Title: Parasite traits shape the association between forest loss and infection: A global meta-analysis

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Abstract:

Forest loss can affect host–parasite dynamics, posing risks to wildlife and human health. Most work has investigated how host traits moderate associations between forest loss and prevalence, but the role that parasite traits play is less understood. We synthesized parasite prevalence and parasite trait data from publicly available databases representing carnivores, ungulates, and primate host species. We combined these data with open-source, remote-sensing forest loss data and conducted multi-level phylogenetic meta-analyses. While we found no overall association between forest loss and prevalence across parasites, trends emerged when considering different parasite taxa. Further, although prevalence did not differ by transmission mode overall, forest-loss prevalence associations varied by transmission mode within parasite taxa. For instance, prevalence decreased with forest loss for closely transmitted helminths but increased for *not* closely transmitted helminths. These results illustrate that parasite traits must be considered to understand complex associations between environmental change and infection outcomes.

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

Introduction

Globally accelerating environmental change poses risks to wildlife and human health owing to effects on host–parasite interactions (Daszak et al. 2001, Acevedo-Whitehouse and Duffus 2009, Brearley et al. 2013). Recent upticks in the frequency of pandemics and panzootics underscore the role that environmental change has on parasite risks and emphasize the need for holistic approaches to safeguard environmental, wildlife, and human health (Plowright et al. 2017, Scheele et al. 2019). Over the past century, forest loss has accelerated globally and has thus received increasing attention as a critical environmental issue (Curtis et al. 2018, Leberger et al. 2020). Forest loss and other sources of habitat loss or modification can alter wildlife infection dynamics via changes in host community composition, host stress physiology and susceptibility, and host behaviors (Messina et al. 2018, Becker et al. 2020, 2023, Keesing and Ostfeld 2021).

Traits of the parasites themselves (rather than the hosts) can also shape associations between forest loss and infection outcomes (e.g., Froeschke et al. 2013, Faust et al. 2017). Prevalence, for instance, is typically expected to be higher for vector-borne pathogens following forest loss because vectors, like their hosts, are also susceptible to change in the external environment (e.g., temperature; Mordecai et al. 2019). This expectation has likely contributed to why most studies investigating associations between land-use change and infectious disease have focused on vector-borne or multi-host parasites (Gottdenker et al. 2014).

Studies that synthesize the effects of forest loss, and other environmental disturbances, on parasite prevalence typically focus on the role of host traits in moderating these outcomes (e.g., Becker et al. 2019, Vicente-Santos et al. 2023). As a result, we lack a broad-scale understanding of how important parasite traits are for shaping these associations. Identifying parasite groups

that most strongly shape the association between forest loss and prevalence could be important for prioritizing surveillance and, in the case of zoonotic parasites, spillover prevention.

To improve our understanding of how parasite traits shape associations between forest loss and parasite outcomes, we here synthesized parasite prevalence data, parasite trait data, and host trait data from publicly available databases representing data for carnivores, ungulates, and primate host species. These data were combined with publicly available remote-sensing forest loss data and analyzed using multi-level phylogenetic meta-analytic models.

Data synthesis

Host and parasite data

To obtain data on parasite prevalence and transmission mode, we used the Global Mammal Parasite Database 2.0 ('GMPD') (Stephens et al. 2017). We excluded records with no host binomial name, where spatial coordinates or prevalence were not reported, and where prevalence was estimated from pooled samples from multiple individuals. We also excluded marine host species (given our focus on forest loss), and we excluded prions given their small sample size (19/24323 records in the GMPD). For carnivores and ungulates, we only included wild and wild, non-managed hosts. Because all primates in the GMPD have uncategorized 'population type' status, we included all primate records.

To determine if each parasite in our dataset is zoonotic, we used VIRION (Carlson et al. 2022) and CLOVER (Gibb et al. 2021), two comprehensive databases on host–pathogen associations. VIRION only includes viruses, whereas CLOVER spans viruses, bacteria, helminths, protozoa, and fungi. Because VIRION integrates CLOVER, we used VIRION for

viruses and CLOVER for all other parasites. We defined zoonotic parasites as those parasites in the GMPD known to associate with *Homo sapiens* in VIRION or CLOVER.

To account for host phylogeny in our analyses, we used a mammal-wide phylogeny (Upham et al., 2019). We trimmed this phylogeny to the species in our dataset using the 'ape' package (Paradis and Schliep 2019). We excluded two host species (*Cercopithecus denti, Taurotragus oryx*) owing to incongruence with the phylogenetic tree and for which we could not find alternate (synonymous or updated) species names. We used 'ape' to compute a phylogenetic correlation matrix from this trimmed tree for downstream meta-analysis.

Finally, the GMPD provides data on parasite transmission mode as a binary variable in each of four categories: close (aerosol, close contact, sexual transmission), non-close (environmental transmission), intermediate (complex life cycles and trophic transmission), and vector (vector-borne transmission). Because many parasites have multiple transmission modes, we created two transmission mode variables. In the first, parasites were assigned into one of five groups: 'only close', 'only non-close', 'only intermediate', 'only vector' or 'multiple transmission modes'. In the second, parasites were categorized based on their number of transmission modes, ranging from one to three.

Home range data

We next added home range data using from the 'HomeRange' R package (Broekman et al. 2023). We used the most updated version of the database at the time of writing: 'HomeRangeData_2024_07_09_1.zip'.

All species need home range data to be included in our analyses, because this information is required to extract forest loss data for each species at biologically relevant spatial scales (see

'Forest Loss Data'). We therefore excluded any species in the GMPD that lacked home range estimates in HomeRange. To reduce intra-specific variation in the home range database, we primarily followed Broekman et al. (2024). Specifically, we excluded daily, monthly, and seasonal sampling, and we excluded non-wild (experimental) animals. We only included home range estimates that were longer than 5 months in duration and isopleths larger than or equal to 90, which improves home range estimates over core area usage. Because multiple home range estimates typically exist for a given species, excluding smaller isopleths did not eliminate any species in our dataset.

We then calculated weighted means for home ranges based on intraspecific sample sizes, as most species in HomeRange have multiple home range estimates. Prior to calculating these weighted means, we excluded any observations where the number of individuals sampled was not reported or not numeric. Weighted means were calculated in two ways. First, we calculated a general weighted mean at the species-level. Second, we calculated a weighted mean for each host species, specific to host age and sex. If the GMPD had sex and/or age data available for a given prevalence estimate, we paired the more specific home range estimate with that observation (46% of total observations). If the GMPD did not have sex and/or age data for that observation, we relied on the species-level weighted mean home range.

Forest loss data

We next used Google Earth Engine to extract forest loss data, using the Hansen Global Forest Change v 1.11 dataset (Hansen et al. 2013). This dataset provides forest cover loss data from 2000-2023. To extract forest loss data at a biologically relevant spatial scale for each prevalence estimate in the GMPD, we used the above mean home range estimates to create buffers around

the coordinates of animal sampling. We then extracted forest loss within each buffer. To improve feasibility of extracting forest loss estimates, we first collapsed continuous home ranges into broader groupings.

Home ranges of our included mammal species were heavily skewed towards small values; 51% of mean home ranges were under 4 km^2, and 80% were above 100 km^2. We therefore binned home range estimates under 100 km^2 into ten equally sized groups. Given that our home range estimates are means, and thus could be conservative estimates of movement, we extracted slightly larger buffer sizes per group via rounding up to account for this variation. For home ranges under 1 km^2, we rounded the value of a given group up to the nearest 0.125 km^2; from 1 km^2 to 10 km^2, we rounded up to the nearest 0.50 km^2; and from 10 km^2 to 100 km^2, we rounded up to the nearest 5 km^2. For home ranges between 100 km^2 and 1000 km^2, we rounded to the nearest 100 km^2; and for home ranges above 1000 km^2, we rounded to the nearest 500 km^2. We ended with 20 different groups with which to create buffers and extract forest loss data in Google Earth Engine: 0.375 km^2, 0.75 km^2, 1.5 km^2, 2 km, 3.5 km^2, 7 km^2, 15 km^2, 25 km^2, 50 km^2, 100 km^2, 200 km^2, 300 km^2, 400 km^2, 500 km^2, 600 km^2, 700 km^2, 800 km^2 1500 km^2, 2000 km^2, and 55500 km^2. We converted these home ranges (km^2) to meter radius for data extraction.

Phylogenetic meta-analysis

We used phylogenetic meta-analysis to estimate the effects of forest loss on parasite prevalence and how this association can be moderated by parasite traits. Our models used the *metafor* package and accounted for sampling variance, random effects to account for within- and between-study variance, and additional random effects of host species, parasite genus, and host

phylogeny (Viechtbauer 2010, Cinar et al. 2022). Detailed methods for these analyses are provided in the supplement.

Dataset description

Our final dataset (n = 5262) comprised 765 records for arthropods (15%), 397 records for bacteria (8%), 38 records for fungi (less than 1%), 3297 records for helminths (63%), 460 records for protozoa (9%), and 305 records for viruses (6%). Most parasites were transmitted via multiple transmission modes (n = 1861; 36%). The second best-represented transmission mode was intermediate only (n = 1377; 26%), followed by non-close only (n = 1194; 23%), close only (n = 471; 9%), and vector-borne only transmission (n = 359; 7%). Most observations were for parasites with a single transmission mode (n = 3401; 65%), with remaining data for parasites with two (n = 1752; 33%) or three (n = 109; 2%) transmission modes.

The subset of our dataset with only zoonotic parasites (n = 2365) comprised 370 records for bacteria (16%), 30 records for fungi (1%), 1518 records for helminths (64%), 259 records for protozoa (11%), and 188 records for viruses (8%). Most zoonotic parasites were transmitted via multiple transmission modes (n = 813; 34%), followed by intermediate only (n = 505; 21%), non-close only (n = 496; 21%), close only (n = 301; 13%), and vector-borne only transmission (n = 250; 11%). Parasites with a single transmission mode remained the best represented (n = 1552; 66%), followed by parasites with two (n = 718; 30%) or three (n = 95; 4%) transmission modes.

Most records in our dataset were of parasites sampled in North America and Europe (figure 1; figure S1). In the northern hemisphere, all parasite groups had records representing parasites sampled in areas with low forest loss and in areas with high forest loss. By contrast, most records in the southern hemisphere represented only areas with low forest loss. The general

exception to this was for protozoans, which have been sampled in the most diverse sites in terms of forest loss, particularly in South America. No records representing parasites sampled in Africa were collected in areas with high forest loss. These trends suggest that researchers are sampling parasites for carnivore, ungulate, and primate hosts in regions that have not suffered high extents of forest loss. Of particular concern, some of the most heavily deforested areas globally (e.g., the Amazon Basin and Southeast Asia) are very poorly sampled for most parasite groups and transmission modes. Because the GMPD comprises only primates, ungulates, and carnivores, these data gaps with respect to forest loss reflect the current state of the literature for these three host taxa. Filling these data gaps will require deliberate sampling with respect to forest loss – especially in under-sampled regions.

Forest loss is not associated with prevalence overall

When initially analyzing data across all parasite taxa and transmission modes, forest loss had no overall association with prevalence ($\beta = 0.00$, $p = 0.50$; table S1; figure 2A). We also found no difference in the association between forest loss and prevalence for parasites transmitted via one, two, or three transmission modes (1 mode: $\beta = 0.01$, $p = 0.56$; 2 modes: $\beta = 0.01$, $p = 0.64$; three modes: $\beta = 0.04$, $p = 0.64$; tables S2-S3; figure 2B). These trends persisted in the subset of our dataset for only zoonotic parasites (tables S13-S15; figure S2).

This overall weak effect of forest loss on prevalence aligns with a recent meta-analysis that investigated multiple drivers of infectious disease outcomes and concluded that habitat change was unimportant relative to other disturbances (Mahon et al. 2024). However, other meta-analyses have shown that multiple parasite outcomes (including but not limited to prevalence) are sensitive to forest loss (e.g., Messina et al. 2018, Ferraguti et al. 2023, Heckley

and Becker 2023, Heckley et al. 2023, Skinner et al. 2023). These studies typically find that associations between anthropogenic activity and infection risk materialize once ecological or evolutionary factors are considered, indicating that null overall effects can mask epidemiologically relevant moderator variables, including parasite traits.

