IBIS
BOU international journal of avian science
Ibis (2021) doi: 10.1111/ibi.12927

The effect of habitat quality on the blood parasite assemblage in understorey avian insectivores in the Eastern Himalaya, India

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The anthropogenic alteration of natural habitats can modify interactions between various biotic and abiotic factors. The prevalence of avian blood parasites in free-living host species in the tropics has shown contrasting patterns in altered landscapes. Here, we investigate these potential associations between understorey insectivorous bird species of the Eastern Himalayas and avian haemosporidians in primary and selectively logged forests. We describe patterns related to host–parasite associations, host life-history traits and host specificity in primary and logged forests. Using parasite-specific cytochrome-*b* gene markers, we screened 545 individual birds from nine families, 33 genera and 57 species. Of these, 34.67% were infected with *Leucocytozoon* spp., 13.94% with *Haemoproteus* spp., 3.30% with *Plasmodium* spp. and 8.44% with co-infections. We found that parasite prevalence did not change with logging; however, host specificity and life-history traits did have associations with infection prevalence. We report a vertical stratification in genera-specific infections driven by vector groups – upper canopy and midstorey foragers had high *Leucocytozoon* and *Haemoproteus* prevalence, respectively. In addition, species foraging in mixed-species flocks showed increased infection risk with *Leucocytozoon*, whereas solitary foragers had a high prevalence of *Plasmodium*. This study also highlights that avian parasite lineages are genetically more distinct in primary forest than in logged forest plots. Although our study demonstrates no influence of selective logging on parasite prevalence, it does reflect a positive influence of host abundance and logged habitats on parasite diversity. Our work reveals valuable patterns in terms of phylospecificity and genetic variation in parasite assemblages. Further research with a focus on parasite intensity and vector abundance will help us to understand anthropogenic impacts on parasite transmission dynamics in Eastern Himalayan birds.

Keywords: avian haemosporidians, avian malaria, community assembly, disease ecology, Eastern Himalayas, selective logging.

Tropical biodiversity is imperiled by a suite of anthropogenic factors, most of which are ultimately driven by climate change and the loss, degradation and fragmentation of natural habitats (Morris, 2010, Pimm 2008). In addition, the combined effects of different threats can further intensify the impacts of others (BirdLife International 2018) – for example, climate change is expanding the area of habitat suitable for malaria-transmitting mosquitoes, thereby increasing the threat posed by avian malaria (Benning et al. 2002). The conversion of forests to alternative land uses such as agriculture and selectively logged forest is particularly detrimental to understorey insectivorous bird species, which often disappear

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from anthropogenically modified habitats (Powell *et al.* 2015). However, the causal mechanisms underlying these observed patterns remain unclear, and potential interactions between threats such as land use change and disease dynamics have largely been unexplored (but see Chasar *et al.* 2009, Sehgal, 2010). With the growing prevalence of potentially suboptimal habitats for wildlife (Walsh *et al.* 1993, Andrén 1994, Schleuning *et al.* 2011) and an increase in the range of disease vectors, it is especially important to understand how land use change might influence pathogen communities and alter interactions with vulnerable host communities. Further, it is important to understand how species traits might influence susceptibility to disease in human-modified habitats.

Wild birds harbour a diversity of intracellular blood parasites in three main genera – *Plasmodium*, *Haemoproteus* and *Leucocytozoon* (hereafter, avian haemosporidians), which are globally distributed (except Antarctica, Valkiūnas, 2005). Chronic infections with avian haemosporidians have a significant negative influence on host population dynamics by decreasing reproductive success, immunity and fitness (Merino et al. 2000, Marzal et al. 2005, Asghar et al. 2015). In addition, avian blood parasites exhibit different degrees of host-specificity; parasite species can either be specialists, restricted to a single host bird species, or generalists, exploiting a broad range of species. Generalists are more successful at establishing in novel host communities (Poulin 2007). Vector-borne parasites often rely on frequency-dependent transmission, wherein the vector's biting rate determines the frequency of the infection in the host (e.g. Thrall *et al.* 1993). Conversely, an increase in pathogen species diversity reduces pathogen transmission, a phenomenon known as the dilution effect (Keesing *et al.* 2006, Nah *et al.* 2010). Finally, the density of infected host individuals governs density-dependent transmission – an increase in host diversity amplifies pathogen transmission of generalists, whereas the addition of a new host species leads to increased host abundance and species richness (Keesing *et al.* 2006).

