control for different sources of non-independence: 1) host species; 2) bat phylogeny; 3) study; 4) observation; and 5) country of sampling. These effects account for: 1) multiple observations of the same bat species; 2) similarity in responses owing to the degree of relatedness among bat species (Cinar et al. 2020); heterogeneity 3) within and 4) between studies (Konstantopoulos 2011); and 5) multiple observations from the same country. For the initial two random effects, simulation studies suggest both species-level and phylogenetic terms are necessary to obtain unbiased estimates of the fixed effects when phylogenetic relatedness is moderate or greater; for our included bat species, the mean phylogenetic correlation (excluding the diagonal) was 0.31, justifying both terms (Cinar et al. 2020). For prevalence, we also included a sixth random effect of virus family to account for differences among viruses; this random
effect was not included in seroprevalence models, given that only two virus families were represented. To select a final random effects structure, the full list of five or six random effects was simplified and compared using restricted maximum likelihood (REML) and Akaike’s information criterion (AIC; i.e. the ‘top–down’ method: Zuur et al. 2009), and models with ΔAIC < 2 were considered competitive (Burnham and Anderson 2004). Models were weighted by inverse sampling variance (the most common weighting scheme used in meta-analysis models; Koricheva et al. 2013) and were fit using the rma.mv() function in ‘metafor’, using the Quasi-Newton BFGS optimizer and REML. The Quasi-Newton BFGS optimizer is one of many optimizers available in ‘metafor’ and was selected because it facilitated convergence of all candidate models. Heterogeneity was calculated overall and for each random effect; and, consistent with other ecological studies, we interpreted heterogeneity as low (F ~ 25%), moderate (F ~ 50%), or high (F ~ 75%; Higgins 2003). To compare the predictive power of our three habitat degradation datasets, we fit equivalent meta-analysis models with derived habitat degradation (i.e. within 10 km, scaled for standardization) for HF, GHMT and HGFC. To facilitate comparison among these three datasets, we scaled and centered each variable for standardization, such that negative values correspond to relative lower habitat degradation or forest cover loss. The prevalence models included diagnostic method (single assay or multi assay) as a precision covariate; diagnostic method was the only precision covariate considered because of high collinearity with sample type and virus family (Supporting information). We did not include any additional covariates in the seroprevalence models because all data included neutralization tests. Although serological responses can vary among viruses and based on the antibody measured, this information was not available in a standardized fashion to include in statistical analyses. Candidate models were again compared with AIC and fit with maximum likelihood (ML), whereas final models were refit with REML. Because the time between habitat degradation and bat sampling could affect the relationship between habitat degradation and (sero)prevalence, we built additional models with the HGFC dataset (the only dataset with annual data) representing different lag times. Owing to differences in database sizes, we built five lag models for seroprevalence and ten lag models for prevalence. We did not build zero-lag models, because forest cover change could have occurred in months prior to bat sampling. We again compared these lag models separately for both response variables using AIC, with the final model refit using REML.

Owing to our dataset being dominated by rhabdovirus testing in Desmodus rotundus (common vampire bat), we also ran the above analyses with the subset of our dataset that only included vampire bat rhabdovirus records. Because this dataset represents a single host species and virus family, the associated models only included random effects of study and observation for seroprevalence, and study, observation, and country for prevalence. The moderator analyses described below were only conducted with the full dataset.

To investigate the role of ecologically relevant bat traits in moderating the relationship between degradation and (sero)prevalence, we first conducted a principal component analysis (PCA) on the three echolocation traits to collapse these variables into a single echolocation trait. Given that 70% of the explained variance loaded onto the first principal component (PC1), subsequent analyses used PC1 (hereafter, ‘echolocation traits’; Supporting information). Next, we constructed meta-analysis models with our five bat traits included as moderators. Owing to sample size disparities for both the prevalence and seroprevalence analyses, we collapsed the diet categories into animalivorous (i.e. bats that primarily eat vertebrates) and non-animalivorous (i.e. bats that eat fruit, nectar, or have variable diets). We also collapsed wing aspect ratio into low (< 6.73; n = 77) or medium-high (> 6.73; n = 142) bins for the seroprevalence analyses.