Parasite taxa respond differently to forest loss

In our full analysis with both non-zoonotic and zoonotic parasites, the association between forest loss and prevalence varied for different groups of parasites (tables S4-S5; figure 3). Prevalence of arthropods and bacteria significantly decreased in areas with more forest loss (arthropods: β = -0.10, p = 0.01; bacteria: β = -0.09, p = 0.05), and helminth prevalence increased in areas with more forest loss (β = 0.04, p = 0.02). No association existed between forest loss and prevalence for other parasites (fungi: β = -0.03, p = 0.87; protozoa: β = 0.04, p = 0.33; viruses: β = 0.00, p = 0.98), which contradicts previous reports that transmission of protozoa and viruses tends to increase in response to anthropogenic change (Gottdenker et al. 2014). Interestingly, the significant trends for bacteria and helminths observed here did not exist when only analyzing zoonotic parasites (the zoonotic dataset does not consider arthropods) (tables S16-S17; figure S3). For zoonotic parasites, the association between forest loss and prevalence did not differ for any parasite taxon.

Prevalence tends to increase with forest loss for vector-borne zoonotic parasites

We did not find relationships between forest loss and prevalence within any transmission mode (only close, only non-close, only intermediate, only vector, or multiple) with the full dataset (tables S6-S7; figure 4). However, when only considering zoonotic parasites, prevalence was

affected by transmission mode, with prevalence tending to increase with more forest loss for only vector-transmitted parasites ($\beta = 0.07$, $p = 0.08$; tables S18-S19; figure S4). This positive trend is consistent with some other meta-analyses that have found positive associations between forest cover or land change and vector species of human parasites (Burkett-Cadena and Vittor 2018) as well as vector-borne parasites (e.g., Ferraguti et al. 2023). These effects could stem from shifts in the abiotic or biotic environments following forest loss; for instance, forest loss can increase local air temperature, and temperature is well-established to affect vector-borne parasite transmission (Cohn et al. 2019, Mordecai et al. 2019). Vector abundance could also increase following forest loss if fewer predators of vectors (e.g., fish that consume mosquito larvae) are present in degraded areas (Burkett-Cadena and Vittor 2018). That this suggestive trend only exists for zoonotic vector-borne parasites, but not across all vector-borne parasites, could reflect an advantage for human-tolerant host species or local adaptation of human-associated vector species to anthropogenic landscapes (Burkett-Cadena and Vittor 2018, Guo et al. 2019). Vector-borne parasites infect hundreds of millions of people per year, are responsible for over 700,000 deaths annually, and represent nearly 20% of human infectious diseases (World Health Organization 2024). This positive trend for zoonotic vector-borne parasites could thus have important human health implications.

Transmission mode affects these associations within different parasite groups

Additional insights emerged when investigating different transmission modes within each parasite group (tables S8-S12; figure 5). Starting with close transmission, prevalence decreased with forest loss for closely transmitted arthropods ($\beta = -0.14$, $p < 0.01$) and helminths ($\beta = -0.08$, $p = 0.04$) as well as for bacteria that are not closely transmitted ($\beta = -0.16$, $p = 0.04$). By contrast,

prevalence of not closely transmitted helminths increased in areas with more forest loss (β = 0.05, $p < 0.01$; tables S8, S12; figure 5). The negative associations for arthropods and bacteria, as well as the positive association for not closely transmitted helminths, are all consistent with our overall analyses ignoring within-group transmission mode; however, the significant negative association between forest loss and prevalence for helminths transmitted through close contact is in the opposite direction of the general association.

For non-close transmission, prevalence decreased with more forest loss for non-closely transmitted arthropods (β = -0.10, $p = 0.01$) and for bacteria that are not non-closely transmitted (β = -0.15, $p = 0.03$; tables S9, S12; figure 6). Prevalence increased with forest loss for helminths that are not non-closely transmitted (β = 0.04, $p = 0.04$), but no association existed for non-closely transmitted helminths (β = 0.04, $p = 0.11$). For intermediate transmission, prevalence was higher for intermediately transmitted helminths in areas with more forest loss (β = 0.06, $p < 0.01$; tables S10, S12; figure 7). Finally, for vector-borne transmission, prevalence trended higher for helminths that are both vector-borne (β = 0.12, $p = 0.06$) and not vector-borne (β = 0.03, p = 0.07). Prevalence also trended higher for vector-borne protozoa (β = 0.11, $p = 0.07$) and trended lower for vector-borne bacteria (β = -0.13, $p = 0.06$). No differences emerged for non-vector-borne parasites from those same groups (tables S11, S12; figure 8).

Within only zoonotic parasites, prevalence decreased with forest loss for closely transmitted zoonotic helminths (β = -0.15, $p < 0.01$) but not for not closely transmitted zoonotic helminths (β = 0.02, $p = 0.37$; table S20, S24; figure S5). Prevalence was also higher for vector-borne zoonotic helminths in areas with more forest loss (β = 0.13, $p = 0.04$) but not for non-vector-borne zoonotic helminths (β = -0.01, $p = 0.63$; table S23-S24; figure S8). Prevalence did

not vary with forest loss for non-close versus not non-close or intermediate versus not intermediate comparisons (tables S21, S23, S24; figures S6-S7).

Taken together, these findings emphasize that parasite outcomes (i.e., prevalence) in response to forest loss can be dependent both on the parasite taxa and the specific transmission mode, aligning with the general consensus that parasite responses to forest loss are complex and context-dependent (Gottdenker et al. 2014). This within-group variability raises questions about why particular trends only emerge within certain taxa. For instance, we found that prevalence decreases with forest loss for closely transmitted arthropods and helminths. This finding could point to possible negative effects of forest loss on host density, as contact rates - and thus transmission of closely transmitted parasites - should be higher in denser areas (Suzan et al. 2012). However, this general effect of density might have been expected to drive consistent associations between forest loss and closely transmitted parasites across all taxa. One could have alternatively predicted that prevalence could increase following forest loss if animals congregate in remaining forest patches, thereby increasing density (Suzan et al. 2012). Regardless, we did not see differences - either positive or negative - for closely transmitted bacteria, fungi, protozoa, or viruses. Although arthropods and helminths have the highest number of records for close-contact transmission in the GMPD, bacteria, protozoa, and viruses are also well-represented. This suggests that the null associations for these taxa are unlikely to stem from low statistical power. Instead, this finding suggests that these parasite groups might generally respond differently to forest loss or that variability within these groups could mask ecologically relevant associations. Indeed, perhaps for bacteria, fungi, protozoa, and viruses, this taxonomic level is too coarse to parse out biologically relevant associations. While the synthetic nature of the present study prevented us from identifying mechanistic explanations for these parasite taxa–

and-transmission-specific responses to forest loss, the trends we identified can help generate testable hypotheses for future empirical work.

The strength of forest loss–prevalence associations

Despite identifying that parasite traits play an important role in shaping complex interactions among forest loss and infection, effect sizes across all models were consistently weak (see figures 2-8; figures S2-S8). The highest marginal R^2 was 2% (4% for zoonotic parasites). By contrast, the highest conditional R^2 was 62% across all models (74% for zoonotic parasites), indicating that far more variance in prevalence can be explained by idiosyncrasies of studies, host species (and phylogeny), and parasite genera through our random effects.

Several explanations can be put forward to explain these weak effects. First, the dataset we leveraged to quantify forest loss (Hansen Global Forest Change) does not specifically quantify anthropogenic drivers, and so our estimates might be weaker if human-driven disturbances, such as urbanization or agricultural land use, generate stronger trends (e.g., Skinner et al. 2023). Second, our use of a broad database (GMPD) that was not specifically compiled to assess the effects of disturbances on parasites likely acquires a broader and, presumably, less biased estimate than if we had explicitly searched for individual studies only investigating forest loss and prevalence. Finally, rather than using qualitative descriptions of forest loss from the literature, we quantified continuous estimates of forest loss based on ecologically relevant host home range sizes. This methodological decision could again favor less extreme contrasts and, therefore, reduce the strength of estimated effects. This last point warrants re-emphasizing the possible implications of the geographic biases in our dataset – specifically, parasites in regions suffering from the highest extents of forest loss are undersampled. In short, the use of these

publicly available databases likely reduces biases in our analyses and may even underestimate the strength of the associations between forest loss and prevalence.

Conclusions, implications, and future directions

We synthesized publicly available parasite prevalence and trait data, open-source forest loss data, and phylogenetic meta-analysis to investigate the association between forest loss and parasite prevalence across three groups of mammals. Although forest loss had no effect on prevalence across all GMPD data, trends emerged when we investigated these associations for specific parasite types (in the case of zoonotic parasites) or transmission modes. We also identified additional associations when assessing how the relationships between forest loss and prevalence vary for different transmission modes within each parasite taxon. Taken together, these results illustrate that parasite traits must be considered to understand complex associations between forest loss and infection outcomes.

Our synthesis highlights many opportunities for future studies. To start, work is needed to identify why forest loss responses are highly variable within parasite taxa (i.e., why transmission mode patterns are not consistent across taxa). Possible avenues could include focused study on specific parasite genera with multiple species and transmission modes, such as *Mycoplasma spp.* or *Mycobacterium spp.* (Stephens et al. 2017). Additionally, the parasite prevalence and trait data used in this study were from the GMPD, which only comprises records for carnivores, primates, and ungulate hosts. The association between parasite traits and infection outcomes could differ for other host species, including (but not limited to) other mammalian groups such as bats and rodents that are highly diverse and harbor many high impact zoonoses (Han et al. 2016). Associations between forest loss and prevalence could differ for these groups, and future studies

could conduct similar analyses with other host groups as systematic parasite datasets expand and grow (e.g., the Pathogen Harmonized Observatory, PHAROS: https://pharos.viralemergence.org/).

Concerning forest loss specifically, we notably found that most records in the GMPD represent parasite sampling from areas that have not suffered the highest extents of forest loss globally. This data gap could result in severely underestimating the effects of forest loss on prevalence. Our synthesis shows that parasite prevalence—both overall and specific to zoonotic parasites—can be shaped by forest loss, depending on particular parasite taxa or transmission modes. Filling these data gaps with respect to forest loss must therefore be prioritized because of the possible implications for both wildlife conservation and human health.

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Data availability: All data required to replicate the analyses are publicly available, as cited in the text.

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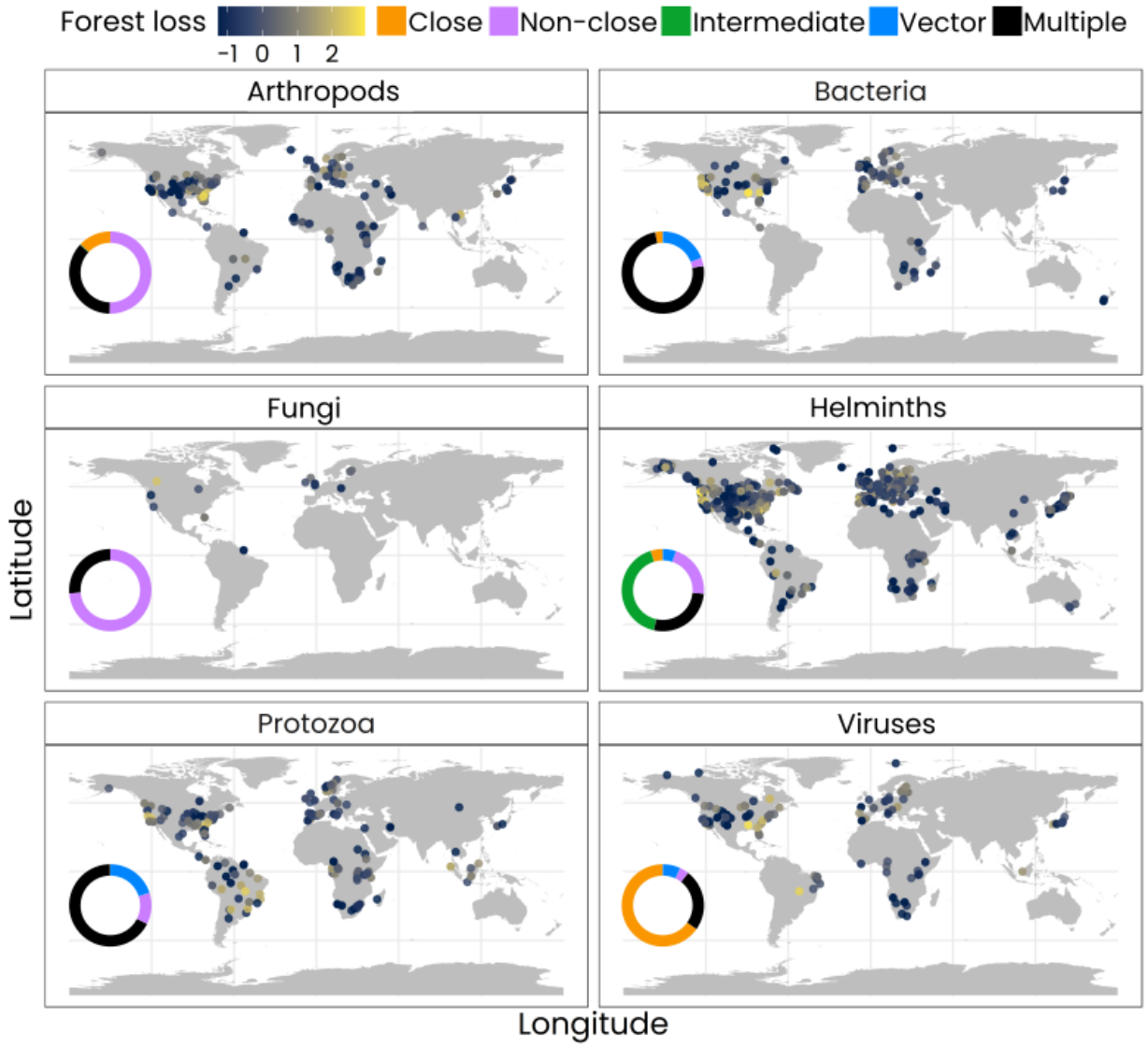