Anthropogenic habitat modification could influence both avian host (Burivalova *et al.* 2015) and vector communities and subsequently influence parasite prevalence and assemblages in many ways (Taylor 1997, Sehgal 2010, Sehgal 2015). Structural changes to forest (e.g. from selective logging) bring about changes in microclimate important to understorey birds (Powell *et al.* 2015) and could reduce immune defence through multiple mechanisms such as thermal stress, increased predation and decreased resource availability (Hua & Sieving 2016). Habitat loss also leads to edge effects, which in turn can result in reduced diversity, gene flow and fecundity in birds. However, the responses of avian guilds to edge effects can have contrasting effects from site to site. For example, road-induced edge effects (Halfwerk *et al.* 2011, Terraube *et al.* 2016) or selective logging and establishment of palm oil plantations can have variable effects on dietary guilds of bird communities (Tchombou *et al.* 2020a). Bregman *et al.* (2016) revealed that assemblages of frugivorous and insectivorous birds remained stable after logging and fire events in primary forests in eastern Amazonian Brazil. Land use change and seasonality can have a strong influence on vector composition and abundance, enabling the spread of vector species into previously uninhabitable areas – tropical deforested habitats are more open and warmer than primary forests (Senior *et al.* 2017), which may increase the survival and growth rates of mosquito larvae (Camargo & Kapos, 1995, Meyer Steiger *et al.* 2016).

From a parasite assemblage perspective, logging creates vacant ecological niches which are beneficial for generalist parasite species by providing high adaptability or certain conditions conducive for host-specific parasite fauna to survive (Agosta & Klemens 2008, Moens & Pérez-Tris 2016). In the tropics, the prevalence of *Plasmodium* infection (generalist parasites) is positively associated with forest cover (Bonneaud *et al.* 2009, Loiseau *et al.* 2010). However, for *Haemoproteus* (specialist parasites), Laurance *et al.* (2013) found infection prevalence to be higher in undisturbed forest patches than in logged forest. The high diversity of host species in undisturbed forest probably facilitates host-switching of the parasite, which could lead to co-speciation, thereby increasing parasite range and diversity (Ricklefs *et al.* 2014, Moens *et al.* 2016). By contrast, a reduction in host diversity in disturbed habitats could limit host-switching and thereby increase prevalence of specialist parasite lineages. In addition, parasite lineages can vary with deforestation even for closely related host species and with the intensity of habitat use or landscape features at a small spatial scale (Chasar *et al.* 2009, Sehgal 2015). Few studies have explored associations between the probability

of haemosporidian infections and life-history traits such as flocking behaviour and foraging stratum (e.g. Laurance *et al.* 2013, González *et al.* 2014, Lutz *et al.* 2015). The patterns observed are largely driven by the diversity of the avian community – a lower infection prevalence in mixed-flock birds or an increase in infection has been perceived as a cost of mixed flocking behaviour (González *et al.* 2014). The vertical stratification of the vector community in forests appears to be concordant with the infection rate of different parasite genera in the canopy vs. understorey foraging birds (Černý *et al.* 2011).

The Eastern Himalayas are exceptionally species-rich globally (Myers 1988, Orme *et al.* 2005), with bird diversity peaking in mid-elevation forests (Orme *et al.* 2005, Price *et al.* 2011). In the mid-elevation forests of the Eastern Himalayas, selective logging is having detrimental effects on large and long-lived avian species, and small, highly fecund insectivorous species at lower trophic levels dominate modified habitats (Srinivasan 2013). Furthermore, the probability of survival of birds is high in primary habitats even with low natal dispersal of individuals from primary (intact) forest plots (Srinivasan *et al.* 2015). In this study, we tested how host life-history traits and changes in abundance between primary and logged forest might influence the prevalence, diversity and host-specificity of avian haemosporidians. Specifically, we predicted the following:

Logging status and prevalence

i We expected that high host diversity in logged habitat would positively influence parasite prevalence.