Because we sought to investigate the relationship between habitat degradation and (sero)prevalence specifically, all moderators (wing aspect ratio, diet, maximum colony size, roost duration, and echolocation traits) were considered in interactions with habitat degradation. We again included diagnostic method as a precision covariate in the prevalence models. For both prevalence and seroprevalence, we used AIC to compare the global model with all included interactions with simpler candidate models, including specific interactions. We compared 30 candidate models for both prevalence and 30 for seroprevalence. Candidate models were compared using datasets free of missing values and were fit with ML, whereas final models were fit with the full dataset using REML (used for unbiased parameter estimation and deriving R²). R² was calculated using the ‘orchRaD’ R package (www.r-project.org) and the r2.ml() function (Nakagawa et al. 2023).

Results

Dataset description

Our dataset consisted of 588 unique records from 16 studies representing 64 bat species. Bats represented six virus families: Phyllostomidae (n = 505; 86% of data records), Vespertilionidae (n = 29; 5%), Molossidae (n = 28; 5%), Nectarciidae (n = 10; 2%), Mormoopidae (n = 10; 2%), and Emballonuridae (n = 6; 1%). Animalivorous bats (n = 336; 57%) were the most heavily represented, of which 67% of observations represented vampire bats (n = 226). Among the non-animalivorous bats, the majority of observations were from phytophagous (n = 209; 36%), followed by omnivorous bats (n = 43; 7%). For species where maximum colony sizes were known (n = 548), our dataset was dominated by bats occupying medium-large colonies (i.e. over 100 bats – n = 473; 86%). Bats were sampled in ten countries: Belize (n = 6; 1%), Brazil (n = 13; 2%), Colombia (n = 152; 26%), Costa Rica (n = 91; 15%), French Guiana (n = 130; 22%), Guatemala (n = 45; 8%), Mexico (n = 16; 3%), Peru (n = 109; 19%), Trinidad (n = 17; 3%) and Uruguay (n = 9; 2%).
Five virus families were represented: Coronaviridae (n = 91; 15%), Hantaviridae (n = 9; 2%), Flaviviridae (n = 112; 19%), Paramyxoviridae (n = 24; 4%) and Rhabdoviridae (n = 352; 60%). Although included in our search, no viruses in the Filoviridae were included. Ten studies sampled rhabdoviruses, four sampled flaviviruses, three sampled coronaviruses, two sampled paramyxoviruses, and only one study sampled hantaviruses. The majority of these studies measured prevalence (n = 363; 62%) rather than seroprevalence (n = 225; 38%). For prevalence, the most heavily sampled viruses were rhabdoviruses (n = 140), followed by flaviviruses (n = 99), coronaviruses (n = 91), paramyxoviruses (n = 24), and hantaviruses (n = 9). However, prevalence was strikingly low: 95% of records (n = 346) represented zero prevalence. All virus families had at least one record where prevalence was greater than zero, with one exception: no bats tested positive for hantaviruses. The seroprevalence dataset, by contrast, only comprised two virus families, of which 94% of records (n = 212; 94%) were rhabdoviruses and the remaining 6% (n = 13) were flaviviruses. Seroprevalence was greater than zero for 55% of records (n = 123).

The vampire bat rhabdovirus virus-specific dataset consisted of 173 unique observations from 10 studies, of which 71% (n = 123) were seroprevalence and 29% were prevalence (n = 50). Vampire bats were sampled in Belize (n = 6; 3%), Brazil (n = 5; 3%), Colombia (n = 2; 1%), French Guiana (n = 39; 23%), Guatemala (n = 9; 5%), Peru (n = 109; 63%), Trinidad (n = 2; 1%) and Uruguay (n = 1; 0%).

### Relationships between habitat degradation and (sero)prevalence across bat-virus systems

The minimal random effects structure was consistently the most parsimonious for seroprevalence (Supporting information). In contrast, models with a country-level random effect consistently had the lowest AIC for prevalence and, in two sets of analyses, the top model included this country-level effect and no competitive alternative. Therefore, all seroprevalence analyses included the minimal random effects of observation nested within study, host species, and host phylogeny, while all prevalence analyses included these random effects in addition to the effect of country. Virus family was a consistently uninformative random effect for prevalence and seroprevalence.

In the intercept-only models, we found moderate-high F for prevalence and seroprevalence (Table 1). For both prevalence and seroprevalence, two random effects had low heterogeneity (bat species and phylogeny), resulting in likewise low phylogenetic signal. Study and observation had similarly low heterogeneity for prevalence, but low-moderate heterogeneity for seroprevalence. The final random effect of country, only considered in the prevalence model, had moderate-high heterogeneity.