Figure 1. Locations where parasites were sampled in the GMPD. Maps are faceted by parasite taxonomy, and the data points are colored by the extent of forest loss. Forest loss is quarter root-transformed and z-score standardized; point color thus reflects the relative extent of forest loss in the dataset. Overlaid donut plots show the distribution of transmission modes within each parasite type close only, non-close only, intermediate only, vector only, or multiple transmission modes).

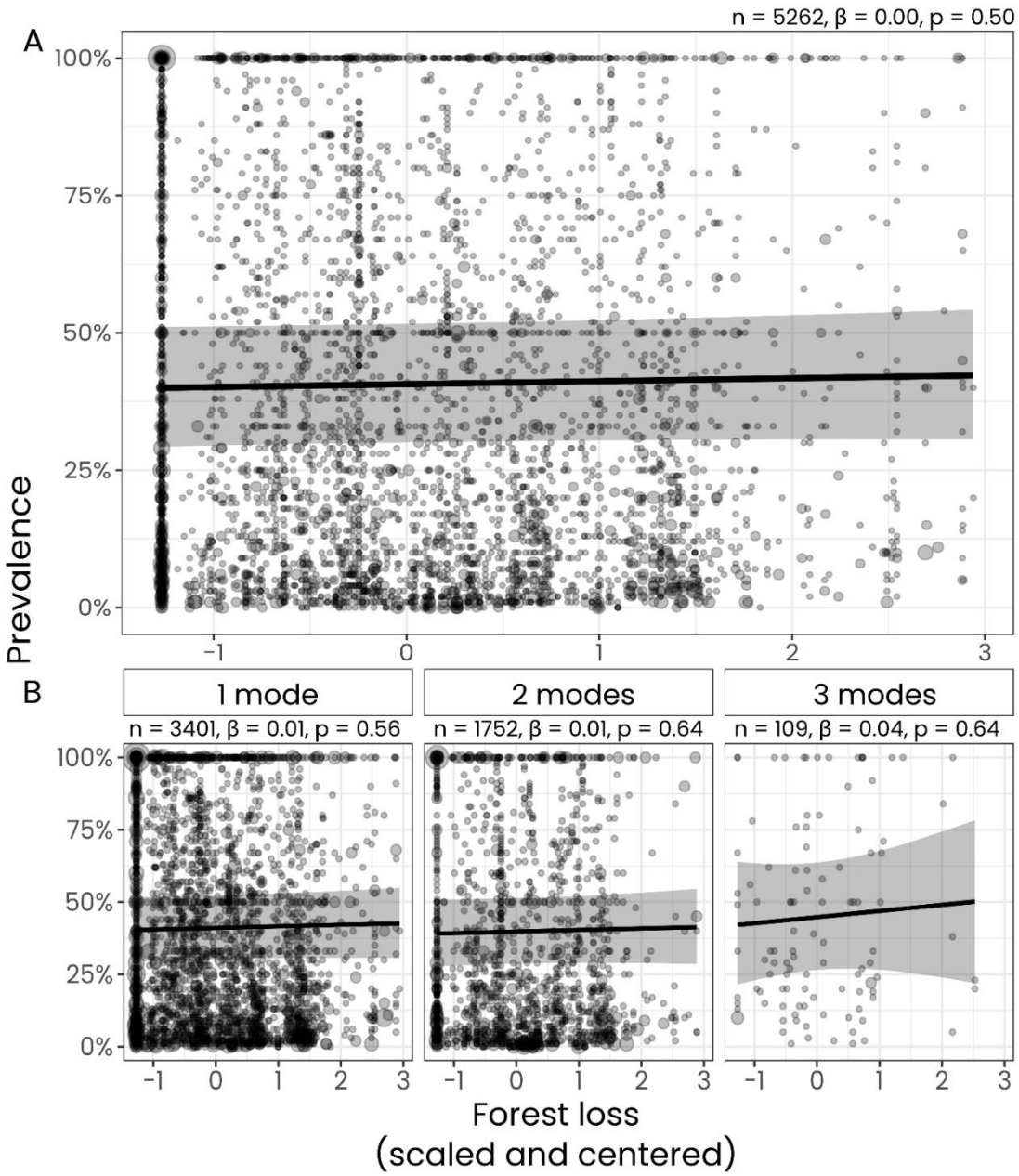

Figure 2. Associations between forest loss and prevalence including all parasite taxa, transmission modes, and both zoonotic and non-zoonotic parasites**,** (A) overall, and (B) for parasites transmitted via one, two, or three transmission modes. Points are scaled by sample size (number of hosts sampled), and the lines and bands represent the modeled trends and 95% confidence intervals from the phylogenetic meta-analyses. Panel A: marginal $R^2 = 0.00$; conditional $R^2 = 0.61$; Panel B: marginal $R^2 = 0.00$; conditional $R^2 = 0.61$.

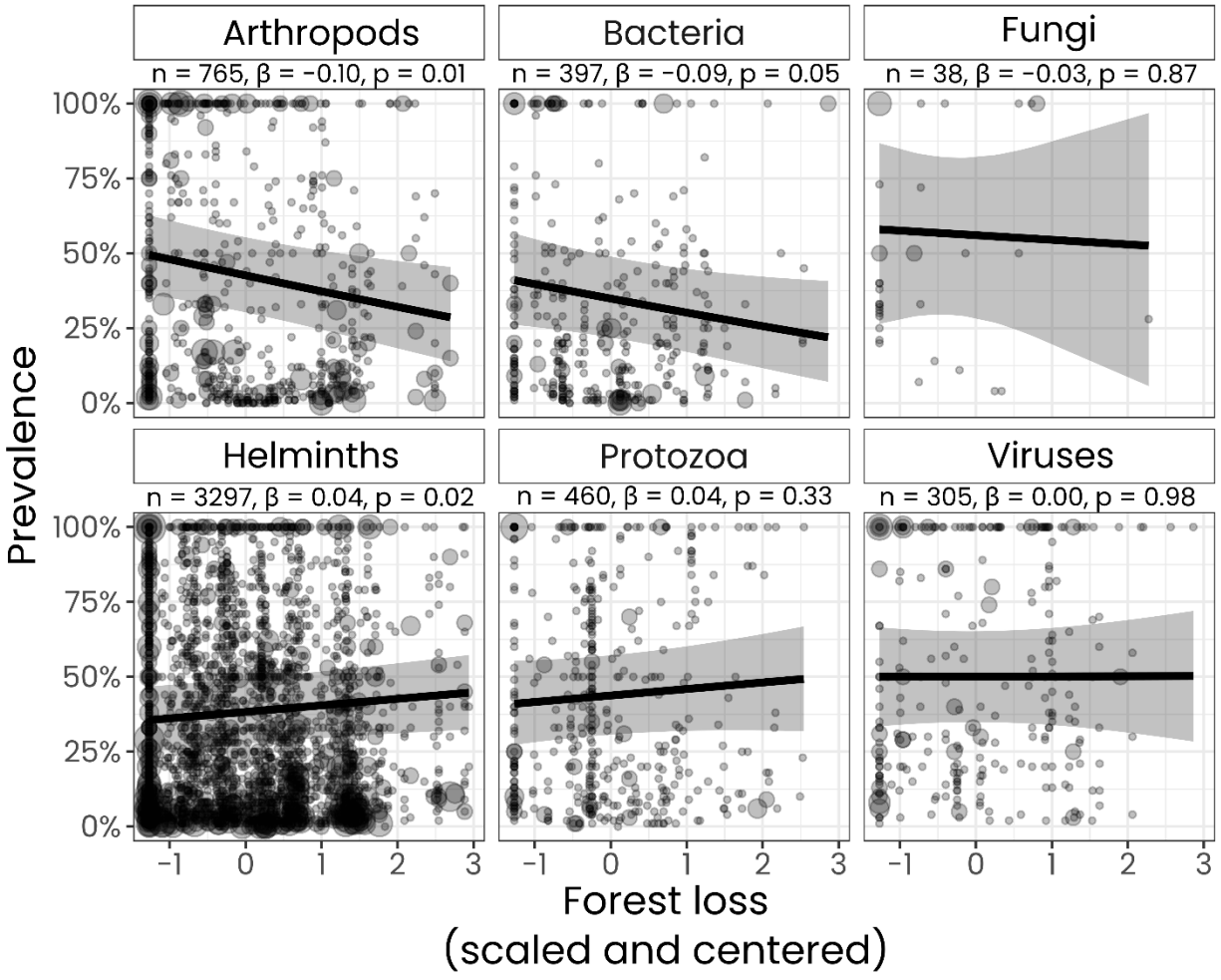

Figure 3. Associations between forest loss and prevalence, for both zoonotic and non-zoonotic parasites, faceted by parasite taxa. Points are scaled by sample size (number of hosts sampled), and the lines and bands represent the modeled trends and 95% confidence intervals from the phylogenetic meta-analyses. Marginal $R^2 = 0.01$; conditional $R^2 = 0.61$.