Logging status, host abundance and parasite diversity

i We expected that high host abundance of edge specialist bird species in logged forest would positively influence parasite diversity. In contrast, primary forest plots should harbour low parasite diversity.

ii We expected that high host abundance in logged forest plots would result in high prevalence of generalist parasite lineages. However, primary forest would harbour more specialist parasite lineages (infecting closely related hosts), as opportunities to infect more distantly related hosts would be low due to low host diversity.

iii Logged forest plots, being warmer and open habitat, would have a greater density of vectors, resulting in higher bite rates, ultimately leading to higher parasite prevalence.

Species traits

i Species participating in mixed-species flocks would have lower parasite prevalence in logged forest compared with solitary foragers because flocking-related anti-predator and foraging benefits would allow flocking species to maintain body condition and survive in logged forest. Solitary foraging species, which show steep declines in survival in logged forest (Srinivasan 2019), should have higher parasite prevalence in logged than in primary forest.

ii Feeding stratum and nest height would exhibit differential parasite prevalence depending on vertical stratification in vector community: for example, with low *Plasmodium* prevalence occurring in canopy-nesting or foraging birds, as *Culex* mosquitoes are mainly restricted to ground-level habitats, and high *Haemoproteus* infections in midstorey foragers and ground-nesting birds.

iii Elevational migrants are exposed to a large suite of parasites. We expected elevational migrants to harbour high parasite diversity and prevalence compared with resident species.

METHODS

Field sampling

We sampled Eastern Himalayan understorey birds in montane broadleaved forest in Eaglenest Wildlife Sanctuary, West Kameng district, Arunachal Pradesh, India (27°06′0″N, 92°24′0″E, 2000 m above sea level; Fig. 1), which is part of the Eastern Himalaya Global Biodiversity Hotspot.

Birds were captured using mist-nets on seven polygonal plots at ~ 2000 m asl ranging in size between 2.5 and 4.0 ha, four plots in primary forest (or very minimally logged forest) with tree density > 10 cm DBH; 168–192 trees per ha, and three plots in logged forest with tree density 76–110 trees per ha (Fig. 1; see Srinivasan 2013, Srinivasan *et al.* 2015 for further details of the