All models fit with HF, GHMT, and HGFC were competitive via ΔAIC for prevalence and seroprevalence (prevalence: HF = 0.00, GHMT = 0.15, HGFC = 0.07; seroprevalence: HF = 0.21, GHMT = 0.00, HGFC = 0.09). For seroprevalence, HGFC explained more variance relative to the other habitat degradation datasets and thus was used in subsequent analyses (conditional $R^2$: HF = 56%; GHMT = 55%; HGFC = 63%). No model was superior for prevalence, and HGFC was therefore selected for consistency (conditional $R^2$: HF = 100%; GHMT = 100%; HGFC = 100%). In the final HGFC models, the extent of forest cover loss did not predict prevalence ($\beta = 0.01$, CI 95% = (−0.04; 0.05), p = 0.76) or seroprevalence ($\beta = 0.02$, CI 95% = (−0.07; 0.02), p = 0.38). We found the same result for the HF and GHFC models (Supporting information). However, despite non-significant trends, all three seroprevalence models did suggest consistent decreases in viral seropositivity with increasing habitat degradation (Fig. 1).

Whereas all time lags were competitive for prevalence, the one-year lag was the top seroprevalence model (Supporting information). For the latter, seroprevalence decreased with increasing forest cover loss one year prior to sampling ($\beta = 0.12$, CI 95% = (−0.18; −0.06), p < 0.0001; marginal $R^2 = 14\%$, conditional $R^2 = 74\%$; Fig. 2B). No effect was observed when we similarly considered the one-year lag for prevalence ($\beta = 0.02$, CI 95% = (−0.01; 0.05), p = 0.22; marginal $R^2 = 1\%$, conditional $R^2 = 100\%$; Fig. 2A). However, prevalence greater than 10% was not reported in areas with low forest cover loss, and prevalence above 50% was only observed in areas with the highest extents of forest cover loss under this one-year lag (Fig. 2A).

When we considered ecological traits to moderate the relationship between forest cover loss and virus positivity, the top prevalence model included the interaction between forest loss and diet and between forest loss and echolocation traits ($\Delta$AIC = 0.00; $w_i = 0.38$; Supporting information). Prevalence differed between animalivorous and non-animalivorous bats, as well as by echolocation traits, but these effects were independent of forest loss (Fig. 3A, Table 2). The top seroprevalence model contained the interaction between forest cover loss and wing aspect ratio (small vs medium-large; $\Delta$AIC = 0.00; $w_i = 0.24$; Supporting information), but trait effects were independent of forest loss. Seroprevalence was significantly higher for bats with medium-high wing aspect ratios (Fig. 3B, Table 2). Two other models were competitive for seroprevalence but excluded for having less Akaike weight and/or greater complexity (Supporting information).

### Vampire bat rhabdoviruses

When considering only rhabdoviruses sampled in vampire bats, heterogeneity was low for prevalence overall and

| Table 1. Heterogeneity (F) and phylogenetic signal (HF) in prevalence and seroprevalence for the intercept-only models. Values are presented as percentages. |
|-----------------|-----------------|-----------------|
| F term          | Prevalence (n = 363) | Seroprevalence (n = 225) |
| Study           | 0.00             | 29.94           |
| Observation     | 0.00             | 33.57           |
| Bat species     | 0.80             | 9.09            |
| Bat phylogeny   | 0.00             | 0.00            |
| Country         | 55.27            | NA              |
| Total F         | 56.07            | 72.59           |
| HF              | 0.00             | 0.00            |

Note: For prevalence, no model was superior, and HGFC was therefore selected for consistency. For seroprevalence, all three models did suggest consistent decreases in viral seropositivity with increasing habitat degradation.
Discussion

Understanding how habitat degradation affects zoonotic infections in wildlife hosts remains critical to predicting pathogen spillover risks (Plowright et al. 2017, Becker et al. 2023). However, this relationship remains poorly understood owing to a lack of large-scale data synthesis to derive broad patterns across host–virus associations as well as methodological and environmental differences. Here, we used Neotropical bats as an initial case study to assess the overall association between habitat degradation or forest loss and virus (sero) prevalence. For prevalence, our dataset contained 50 bat species, representing five virus families. For seroprevalence, our dataset contained over 30 bat species but was dominated by rhabdoviruses (94% of records), and only one other virus family was represented. Thus, we caution that the results of our seroprevalence analyses in particular may not be generalizable to other bat virus families across the Neotropics. These biases serve as an important opportunity to highlight future data needs, and we hope to inspire other researchers to fill some of these gaps.