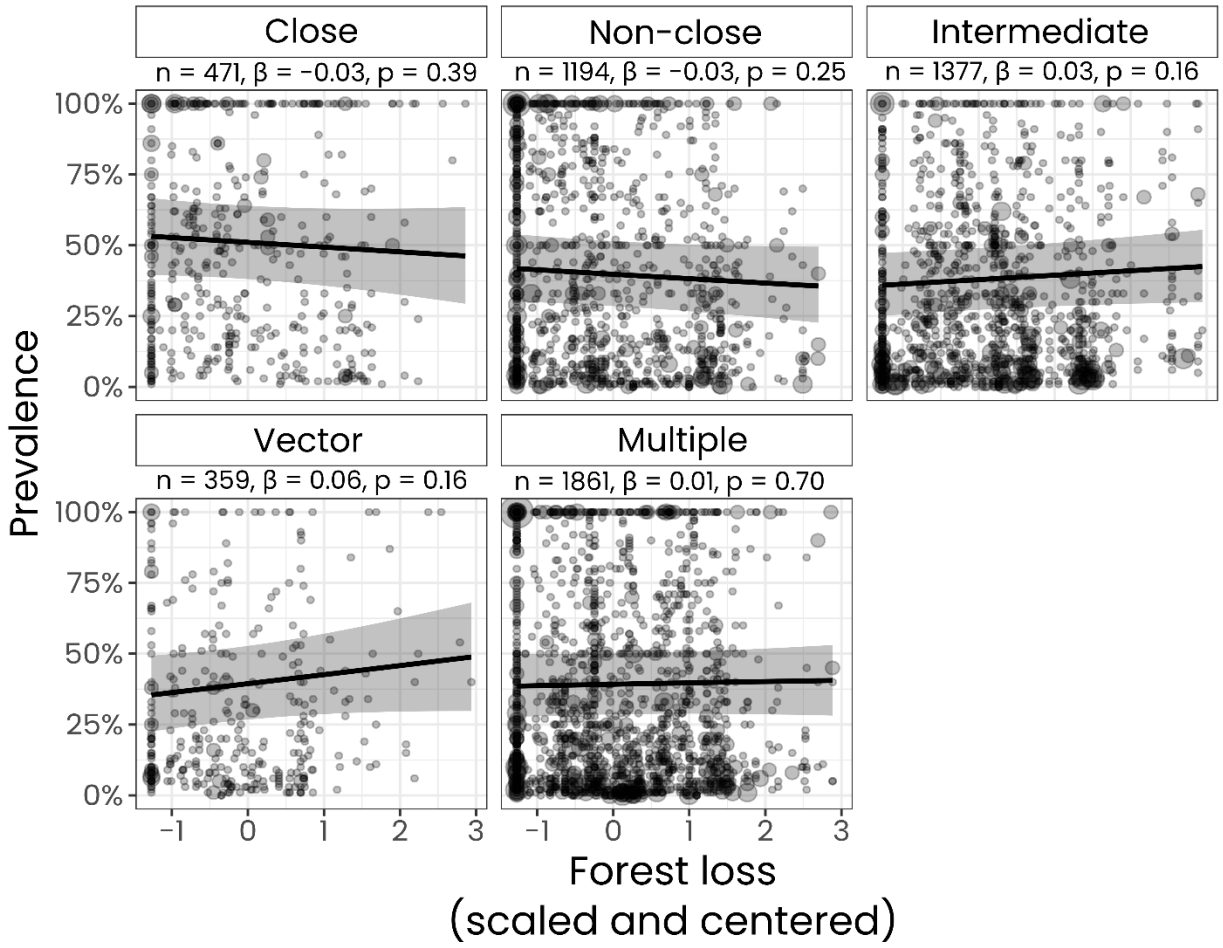

Figure 4. Associations between forest loss and prevalence, for both zoonotic and non-zoonotic parasites, faceted by transmission mode (close only, non-close only, intermediate only, vector only, or multiple transmission modes). Points are scaled by sample size (number of hosts sampled), and the lines and bands represent the modeled trends and 95% confidence intervals from the phylogenetic meta-analyses. Marginal $R^2 = 0.01$; conditional $R^2 = 0.61$.

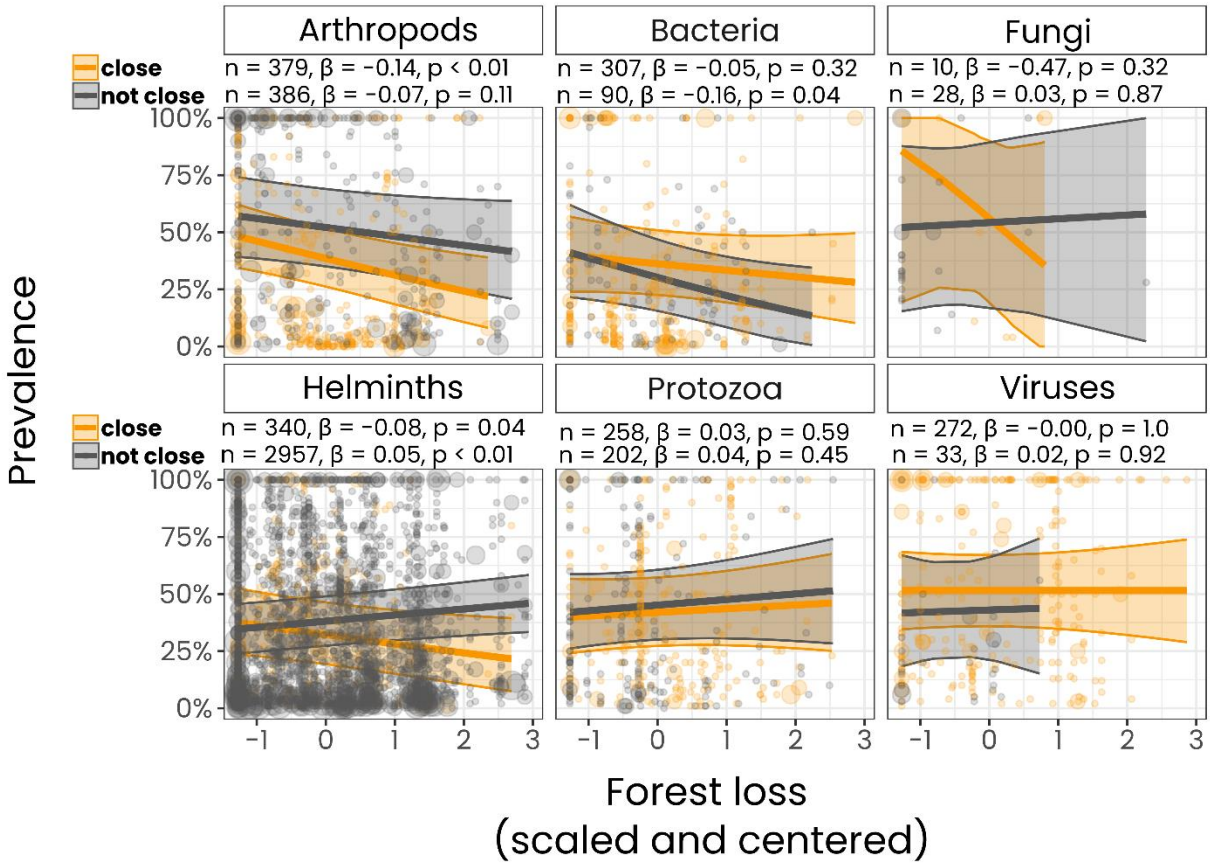

Figure 5. Association between forest loss and prevalence, for both zoonotic and non-zoonotic parasites, faceted by parasite taxa, and coloured by whether the parasite is closely transmitted or not closely transmitted. Points are scaled by sample size (number of hosts sampled), and the lines and bands represent the modeled trends and 95% confidence intervals from the phylogenetic meta-analyses. Marginal $R^2 = 0.02$; conditional $R^2 = 0.62$.

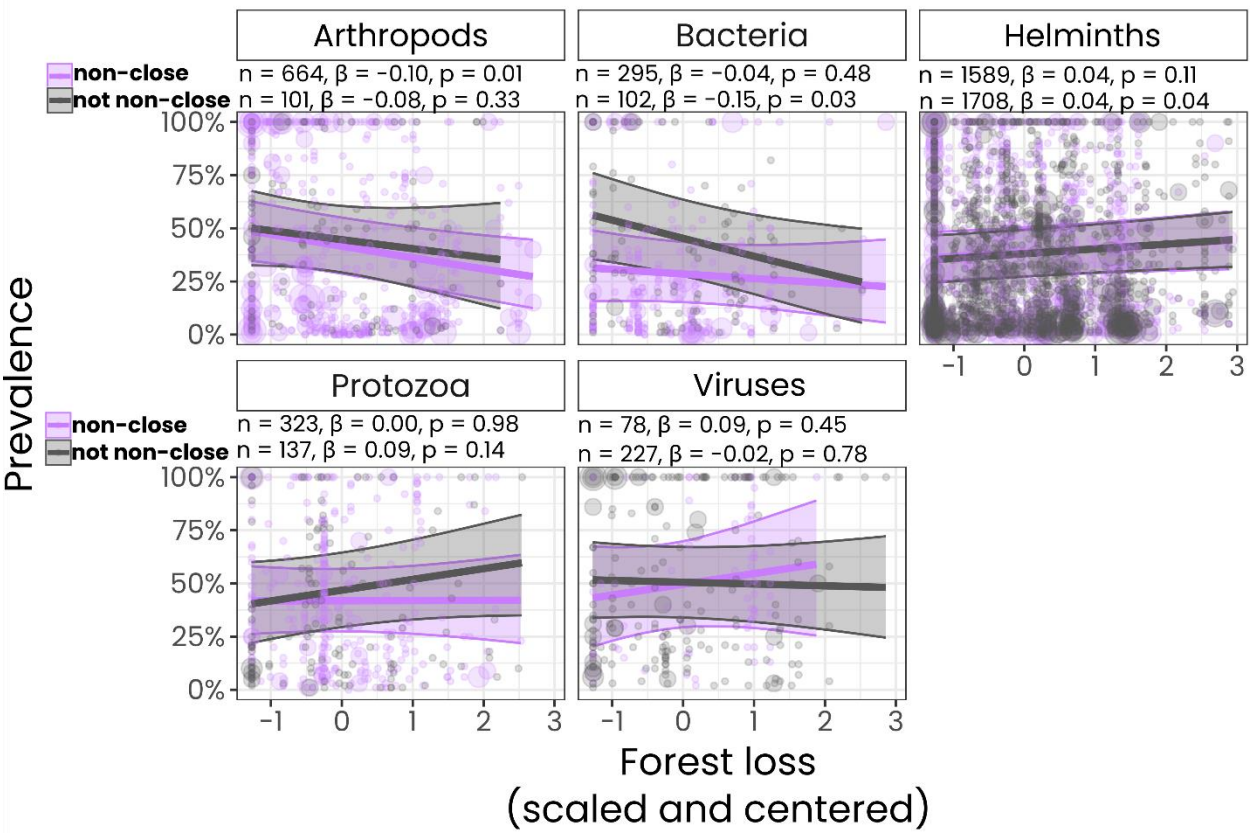

Figure 6. Associations between forest loss and prevalence, for both zoonotic and non-zoonotic parasites, faceted by parasite taxa, and coloured by whether the parasite is non-closely transmitted or not non-closely transmitted. Points are scaled by sample size (number of hosts sampled), and the lines and bands represent the modeled trends and 95% confidence intervals from the phylogenetic meta-analyses. Marginal $R^2 = 0.02$; conditional $R^2 = 0.62$. Fungi are excluded, because fungi are only non-closely transmitted in the GMPD.

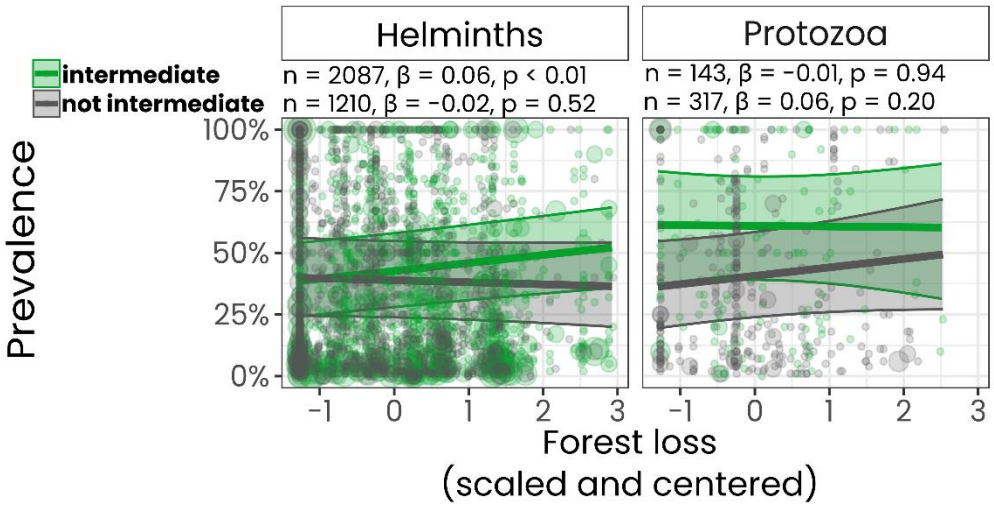

Figure 7. Associations between forest loss and prevalence, for both zoonotic and non-zoonotic parasites, faceted by parasite taxa, and coloured by whether the parasite is intermediately transmitted or not intermediately transmitted. Points are scaled by sample size (number of hosts sampled), and the lines and bands represent the modeled trends and 95% confidence intervals from the phylogenetic meta-analyses. Marginal $R^2 = 0.01$; conditional $R^2 = 0.61$. Arthropods are excluded because of the small sample size for intermediately transmitted arthropods (n = 2). Bacteria, fungus, and viruses are excluded because they are only not intermediately transmitted.