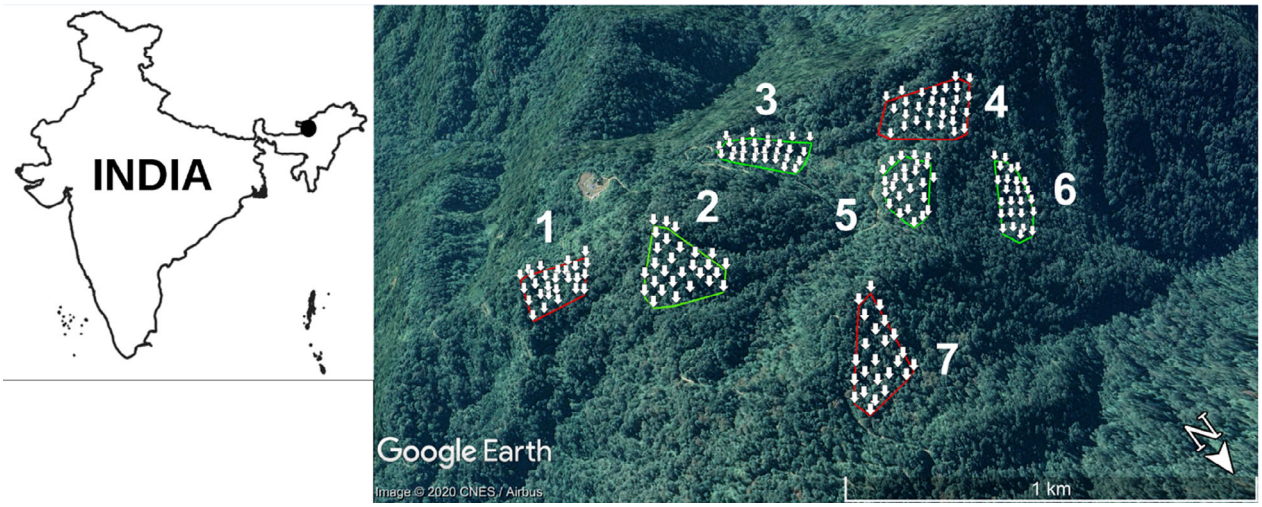

Figure 1. Sampling plots depicted by polygons with the locations of mist-nets (white arrows) in Eaglenest Wildlife Sanctuary (black dot in outline map of India), Arunachal Pradesh, India. Polygon numbers: 1, 4 and 7 are logged forest plots; 2, 3, 5 and 6 are primary forest plots. Image source: GoogleEarth.

study site). We sampled adult birds in April 2014, which is the early breeding season in the mid-elevation Eastern Himalayas (Rasmussen & Anderton 2005, Srinivasan *et al.* 2015), before young birds fledged. We conducted mist-netting (12 m length, 2.4 m height four-shelf nets; between 24 and 28 nets placed systematically per plot and run simultaneously) for three consecutive days in each plot, from 05:00 to 12:00 h. We identified each captured bird to species, then ringed, weighed and collected a blood sample before releasing the bird back to the wild. For each bird, blood samples were collected by sub-brachial venepuncture and stored in an SET buffer (20–40 µL in 500 µL buffer 0.15 M NaCl, 0.05 M Tris, 0.001 M EDTA, pH 8.0) for subsequent parasite screening.

Molecular methods

Genomic DNA was extracted from blood samples using the phenol chloroform isoamyl (PCI) extraction method (Sambrook *et al.* 1989). We followed a two-step screening protocol: (1) detection of the presence of three parasite genera, *Plasmodium*, *Haemoproteus* and *Leucocytozoon* and co-infections using a diagnostic primer 213F/372R (160 bp; Beadell & Fleischer 2005); and (2) a nested PCR was performed on the positives from the first step by PCR-amplifying infections for sequencing using the 478-bp fragment of the cytochrome *b* (cytb) gene following Hellgren *et al.* (2004). Negative and positive controls were included with each PCR round to detect potential contamination. We used a universal primer pair – Cytb-WOW and Cytb-2RC (268 bp; Dumbacher *et al.* 2003) – to confirm the host DNA quality (Ishtiaq *et al.* 2008). Finally, the amplified PCR products were purified using ExoSAP-IT (Affymetrix - USB) and sequenced using Big Dye Terminator v3.1 Cycle Sequencing Kit (Catalogue number: 4458688; Applied Biosystems, Foster City, CA, USA) in both directions. The sequences were aligned and assembled using Sequencher v5.2.4 (Gene Codes Corp., Ann Arbor, MI, USA) and compared against a reference database (e.g. GenBank and MalAvi; Bensch *et al.* 2009) for identification of parasite genera and lineage distribution across hosts. All sequences were deposited in GenBank under accession numbers MW023106–MW023200.

Phylogenetic analysis

We used 96 distinct cytochrome-*b* lineages for phylogenetic analyses. Using an Akaike's information criterion (AIC)-based approach in Modeltest v3.7 (Posada & Crandall 1998), we determined the most appropriate evolutionary model (GTR + I+G). Phylogenetic reconstruction was implemented in Mega5 (Tamura *et al.* 2011) and the best tree was obtained using a heuristic search using the nearest-neighbour interchange algorithm. Similar results were obtained when using maximum likelihood (data not shown).