When we assessed habitat degradation irrespective of bat sampling time, we did not observe significant effects of per random effect but high for seroprevalence overall, with study and observation each having low-moderate heterogeneity (Supporting information). All degradation datasets were competitive for prevalence (ΔAIC: HF = 1.27; GHMT = 0.00; HGFC = 1.31) and seroprevalence (ΔAIC: HF = 0.40; GHMT = 0.00; HGFC = 1.27). Across all three degradation datasets, degradation had no significant effect on prevalence or seroprevalence (Supporting information). Nevertheless, the direction of nonsignificant trends remained consistent with the full dataset for seroprevalence (i.e. a consistent negative relationship; Fig. 4B).

Consistent with our full analysis, the top seroprevalence model considered the one-year lag (with no competitive alternative; ΔAIC of next-best model = 6.51; Supporting information), and all prevalence models were competitive with AIC (Supporting information). Rhabdovirus seroprevalence decreased with increasing forest cover loss when forest loss occurred one year prior to bat sampling (β = −0.13, CI 95% = (−0.21; −0.06), p = 0.0004; marginal $R^2$ = 14%; conditional $R^2$ = 72%; Fig. 2D, Supporting information). No effect was observed for prevalence (β = −0.00, CI 95% = (−0.07; 0.06), p = 0.90; marginal $R^2$ = 100%, conditional $R^2$ = 100%; Fig. 2C, Supporting information).

Figure 1. Effects of habitat degradation on bat virus (A) prevalence and (B) seroprevalence across the three datasets: HGFC, HF, GHMT. Raw data points are scaled by sample size alongside trend lines and 95% confidence intervals predicted by the models. Diagnostic method was held constant for visualizing fitted values for prevalence. The x-axes are scaled and centered. HF = Human Footprint; GHMT = Global Human Modification of Terrestrial Systems; HGFC = Hansen Global Forest Change.
habitat degradation on bat virus prevalence or seroprevalence. However, although we did not detect any effects statistically, weak but consistent trends among all datasets suggest a negative relationship for seroprevalence. In contrast, when forest loss (i.e. the HGFC dataset) was considered the year prior to bat sampling, we found significant negative associations between forest loss and seroprevalence as well as suggestive, but still non-significant, positive trends for prevalence across our multi-species dataset (but not the vampire bat–rhabdovirus dataset). Our analyses therefore show these observed weak effects could be due to time lags between forest loss and viral dynamics in bats as well as how certain bat guilds respond differently to the effects of habitat degradation.

Effects of time

Time lags have frequently been used to explain the delayed impacts of habitat change on communities (Krauss et al. 2010, Lira et al. 2019). Time lags may be especially important for assessing effects of habitat degradation on prevalence and seroprevalence, given that the trajectory of these outcomes should differ over time. Because prevalence represents active infections (often relatively short for bat viruses; Gentles et al. 2020), prevalence should decrease as individuals acquire immunity; in contrast, because seroprevalence indicates both active and recent infections, seroprevalence could be expected to increase over time as individuals are exposed to viruses. When forest loss was considered annually in relation to the timing of bat sampling, we found the one-year lag was most predictive for seroprevalence. Seroprevalence significantly decreased in regions with the greatest extents of forest cover loss when loss occurred the year prior to bat sampling, with weaker effects observed as the time between forest loss and sampling increased (possibly owing to waning immunity over time for many of the viral families included here; Blackwood et al. 2013, Gentles et al. 2020). Such results suggest a critical role of knowing the history of land conversion when assessing viral risks. Sampling in cleared versus forested sites without knowledge of when habitat degradation occurred could obscure associations between habitat degradation and seroprevalence.