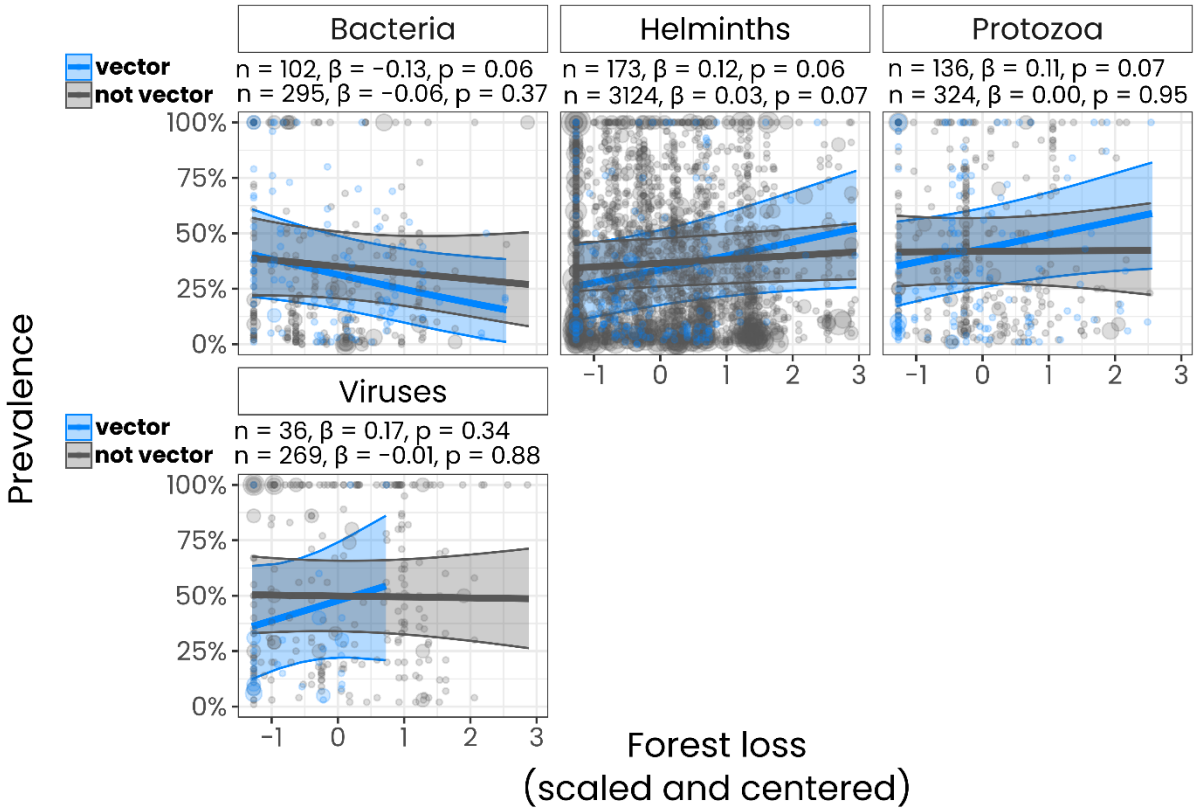

Figure 8. Associations between forest loss and prevalence, for both zoonotic and non-zoonotic parasites, faceted by parasite taxa, and coloured by whether the parasite is vector-borne or not vector-borne. Points are scaled by sample size (number of hosts sampled), and the lines and bands represent the modeled trends and 95% confidence intervals from the phylogenetic meta-analyses. Marginal $R^2 = 0.01$; conditional $R^2 = 0.61$. Arthropods and fungi are excluded, because no arthropods or fungi in the GMPD are vector-borne.

Supplementary materials for 'Parasite traits shape the association between forest loss and infection outcomes: A global meta-analysis'

Meta-analysis methods

We used the 'metafor' escalc() function and the Freeman-Tukey double arcsine transformed proportion ('PFT') to normalize prevalence and calculate corresponding sampling variances. This measure was selected because PFT efficiently accounts for the high zero inflation that often characterizes prevalence data sampled from wild animals and can effectively handle zero prevalence values (in contrast to the logit transformation). Because forest loss in our dataset is also heavily skewed towards zero, forest loss was quarter-root transformed. We also scaled this forest loss variable by transforming it into a z-score.

We built hierarchical meta-analytic models using the rma.mv() function in 'metafor'. The random effect structure in all our models was as follows. To account for heterogeneity within and among studies, we included random effects of 'observation' nested within 'study'. To account for variation among hosts, we included random effects of 'host phylogeny' (see 'Host and parasite data') and 'host species'; the former random effect accounts for relatedness among species, whereas the latter accounts for multiple observations of the same species. The mean phylogenetic correlation was 0.27 (excluding the diagonal), indicating that the phylogenetic relationships are sufficiently strong to justify both terms (Cinar et al. 2022). Our final random effect, 'parasite genus', was included to account for non-independence among parasites sampled.

Our first series of models included all observations in our dataset (n = 5262). First, we built an overall forest loss model, which only included the fixed effect of forest loss. We then added additional moderators to untangle the factors that could moderate the association between

forest loss and prevalence. These moderators were always considered in interactions with forest loss (i.e., main effects and their interaction). The first model investigated the effects of 'parasite type' (helminth, protozoa, virus, bacteria, fungi). The next two of these models investigated the effects of transmission mode. In one model, the number of transmission modes was included (1-3), and in the second model, the more specific transmission mode was included (close only, non-close only, intermediate only, vector only, multiple).

We next build a series of models with forest loss, parasite type, and the binary transmission mode (e.g., vector: yes or no) in a three-way interaction. We created four of these models, one for each transmission mode: close, non-close, intermediate, vector. For the close model, we used the full dataset with all parasite groups. For the non-close model, we included all parasite groups except for fungi (all fungi in our dataset are non-closely transmitted). For the vector-borne models, we included all parasite groups except for fungi and arthropods (all fungi and arthropods in our dataset are not vector-borne). Finally, for the intermediate model we only compared helminths and protozoa (all bacteria, fungi and viruses in our dataset are not intermediately transmitted; and only 2 arthropod records represent intermediate transmission).

In a final series of models, we sought to better understand how associations between forest loss and prevalence specifically differ for potentially zoonotic parasites. We therefore replicated the above-described analyses using only data representing parasites that are known to infect humans (n = 2365). Because VIRION and COVER do not consider arthropods, parasite type for zoonotic parasites consisted of only five levels: helminth, protozoa, bacteria, virus, and fungi.

All models were fit using restricted maximum likelihood using the Quasi-Newton BFGS optimizer, and included weighting by the inverse of sampling variance. For each model, we calculated R^2 using the 'orchaRd' package and the r2_ml() function (Nakagawa et al. 2023).

Because our models included forest loss (a continuous variable) in an interaction with one or more categorical variables, we estimated the forest loss slope for each level of our interacting categorical variables using the 'emmeans' package (Lenth 2024). We computed a reference grid for each meta-analytic model with forest loss fixed at two levels. We estimated consecutive pairwise comparisons between the slopes predicted for each level of forest loss within each grouping category (transmission mode or parasite type).

References (cited in supplement)

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Supplemental tables and figures

Table S1. Wald-type test for the overall model with only forest loss as a fixed effect.

Term	Q	df	p
Forest loss	0.45	1	0.50

Table S2. Wald-type test for the model with the number of transmission modes in interaction with forest loss.

Term	Q	df	p
Forest loss	0.34	1	0.56
Number of transmission modes	0.56	2	0.76
Forest loss: Number of transmission modes	0.13	2	0.94

Table S3. Post hoc comparisons between differing extents of forest cover loss within groups of parasites that have one, two or three transmission modes.

Number of transmission modes	β	SE	t	p
1 mode	0.01	0.02	0.58	0.56
2 modes	0.01	0.02	0.46	0.64
3 modes	0.04	0.08	0.47	0.64

Table S4. Wald type test for the model with parasite taxa in interaction with forest loss.

Term	Q	df	p
Forest loss	6.96	1	0.01
Parasite taxa	7.60	5	0.18
Forest loss: Parasite taxa	17.72	5	<0.01

Table S5. Post hoc comparisons between differing extents of forest cover loss for different parasite taxa.

Parasite type	β	SE	t	p
Arthropod	-0.10	0.04	-2.64	0.01
Bacteria	-0.09	0.05	-1.93	0.05
Fungus	-0.03	0.1672	-0.17	0.87
Helminth	0.04	0.02	2.26	0.02
Protozoa	0.04	0.04	0.97	0.33
Virus	0.00	0.05	0.02	0.98

Table S6. Wald type test for the model with the specific transmission mode (close only, non-close only, intermediate only, vector only, multiple) in interaction with forest loss.

Term	Q	df	p
Forest loss	0.75	1	0.39
Transmission mode	7.91	4	0.10
Forest loss: Transmission mode	6.55	4	0.16

Table S7. Post hoc comparisons between differing extents of forest cover loss based on different transmission modes.

Transmission mode	β	SE	t	p
Only close	-0.03	0.04	-0.86	0.39
Only non-close	-0.03	0.02	-1.15	0.25
Only intermediate	0.03	0.02	1.41	0.16
Only vector	0.06	0.04	1.42	0.16
Multiple transmission modes	0.01	0.02	0.39	0.70

Table S8. Wald type test for the model with ‘close or not close’ transmission in interactions with parasite taxa and forest loss.

Term	Q	df	p
Forest loss	9.00	1	<0.01
Close or not close	3.00	1	0.08
Parasite taxa	7.13	5	0.21
Forest loss: Close or not close	1.66	1	0.20
Forest loss : Parasite taxa	7.81	5	0.17
Close or not close : Parasite taxa	4.88	5	0.43
Forest loss : Close or not close : Parasite taxa	7.05	5	0.22

Table S9. Wald type test for the model with ‘non-close or not non-close’ transmission in interactions with parasite taxa and forest loss.

Term	Q	df	p
Forest loss	7.03	1	0.01
Non-close or not non-close	0.19	1	0.67
Parasite taxa	5.23	4	0.26
Forest loss: Non-close or not non-close	0.09	1	0.76
Forest loss : Parasite taxa	11.63	4	0.02
Non-close or not non-close : Parasite taxa	3.54	4	0.47
Forest loss : Non-close or not non-close : Parasite taxa	3.62	4	0.46

Table S10. Wald type test for the model with ‘intermediate or not intermediate’ transmission in interactions with parasite taxa and forest loss.

Term	Q	df	p
Forest loss	9.41	1	<0.01
Intermediate or not intermediate	0.87	1	0.35
Parasite taxa	4.45	1	0.03
Forest loss: Intermediate or not intermediate	8.82	1	<0.01
Forest loss : Parasite taxa	0.74	1	0.39
Intermediate or not intermediate : Parasite taxa	2.29	1	0.13
Forest loss : Intermediate or not intermediate : Parasite taxa	2.49	1	0.11

Table S11. Wald type test for the model with ‘vector-borne or not vector-borne’ transmission in interactions with parasite taxa and forest loss.

Term	Q	df	p
Forest loss	0.82	1	0.37
Vector-borne or not vector-borne	0.19	1	0.67
Parasite taxa	4.73	3	0.19
Forest loss : Vector-borne or not vector-borne	0.71	1	0.40
Forest loss : Parasite taxa	2.34	3	0.50
Vector or not vector-borne : Parasite taxa	0.18	3	0.98
Forest loss : Vector or not vector-borne : Parasite taxa	3.11	3	0.37

Table S12. Post hoc comparisons between differing extents of forest cover loss for each parasite taxa and transmission mode.

Parasite group	Binary transmission mode	β	SE	t	p
Arthropod	Close	-0.14	0.05	-3.00	<0.01
	Not close	-0.07	0.04	-1.59	0.11
Bacteria	Close	-0.05	0.06	-0.99	0.32
	Not close	-0.16	0.08	-2.05	0.04
Fungus	Close	-0.47	0.47	-0.99	0.32
	Not close	0.03	0.18	0.17	0.87
Helminth	Close	-0.08	0.04	-2.01	0.04
	Not close	0.05	0.02	2.67	<0.01

Protozoa	Close	0.03	0.05	0.54	0.59
	Not close	0.04	0.06	0.76	0.45
Virus	Close	-0.00	0.05	-0.00	0.10
	Not close	0.02	0.17	0.11	0.92
Arthropod	**Non-close**	**-0.10**	**0.04**	**-2.65**	**<0.01**
	Not non-close	-0.08	0.08	-0.97	0.33
Bacteria	Non-close	-0.04	0.06	-0.71	0.48
	Not non-close	**-0.16**	**0.07**	**-2.22**	**0.03**
Helminth	Non-close	0.04	0.02	1.59	0.11
	Not non-close	**0.04**	**0.02**	**2.07**	**0.04**

Protozoa	Non-close	0.00	0.05	0.03	0.98
	Not non-close	0.09	0.06	1.48	0.14
Virus	Non-close	0.09	0.12	0.76	0.45
	Not non-close	-0.02	0.06	-0.28	0.78
Helminth	Intermediate	0.06	0.02	3.07	<0.01
	Not intermediate	-0.02	0.03	-0.65	0.52
Protozoa	Intermediate	-0.01	0.07	-0.07	0.94
	Not intermediate	0.06	0.05	1.283	0.20
Bacteria	Vector-borne	-0.13	0.07	-1.911	0.06
	Not vector-borne	-0.06	0.06	-0.91	0.37

Helminth	Vector-borne	0.12	0.06	1.88	0.06
	Not vector-borne	0.03	0.02	1.79	0.07
Protozoa	Vector-borne	0.11	0.06	1.83	0.07
	Not vector-borne	0.00	0.05	0.07	0.95
Virus	Vector-borne	0.17	0.17	0.96	0.34
	Not vector-borne	-0.01	0.05	-0.15	0.88

The tables below are for the subset of analyses with only zoonotic parasites

Table S13. Wald-type test for the overall model with only forest loss as a fixed effect conducted with the subset of our dataset only representing zoonotic parasites.