Statistical analyses

All statistics were performed in R v3.3.1 (R Development Core Team 2015). We calculated the prevalence of each parasite genus in all sampled birds with 95% confidence intervals (95% CI) using the Sterne exact method (Reiczigel 2003) in the 'prevalence' package (Devleesschauwer *et al.* 2014). Based on logging status, each sampled plot was categorized as logged or primary forest. We investigated the relationship between logging status and standard community indices (such as the Chao1 estimator and Shannon–Weiner Index). We used detection-corrected abundances to calculate bird species diversity (Shannon–Weiner Index), parasite diversity (Shannon–Wiener index) and species richness (Chao1 estimator), calculated using the 'vegan' package (Oksanen *et al.* 2015). To estimate detection-corrected abundances of host species, we classified species into five detection classes based on body size (small and large species) and foraging height (terrestrial, understorey, lower midstorey and upper midstorey). We then used Cormack–Jolly–Seber open population mark–recapture models in the package 'RMark' (Laake 2013) to estimate capture probability for each of these detection classes in primary and logged forest plots separately (for a mark–recapture dataset spanning 2011 to 2018; Srinivasan 2019). We then divided the raw counts of each species in primary and logged forest by habitat and class-specific detection probability, to calculate detection-corrected abundances at the plot level.

Finally, for bird species that were captured in almost all plots, relative avian abundance – the number of individuals captured (excluding recaptures) – was standardized by effort (number of net hours per plot) for each species and used as a proxy for abundance.

We considered species-specific life-history traits that are ecologically relevant in driving host–vector interactions: social behaviour (solitary, mixed-species flocks, intraspecific flocks), feeding stratum (upper canopy, midstorey, understorey), average nest height (<1 m, 1–5 m, >5 m) and migratory status (elevational migrant or resident). We did not include dietary guilds, as our sampled bird community largely consisted of understorey insectivores. We obtained species-level data on host life-history traits from the Handbook of the Birds of the World (del Hoyo *et al.* 2019) and Rasmussen and Anderton (2005) (Table S1 and Fig. S1a–d).

First, we identified variables that best predicted the *Leucocytozoon* infections in understorey birds using generalized linear mixed-effects models (GLMMs). Host bird families with fewer than four individuals were excluded from the analysis (n = 59). Our full model consisted of the infection status (infected vs. non-infected, binomial distribution) as a response variable and the variables logging status (logged vs. primary forest), host Shannon diversity (at the plot level) and logging status as interactive terms for species-specific traits (social structure, feeding stratum and nest height) as fixed effects. We controlled for host phylogeny by including nested random effects (see Lutz *et al.* 2015, Ishtiaq *et al.* 2017). We used generalized linear models (GLMs) with binary error structure for *Haemoproteus* and *Plasmodium* infections and the best-fit global model was selected without the random effects (for these genera, the GLMM with the random effects was over-parameterized and failed to converge).

Secondly, we asked whether parasite lineage diversity (Shannon Diversity Index) is influenced by host abundance and logging status using linear mixed effect models. We included 'species' as a random intercept effect.

For all models included in the top-model set, we calculated pseudo-R^2 values to estimate model-fit by accounting for the variation explained by both fixed and random effects using the '*rsquared.glmm()*' function from the R package MuMIn (Barton, 2012) and McFadden's pseudo-R^2 for GLM, for which larger values suggest a better fit. We scaled the fixed variables and tested for multicollinearity using variance inflation factors (VIFs). All GLMMs were conducted using the '*glmer*' function from the 'lme4' package (Bates *et al.* 2015). Next, we generated a full submodel set (including the null model) from the global model using the '*dredge*' function implemented in the MuMIn package.

Multi-model inference tested all possible combinations of explanatory variables, yielding 195 logistic multiple regressions. We used the AIC (Burnham *et al.* 2011) to select the best-fit model and models were ranked using small-sample-corrected AIC (AICc). Models with a difference (ΔAICc) of ≤ 7 are as parsimonious as the best-fit model (lowest AICc; Table S2). The relative

importance of the traits was assessed and model-averaged estimates were derived (for models with ΔAICc < 7; Burnham & Anderson 2004) to account for model uncertainty. We consider each explanatory variable to be a useful predictor of parasite infection if their 95% CI does not cross zero.