The negative relationship between recent forest cover loss and seroprevalence could be explained by infection or habitat degradation increasing bat mortality or emigration, thereby decreasing bat abundance and density-dependent virus transmission. Indeed, habitat degradation often has adverse health
effects on wildlife, including altered stress physiology and immune traits (Messina et al. 2018); higher seroprevalence could be observed in more forested areas without recent degradation, because bats are healthier overall and suffer lower disease-induced mortality. This negative association between recent forest loss and seroprevalence persisted in our focused analyses of only vampire bat rhabdoviruses. Seroprevalence is often high in vampire bat populations owing to abortive infections and a high probability of developing temporary immunity (Blackwood et al. 2013), and higher seroprevalence in denser forests has similarly been found when sampling vampire bats as well as other bat species (de Thoisy et al. 2016, Fisher et al. 2018). Because one cause of habitat degradation is clearance for livestock pasture, abundant cattle could provide a more accessible food resource for vampire bats that manifests in greater resistance against rabies virus

Figure 3. The effects of diet, the top moderator variable for predicting (A) prevalence, and wing aspect ratio, the top moderator for predicting (B) seroprevalence, in bats sampled from sites with varying degrees of forest cover loss. Raw data points are scaled by sample size alongside trend lines and 95% confidence intervals predicted by the models. Diagnostic method and echolocation traits were held constant for visualizing fitted values for prevalence. The x-axes are scaled and centered.

Table 2. Summary of the top prevalence and seroprevalence models with moderators. Variables with significant p-values (< 0.05) are bolded.

<table>
<thead>
<tr>
<th>Outcome variable</th>
<th>β</th>
<th>SE</th>
<th>z</th>
<th>p</th>
<th>95% Confidence intervals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prevalence</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>0.38</td>
<td>0.09</td>
<td>4.20</td>
<td>0.00</td>
<td>0.21; 0.56</td>
</tr>
<tr>
<td>Habitat degradation</td>
<td>0.02</td>
<td>0.03</td>
<td>0.63</td>
<td>0.53</td>
<td>−0.04; 0.07</td>
</tr>
<tr>
<td>Diet (non-animalivorous)</td>
<td>−0.14</td>
<td>0.05</td>
<td>−2.87</td>
<td>0.00</td>
<td>−0.24; −0.05</td>
</tr>
<tr>
<td>Echolocation</td>
<td>0.06</td>
<td>0.02</td>
<td>2.89</td>
<td>0.00</td>
<td>0.02; 0.10</td>
</tr>
<tr>
<td>Diagnostic method</td>
<td>−0.10</td>
<td>0.13</td>
<td>−0.79</td>
<td>0.43</td>
<td>−0.36; 0.15</td>
</tr>
<tr>
<td>Habitat degradation: Diet</td>
<td>−0.05</td>
<td>0.04</td>
<td>−1.14</td>
<td>0.25</td>
<td>−0.14; 0.04</td>
</tr>
<tr>
<td>Habitat degradation: Echolocation</td>
<td>0.01</td>
<td>0.03</td>
<td>0.50</td>
<td>0.62</td>
<td>−0.04; 0.07</td>
</tr>
<tr>
<td>Seroprevalence</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>0.31</td>
<td>0.10</td>
<td>3.09</td>
<td>0.00</td>
<td>0.11; 0.51</td>
</tr>
<tr>
<td>Habitat degradation</td>
<td>−0.07</td>
<td>0.07</td>
<td>−0.90</td>
<td>0.37</td>
<td>−0.21; 0.08</td>
</tr>
<tr>
<td>Wing aspect ratio (medium high)</td>
<td>0.18</td>
<td>0.07</td>
<td>2.63</td>
<td>0.01</td>
<td>0.05; 0.32</td>
</tr>
<tr>
<td>Habitat degradation: Wing aspect ratio (medium high)</td>
<td>0.06</td>
<td>0.08</td>
<td>0.76</td>
<td>0.45</td>
<td>−0.09; 0.21</td>
</tr>
</tbody>
</table>
and possibly other viruses, thereby leading to more frequent detections of virus-neutralizing antibodies (as suggested by Meza et al. 2022). However, improved food resource availability does not always lead to increased resistance (Becker et al. 2015), and more work is needed to better understand the mechanisms underlying this relationship. Nevertheless, given that the trends we observed were consistent for both vampire bat rhabdoviruses and other bat species more broadly (there were 32 bat species represented in the full seroprevalence dataset), our results provide general support that these effects may occur more generally across bat species in the Neotropics.