Term	Q	df	p
Forest loss	0.07	1	0.79

Table S14. Wald-type test for the model with the number of transmission modes in interaction with forest loss conducted with the subset of our dataset only representing zoonotic parasites.

Term	Q	df	p
Forest loss	0.02	1	0.89
Number of transmission modes	2.56	2	0.28
Forest loss: Number of transmission modes	1.01	2	0.60

Table S15. Post hoc comparisons between differing extents of forest cover loss within groups of zoonotic parasites that have one, two or three transmission modes.

Number of transmission modes	β	SE	t	p
1 mode	-0.00	0.02	-0.14	0.89
2 modes	0.02	0.03	0.68	0.50
3 modes	0.05	0.07	0.76	0.45

Table S16. Wald type test for the model with parasite taxa in interaction with forest loss conducted with the subset of our dataset only representing zoonotic parasites.

Term	Q	df	p
Forest loss	1.63	1	0.20
Parasite taxa	7.4	4	0.12
Forest loss: Parasite taxa	4.38	4	0.36

Table S17. Post hoc comparisons between differing extents of forest cover loss within different groups of zoonotic parasites.

Parasite type	β	SE	t	p
Bacteria	-0.05	0.04	-1.28	0.20
Fungus	-0.05	0.15	-0.36	0.72
Helminth	0.00	0.02	0.18	0.86
Protozoa	0.06	0.04	1.38	0.17
Virus	0.04	0.06	0.80	0.43

Table S18. Wald type test for the model with the specific transmission mode (close only, non-close only, intermediate only, vector only, multiple) in interaction with forest loss conducted with the subset of our dataset only representing zoonotic parasites.

Term	Q	df	p
Forest loss	1.18	1	0.28
Transmission mode	10.75	4	0.03
Forest loss: Transmission mode	5.22	4	0.27

Table S19. Post hoc comparisons between differing extents of forest cover loss and zoonotic parasites based on different transmission modes.

Transmission mode	β	SE	t	p
Only close	-0.04	0.04	-1.09	0.28
Only non-close	-0.02	0.03	-0.66	0.51
Only intermediate	-0.01	0.03	-0.26	0.80
Only vector	0.07	0.04	1.75	0.08
Multiple transmission modes	0.02	0.03	0.59	0.56

Table S20. Wald type test for the model with ‘close or not close’ transmission in interactions with parasite taxa and forest loss conducted with the subset of our dataset only representing zoonotic parasites.

Term	Q	df	p
Forest loss	0.37	1	0.54
Close or not close	2.16	1	0.14
Parasite taxa	4.06	4	0.40
Forest loss: Close or not close	0.82	1	0.37
Forest loss : Parasite taxa	12.46	4	0.01
Close or not close : Parasite taxa	1.64	4	0.80
Forest loss : Close or not close : Parasite taxa	7.88	4	0.10

Table S21. Wald type test for the model with ‘non-close or not non-close’ transmission in interactions with parasite taxa and forest loss conducted with the subset of our dataset only representing zoonotic parasites.

Term	Q	df	p
Forest loss	0.05	1	0.83
Non-close or not non-close	1.27	1	0.26
Parasite taxa	1.65	3	0.65
Forest loss: Non-close or not non-close	0.04	1	0.85
Forest loss : Parasite taxa	3.25	3	0.35
Non-close or not non-close : Parasite taxa	2.01	3	0.57
Forest loss : Non-close or not non-close : Parasite taxa	2.48	3	0.48

Table S22. Wald type test for the model with ‘intermediate or not intermediate’ transmission in interactions with parasite taxa and forest loss conducted with the subset of our dataset only representing zoonotic parasites.

Term	Q	df	p
Forest loss	1.47	1	0.22
Intermediate or not intermediate	0.38	1	0.54
Parasite taxa	4.22	1	0.04
Forest loss: Intermediate or not intermediate	3.77	1	0.05
Forest loss : Parasite taxa	0.24	1	0.63
Intermediate or not intermediate : Parasite taxa	4.01	1	0.05
Forest loss : Intermediate or not intermediate : Parasite taxa	0.37	1	0.54

Table S23. Wald type test for the model with ‘vector-borne or not vector-borne’ transmission in interactions with parasite taxa and forest loss conducted with the subset of our dataset only representing zoonotic parasites.

Term	Q	df	p
Forest loss	0.23	1	0.63
Vector-borne or not vector-borne	0.00	1	0.99
Parasite taxa	5.12	3	0.16
Forest loss : Vector-borne or not vector-borne	4.73	1	0.03
Forest loss : Parasite taxa	1.59	3	0.66
Vector or not vector-borne : Parasite taxa	0.51	3	0.92
Forest loss : Vector or not vector-borne : Parasite taxa	2.68	3	0.44

Table S24. Post hoc comparisons between differing extents of forest cover loss for each zoonotic parasite taxa and transmission mode.

Parasite group	Binary transmission mode	β	SE	t	p
Bacteria	Close	-0.03	0.05	-0.61	0.54
	Not close	-0.10	0.07	-1.44	0.15
Fungus	Close	-0.45	0.42	-1.09	0.28
	Not close	0.00	0.16	0.02	0.98
Helminth	Close	-0.15	0.04	-3.41	<0.001
	Not close	0.02	0.02	0.90	0.37
Protozoa	Close	0.04	0.05	0.85	0.40
	Not close	0.10	0.08	1.24	0.22

Virus	Close	0.04	0.06	0.72	0.47
	Not close	0.06	0.16	0.35	0.73
Bacteria	Non-close	-0.03	0.05	-0.69	0.49
	Not non-close	-0.09	0.07	-1.28	0.20
Helminth	Non-close	0.01	0.03	0.22	0.83
	Not non-close	-0.00	0.03	-0.00	1.0
Protozoa	Non-close	0.04	0.05	0.87	0.39
	Not non-close	0.11	0.08	1.35	0.18
Virus	Non-close	0.33	0.23	1.43	0.15
	Not non-close	0.03	0.06	0.48	0.63

Helminth	Intermediate	0.03	0.03	1.21	0.23
	Not intermediate	-0.03	0.03	-1.03	0.31
Protozoa	Intermediate	0.07	0.08	0.95	0.34
	Not intermediate	0.07	0.05	1.40	0.16
Bacteria	Vector-borne	-0.07	0.07	-1.09	0.28
	Not vector-borne	-0.04	0.05	-0.83	0.41
Helminth	Vector-borne	0.13	0.06	2.08	0.04
	Not vector-borne	-0.01	0.02	-0.48	0.63
Protozoa	Vector-borne	0.11	0.08	1.37	0.17
	Not vector-borne	0.04	0.05	0.72	0.47

Virus	Vector-borne	0.15	0.15	1.04	0.30
	Not vector-borne	0.02	0.06	0.42	0.68

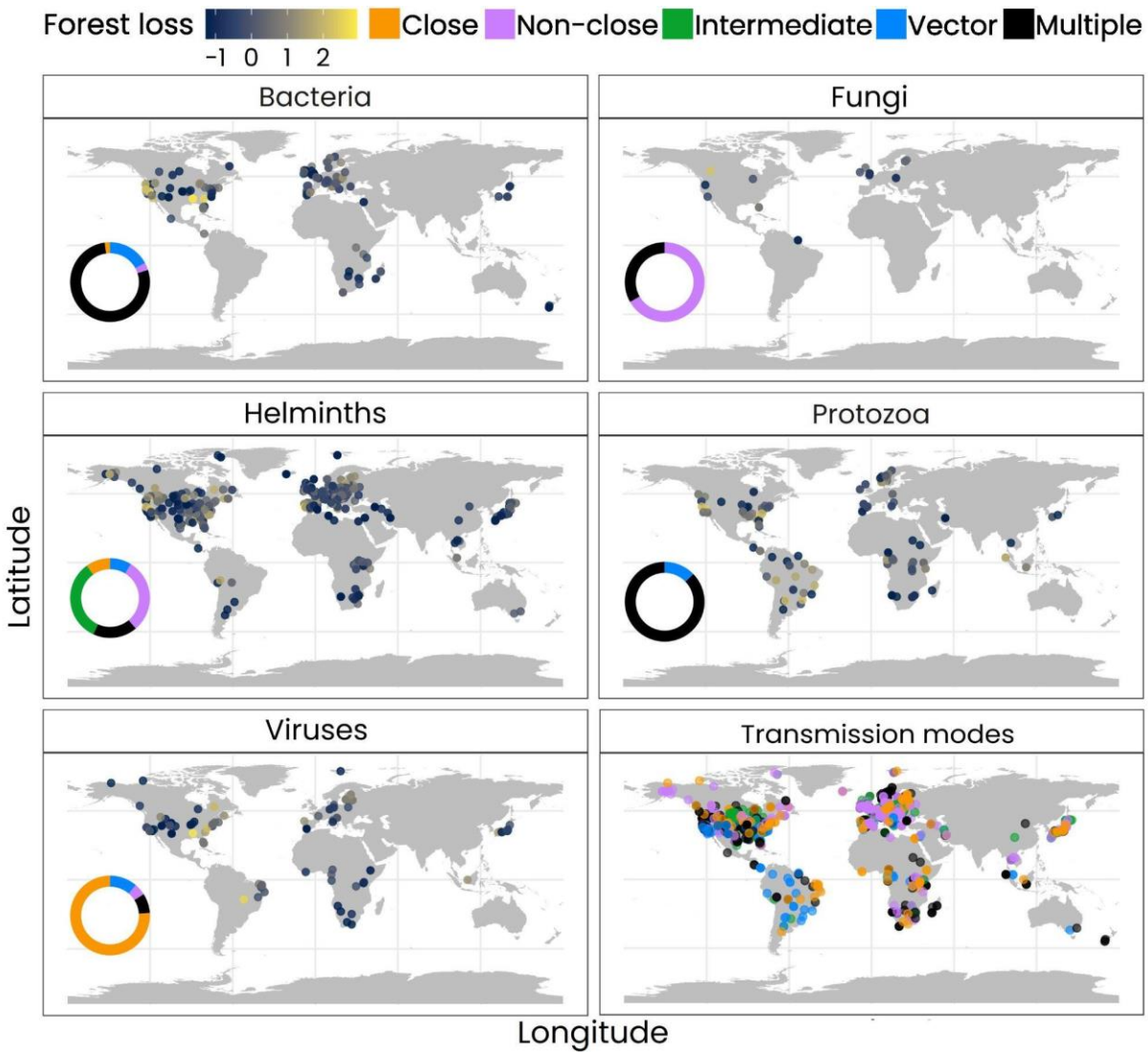

Figure S1. Locations where zoonotic parasites were sampled in the GMPD. Maps are faceted by parasite taxonomy, and the data points are colored by the extent of forest loss. Forest loss is quarter root-transformed and z-score standardized; point color thus reflects the relative extent of forest loss in the dataset. Overlaid donut plots show the distribution of transmission modes within each parasite type close only, non-close only, intermediate only, vector only, or multiple transmission modes).