For consistency, we also considered the one-year lag for prevalence, but we detected no significant association with recent habitat degradation. Nevertheless, non-significant trends also warrant discussion. In contrast with seroprevalence, limitations to detect effects here likely stem from severe zero inflation; 95% of records represented zero prevalence, reflecting the general rarity of detecting active infection of these viruses in wild bats (Becker et al. 2019b, Cohen et al. 2022). Nevertheless, when forest loss was calculated the year prior to bat sampling, relatively high prevalence (> 10%) was only reported in areas with moderate-to-high extents of recent degradation, and the highest prevalence (> 50%) was only observed in areas with the highest extent of recent habitat degradation. These trends are consistent with the idea of impaired immunity in more degraded forests, as immunocompromised bats could be less equipped to resist or clear infections and thus be more likely to develop detectable infections via PCR. Coinciding with this, a recent meta-analysis also found increased bat coronavirus prevalence in areas with higher human impacts globally (Warmuth et al. 2023); however, this study did not consider the effects of time, which we suggest could be important for influencing infection prevalence across a wider range of viral families. Nevertheless, before concrete conclusions about these possible effects can be reached, a need exists for more longitudinal research investigating bat virus prevalence following habitat degradation as well as how these responses can vary by bat species or virus families.

**Vampire bat rhabdoviruses**

In our focused vampire bat analysis, we did not observe increased rhabdovirus prevalence in areas with recent forest
loss. More sampling is needed to determine whether this result is again owing to high zero-inflation or whether the association between habitat degradation and prevalence differs between Neotropical bat species and viruses broadly and vampire bat rhabdoviruses specifically. Given the known economic and human health implications of vampire bat rabies virus in particular (Mayen, 2003, Johnson et al. 2014, Benavides et al. 2017), addressing this knowledge gap should be prioritized in future research.

Our results do suggest, however, that the association between habitat degradation and seroprevalence differs between Neotropical bat species and viruses broadly and vampire bat rhabdoviruses specifically. Vampire bats appeared to have higher seroprevalence overall, irrespective of time, relative to the broader group of bats and viruses included in our meta-analysis. Higher seroprevalence in vampire bats suggests increased opportunities for virus exposure relative to other bat species. Unique aspects of vampire bat behaviour, such as blood sharing, could facilitate higher virus transmission (Wilkinson 1984). Culling could also increase virus exposure owing to age-biased mortality and because culling facilitates bat dispersal and increases pathogen spread throughout landscapes (Viana et al. 2023).

Finally, higher pathogen transmission risks are generally found in bats that consume vertebrate prey. Immunological surveys of Neotropical bats indeed suggest carnivorous and blood-feeding bats have increased white blood cell counts relative to other bat species, reflecting increased pathogen exposure (Schneeberger et al. 2013). Interestingly, we found higher viral prevalence in non-animalivorous bats relative to animalivorous bats. Although the within-host dynamics that dictate prevalence differ from those of seroprevalence (Plowright et al. 2016), this result nevertheless suggests that blood-feeding bats may differ from other animalivorous bats in their responses to degradation.

Effects of shared bat traits

The top moderator variables for predicting viral outcomes were diet and echolocation for prevalence and wing aspect ratio for seroprevalence. Although we observed significant associations between diet and prevalence, echolocation and prevalence, and wing aspect ratio and seroprevalence, these effects were independent of forest cover loss. These results suggest that associations between forest loss and bat virus (sero)prevalence are largely independent of these ecological traits, such that other bat traits or ecological contexts are likely more important for dictating the viral outcomes of forest loss. Indeed, this is likely the case for seroprevalence, and future work could emphasize investigating bat traits or ecological contexts that we did not consider here. Concerning prevalence, however, the high zero-inflation in our dataset again limits our ability to ascertain whether the lack of effects reflect weak associations or a lack of variability in the dataset. In short, more work is therefore needed to understand which bat traits are most important for influencing bat virus (sero) prevalence in degraded habitats.

Conclusions and future directions

Large-scale data syntheses facilitate identifying general ecological patterns that transcend species, regions, and study-specific methods. Our initial results suggest that relationships between habitat degradation and bat rhabdovirus seroprevalence are temporally dependent. Although our results also indicate that time could also be important for influencing prevalence across bat viruses more broadly, future work is needed to support the trends we observed here. Nevertheless, given the possible importance of time, and because pathogen spillover risks are known to vary temporally (Becker et al. 2019a), sampling dates should always be reported to better understand the dynamic associations that exist between habitat degradation and (sero)prevalence. Future work could assess how the association between habitat degradation and (sero)prevalence varies with seasonal factors that can result in virus shedding pulses, such as resource availability, migration, and reproductive cycles (Kessler et al. 2018).