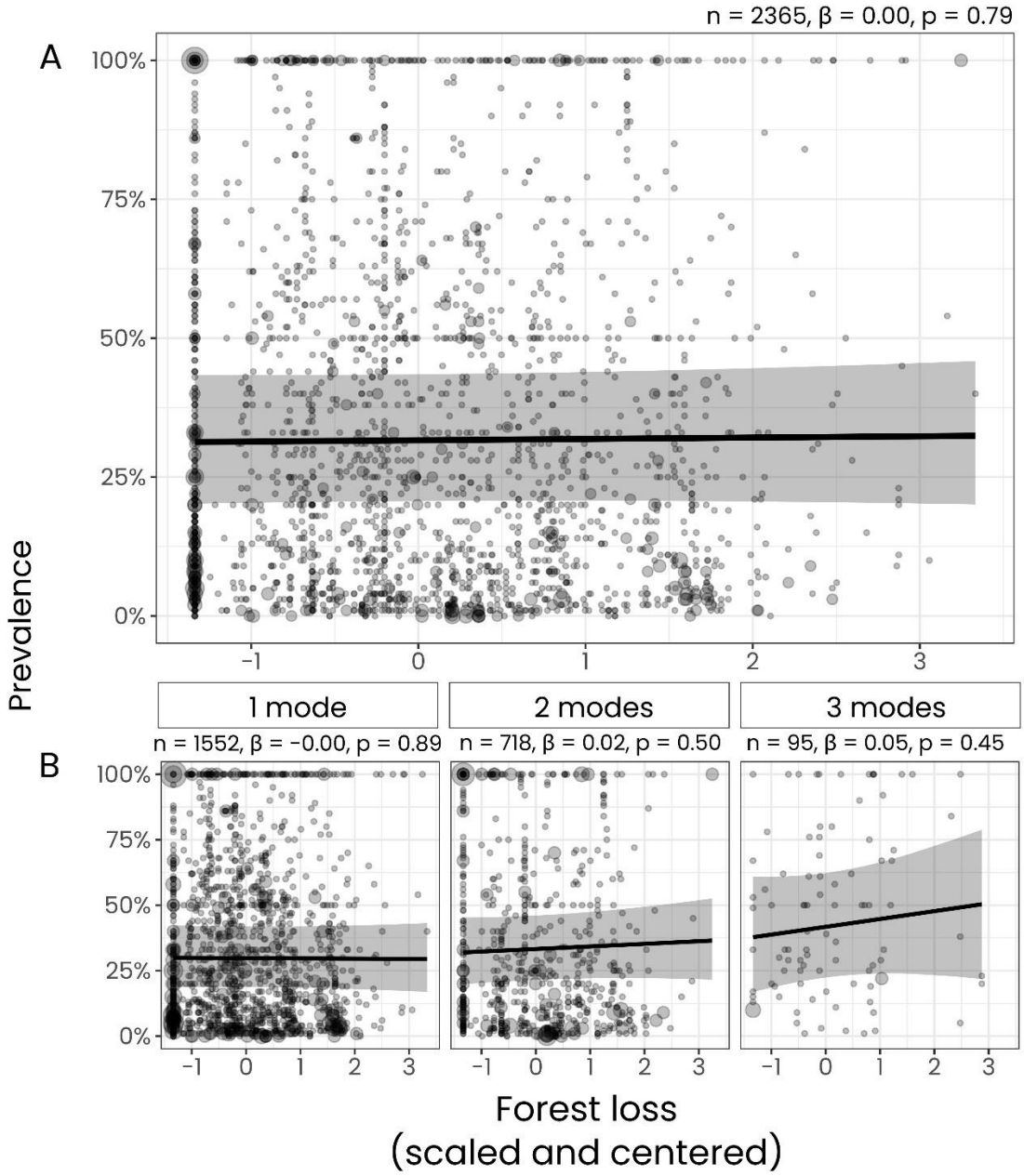

Figure S2. Association between forest loss and zoonotic parasite prevalence including all parasite taxa**,** (A) overall, and (B) for parasites transmitted via one, two, or three transmission modes. Points are scaled by sample size (number of hosts sampled), and the lines and bands represent the modeled trends and 95% confidence intervals from the phylogenetic meta-analyses). Panel A: marginal $R^2 = 0.00$; conditional $R^2 = 0.68$; Panel B: marginal $R^2 = 0.01$; conditional $R^2 = 0.68$.

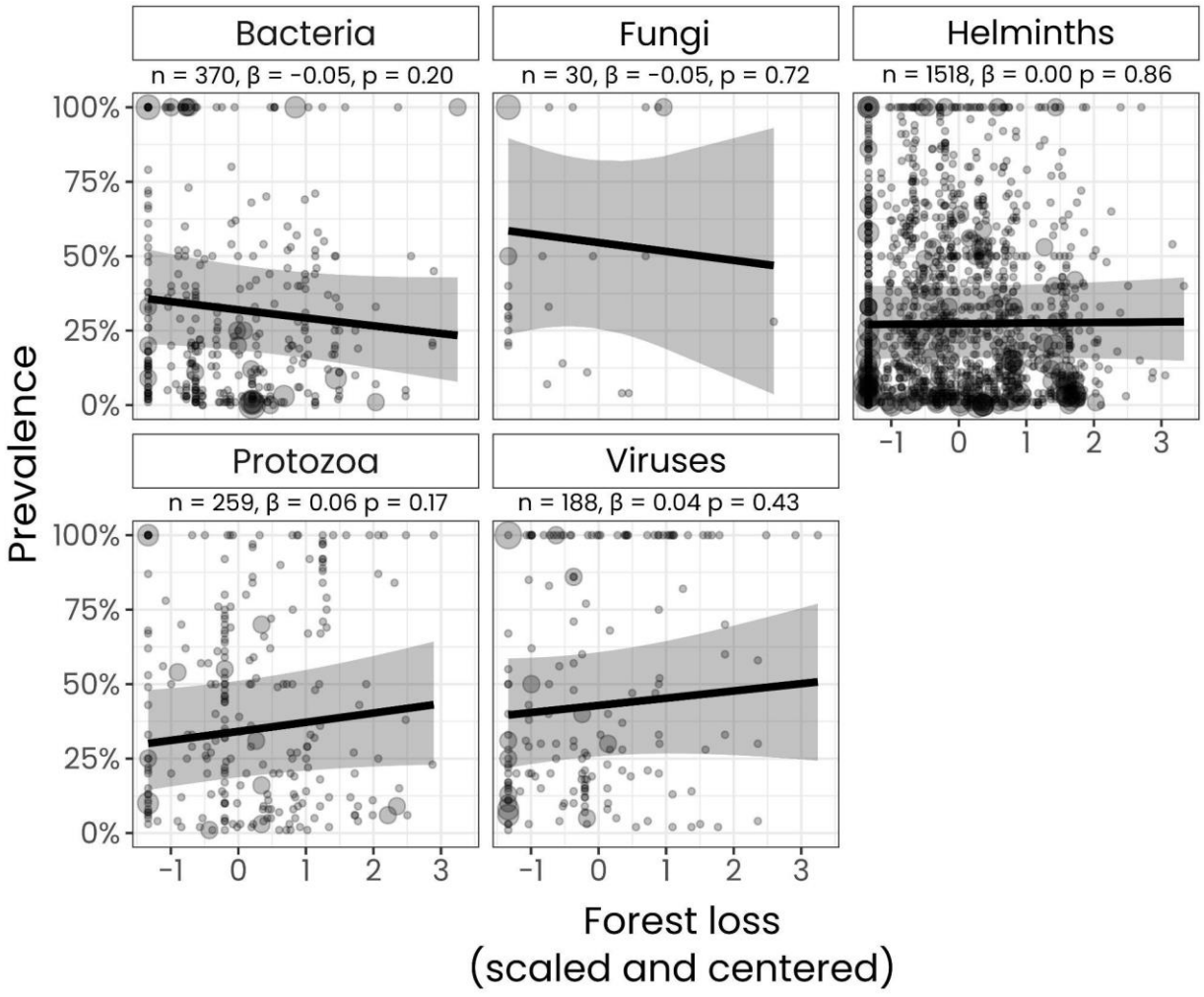

Figure S3. Association between forest loss and zoonotic parasite prevalence, faceted by parasite taxa. Points are scaled by sample size (number of hosts sampled), and the lines and bands represent the modeled trends and 95% confidence intervals from the phylogenetic meta-analyses). Marginal $R^2 = 0.02$; conditional $R^2 = 0.69$.

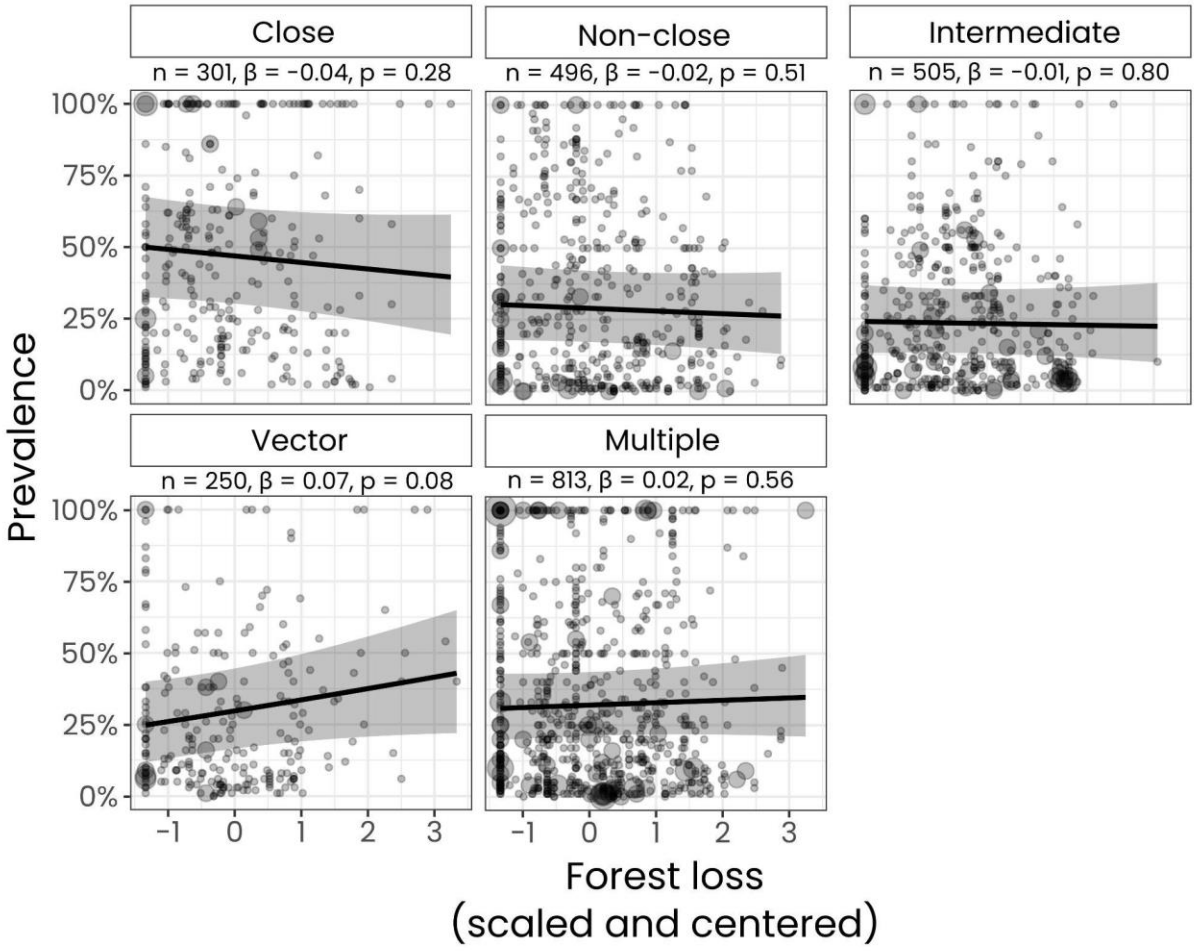

Figure S4. Association between forest loss and zoonotic parasite prevalence, faceted by transmission mode (close only, non-close only, intermediate only, vector only, or multiple transmission modes). Points are scaled by sample size (number of hosts sampled), and the lines and bands represent the modeled trends and 95% confidence intervals from the phylogenetic meta-analyses). Marginal $R^2 = 0.04$; conditional $R^2 = 0.68$.

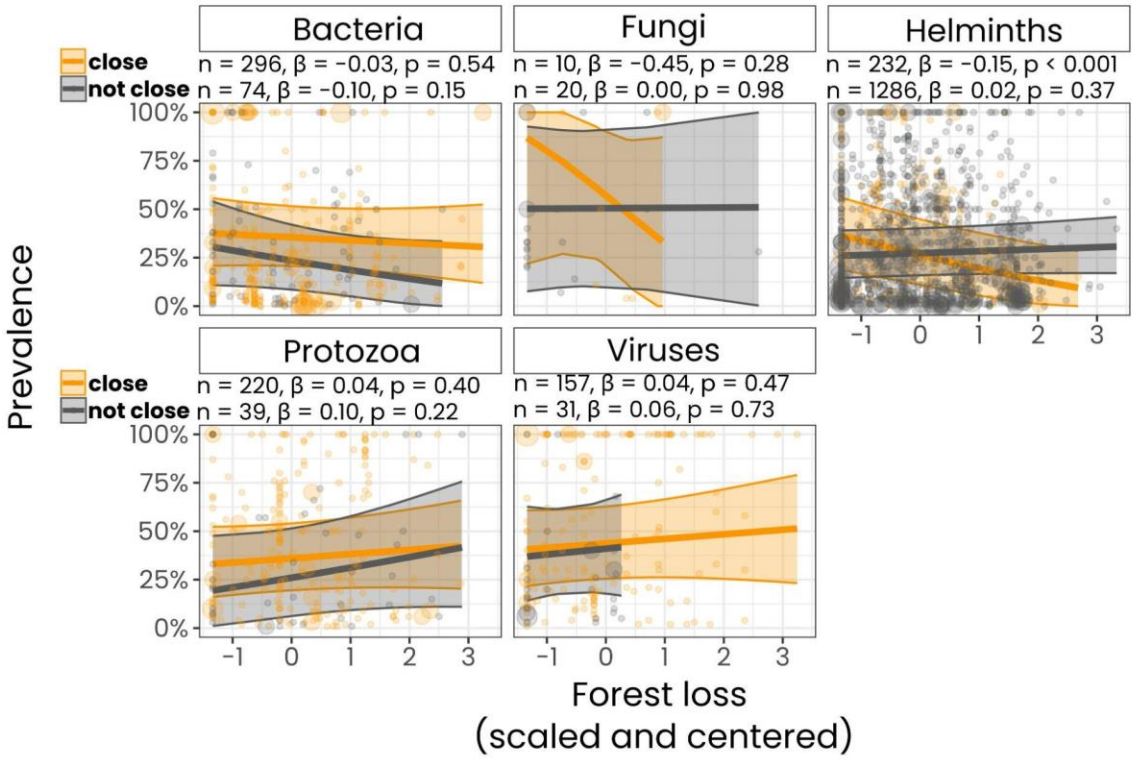

Figure S5. Association between forest loss and zoonotic parasite prevalence faceted by parasite taxa, and coloured by whether the parasite is closely transmitted or not closely transmitted. Points are scaled by sample size (number of hosts sampled), and the lines and bands represent the modeled trends and 95% confidence intervals from the phylogenetic meta-analyses). Marginal R^2 = 0.03; conditional R^2 = 0.70.

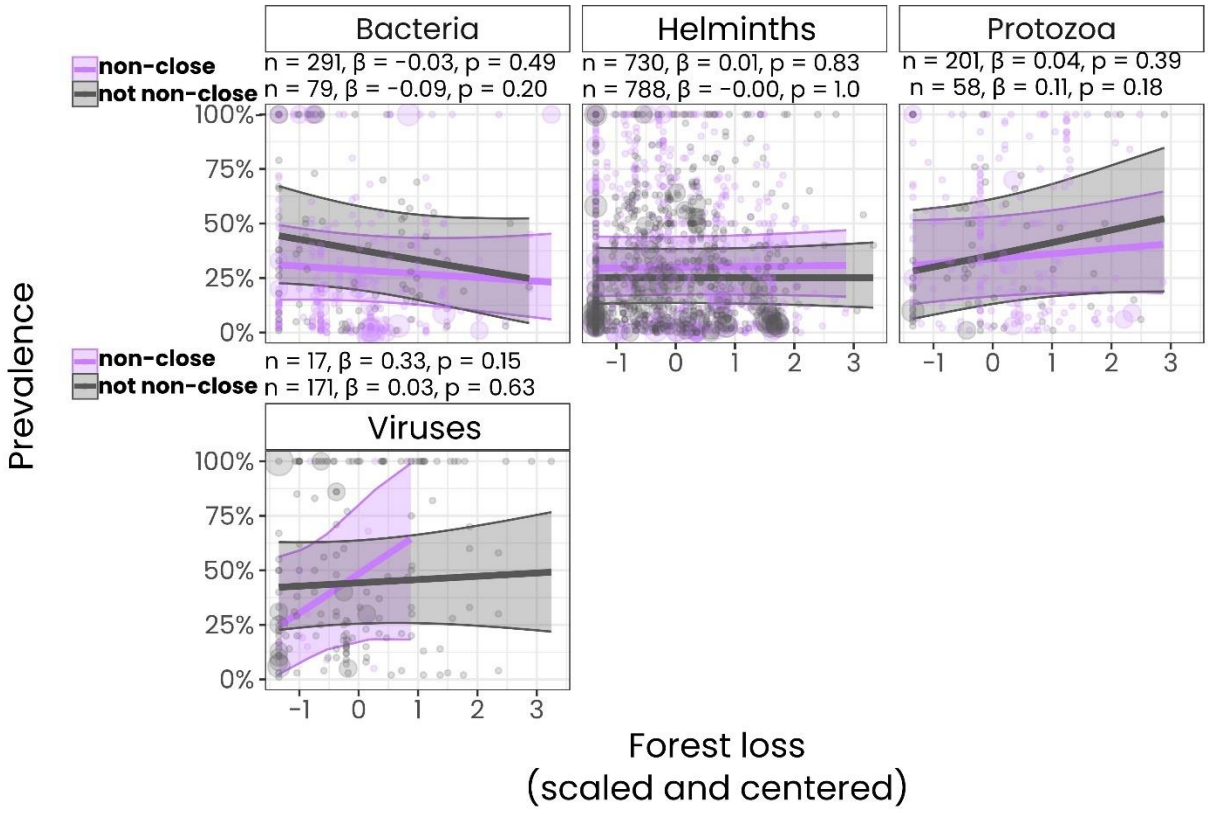

Figure S6. Association between forest loss and zoonotic parasite prevalence faceted by parasite taxa, and coloured by whether the parasite is non-closely transmitted or not non-closely transmitted. Points are scaled by sample size (number of hosts sampled), and the lines and bands represent the modeled trends and 95% confidence intervals from the phylogenetic meta-analyses). Marginal $R^2 = 0.02$; conditional $R^2 = 0.69$. Fungi are excluded because fungi are only non-closely transmitted in the GMPD.

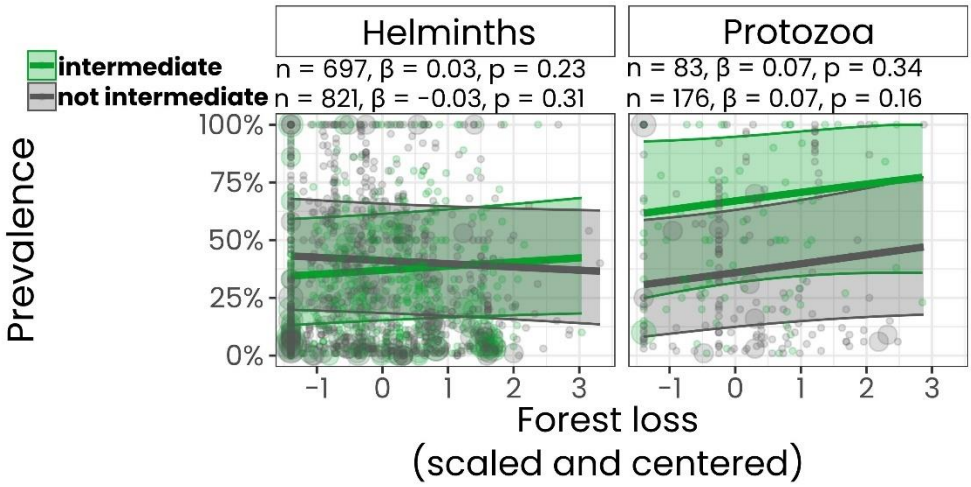

Figure S7. Association between forest loss and zoonotic parasite prevalence faceted by parasite taxa, and coloured by whether the parasite is intermediately transmitted or not intermediately transmitted. Points are scaled by sample size (number of hosts sampled), and the lines and bands represent the modeled trends and 95% confidence intervals from the phylogenetic meta-analyses). Marginal R^2 = 0.02; conditional R^2 = 0.74. Bacteria, fungus, and viruses are excluded because they are only not intermediately transmitted.

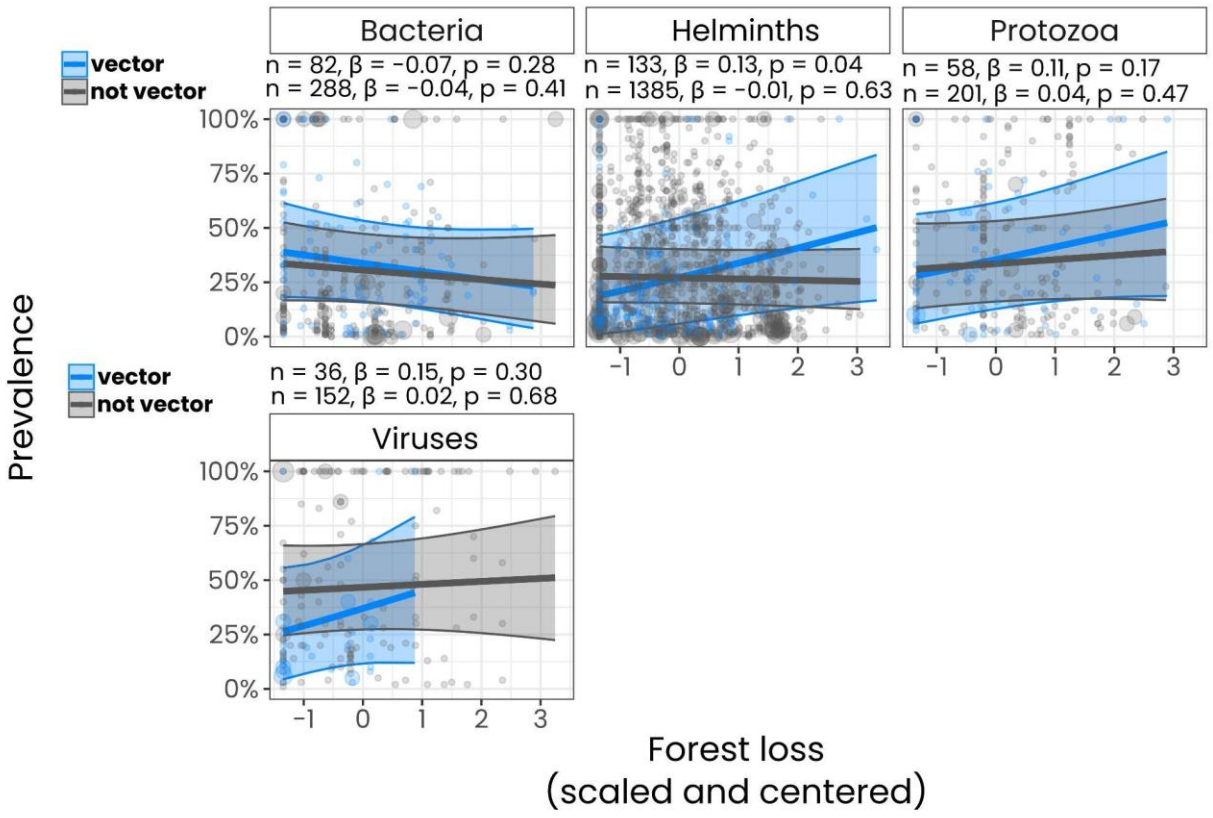

Figure S8. Association between forest loss and zoonotic parasite prevalence faceted by parasite taxa, and coloured by whether the parasite is vector-borne or not vector-borne. Points are scaled by sample size (number of hosts sampled), and the lines and bands represent the modeled trends and 95% confidence intervals from the phylogenetic meta-analyses). Marginal R^2 = 0.02; conditional R^2 = 0.69. Fungi are excluded because no fungi in the GMPD are vector-borne.