Notable biases existed in our dataset regarding the bats and viruses sampled, highlighting additional opportunities for future work and critical data needs. In particular, common vampire bats (family Phyllostomidae) represented the majority of our dataset, and insectivores and omnivores were the least represented dietary guilds. One meta-analysis identified insectivorous, omnivorous, and sanguivorous bats as being particularly sensitive to the effects of habitat disturbance (Carballo-Morales et al. 2021), whereas another found omnivores occur in similar abundances in continuous forests and forests converted for cattle ranching (Gonçalves et al. 2017). Such variable responses to habitat degradation likely alter associations between degradation and virus (sero)prevalence, and bats from other dietary guilds and families should be increasingly sampled across habitat types to better understand these associations.

Lastly, the majority of viruses in our dataset were rhabdoviruses, of which 97% were rabies virus, and flaviviruses were the second most heavily sampled. An important consideration here is that transmission modes are likely highly important for explaining infection outcomes in degraded habitats. Density-dependent transmission could increase (sero)prevalence following degradation, owing to increased density in remaining forest patches. However, transmission of rabies virus is likely not density dependent (Streicker et al. 2012, Blackwood et al. 2013), and neither are many other bat viruses (e.g. flaviviruses; Kading and Schountz 2016). To broadly assess the extent to which varying transmission modes may affect bat virus outcomes in response to degradation, more sampling of underrepresented viruses is needed. A recent global analysis found that bat Coronavirus prevalence increased with increasing intensity of human impact (Warmuth et al. 2023); however, this analysis did not consider the effects of time, a factor which we found to be important for rhabdovirus seroprevalence, and possibly for prevalence across five virus families, in our analyses. Research should particularly focus on sampling coronaviruses, paramyxoviruses, and hantaviruses across habitat gradients, as these viral
families were underrepresented in our included studies, to develop a broader understanding of how habitat degradation affects Neotropical bat virus (sero)prevalence.

Acknowledgements — McGill University is on land which has long served as a site of meeting and exchange amongst Indigenous peoples, including the Haudenosaunee and Anishinabeg nations. We also acknowledge that the Univ. of Oklahoma resides on land that was the traditional home of the “Hasinai” Caddo Nation and “Kirikirïti” Wichita & Affiliated Tribes and that also served as a hunting ground, trade exchange point, and migration route for the Apache, Comanche, Kiowa and Osage nations. We would like to thank the authors who kindly shared data for use in this analysis or helped clarify questions that arose as we extracted data: Jane Megid, Fernando Morecigos, Edith Darcissac, Larissa Bueno, Helena Ferreira, Luzia Quieroz, Ricardo Dias, Alfonso Calderon, Andres Moreira-Soto, Paulo Eduardo Brandão, Ayesha Pedrozo, Julie Blackwood, Eugenia Corrales, Salome Cabrera Romo, Joselyn Lissett Calderón González, Megan Griffiths, David Moran, Kevin Olival, Benoit de Thoisy, Vincent Munster, Amanda Vicente-Santos. Lastly, we thank the Becker Lab at the Univ. of Oklahoma for providing helpful feedback on the manuscript.

Funding — This project was supported by the National Science Foundation (B1I 2213854) and the Research Corporation for Science Advancement (RCSA). This work was conducted as part of Subaward no. 28365, part of a USDA Non-Assistance Cooperative Agreement with RCSA Federal Award no. 58-3022-0-005. AMH was supported by a National Sciences and Engineering Research Council of Canada (NSERC) Postgraduate Scholarship – Doctoral (PGS-D). Financial support was also provided by the University of Oklahoma Libraries’ Open Access Fund.

Author contributions
Alexis M. Heckley: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Writing – original draft (lead); Writing – review and editing (equal). Lauren R. Lock: Conceptualization (equal); Data curation (supporting); Writing – review and editing (equal). Daniel J. Becker: Conceptualization (equal); Formal analysis (supporting); Supervision (lead); Writing – review and editing (equal).

Transparent peer review
The peer review history for this article is available at https://publons.com/publon/10.1111/ecog.07041.

Data availability statement
Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.86661glw (Heckley et al. 2023). One author specifically requested that we not share their data owing to concerns about data ownership, and these rows have been excluded from the publicly available dataset.

References


Schneeberger, K., Czirják, G. Á. and Voigt, C. C. 2013. Measures of the constitutive immune system are linked to diet and roosting habits of Neotropical bats. – PLoS One 8: e54023.