Estimation of phylogenetic host specificity

We quantified the specialization/specificity of parasite lineages at two levels: host and habitat quality (as logged and primary forest).

Host specificity

We used a mean pairwise phylogenetic index (MPD) as a measure to quantify the phylogenetic host specificity to investigate whether haemosporidian lineages (≥ 2) infect more closely related hosts than expected by chance. This was done using the net relatedness index (NRI). MPD was estimated by taking into account the frequency of infected hosts and the phylogenetic relationships among the infected host species (Poulin & Mouillot, 2003). Subsequently, we calculated standardized effect sizes of the MPD values (SES.MPD) as the difference between the observed MPD values (MPDobs) and expected MPD values (MPDexp) under a null model, divided by the standard deviation of the MPD values obtained from the null data. Finally, we tested statistical significance by comparing MPDobs values with those from the 999 randomly generated MPD values by keeping the host topology intact and randomizing tip labels across the host phylogeny using the 'mpd' and 'ses.mpd' functions in the 'picante' package (Kembel *et al.* 2010). The bird phylogeny was retrieved for select species from birdtree.org (https://birdtree.org; Jetz *et al.* 2012), specifying the Ericson all-species backbone tree (Ericson *et al.* 2006).

Phylospecificity by habitat quality

We calculated two metrics of phylogenetic alpha diversity – NRI and the nearest taxon index (NTI), which are mean nearest taxon distances (MNTD) between all parasite lineages in an assemblage (Webb 2000, Webb *et al.* 2002) using the 'picante' package (Kembel *et al.* 2010). NRI detects clustering throughout the phylogenetic tree and NTI detects clustering at the tip of the tree. Significances of NRI and NTI were determined by identifying departures of MPD and MNTD (based on 10 000 permutations) from a null model that shuffled taxon labels on the tips of the phylogeny across all plots, resulting in randomized relationships among parasite lineages (Webb *et al.* 2002, 2008). Negative values of NRI and NTI reflect higher than expected community relatedness or phylogenetic clustering, suggesting that a parasite exploits closely related hosts. Positive values indicate phylogenetic over-dispersion and that a parasite lineage exploits distantly related hosts or a highly generalized community (Webb *et al.* 2002).

RESULTS

We screened 545 birds from nine families, 33 genera and 57 species for haemosporidian parasites. Of these, 238 (43.6%; 95% CI 39.56–47.86%) were infected with haemosporidians. The prevalence of *Leucocytozoon* was high at 34.67% (95% CI 30.80–38.77%), followed by *Haemoproteus* at 13.94% (95% CI 11.27–17.11%) and *Plasmodium* infections at 3.30% (95% CI 2.06–5.19%). We found 8.44% (95% CI 6.36–11.09%) co-infections with multiple parasite genera.

We retrieved 71 *Leucocytozoon*, 17 *Haemoproteus* and eight *Plasmodium* lineages. Of these, 68 *Leucocytozoon*, 15 *Haemoproteus* and three *Plasmodium* were new cytb lineages, whereas three *Leucocytozoon* (HYBOR2, WW6 and SYCON03), two *Haemoproteus* (COLL2, TROERY01) and five *Plasmodium* (GRW04, GRW06, NILSUN01, ALARV04, POMFER01) lineages had previously been reported to GenBank and the MalAvi database (Table S1, Fig. 2).

Effect of logging status on parasite richness and diversity

Parasite richness (Chao1 estimator) was higher in logged plots (observed = 63, Chao1 = 168.11 ± 47.14) than in primary forest plots (observed = 61, Chao1 = 106 ± 20.26). By contrast, bird richness did not vary by logging status (Primary: observed = 46, Chao1 = 57.37 ± 8.08; Logged: observed = 46, Chao1 = 57.14 ± 8.22). Our individual-based rarefaction curves indicated that sampling of the understorey insectivorous bird community almost reached an asymptote, whereas parasite lineage diversity remained under-sampled in both logged and primary forest plots (Fig. S2).

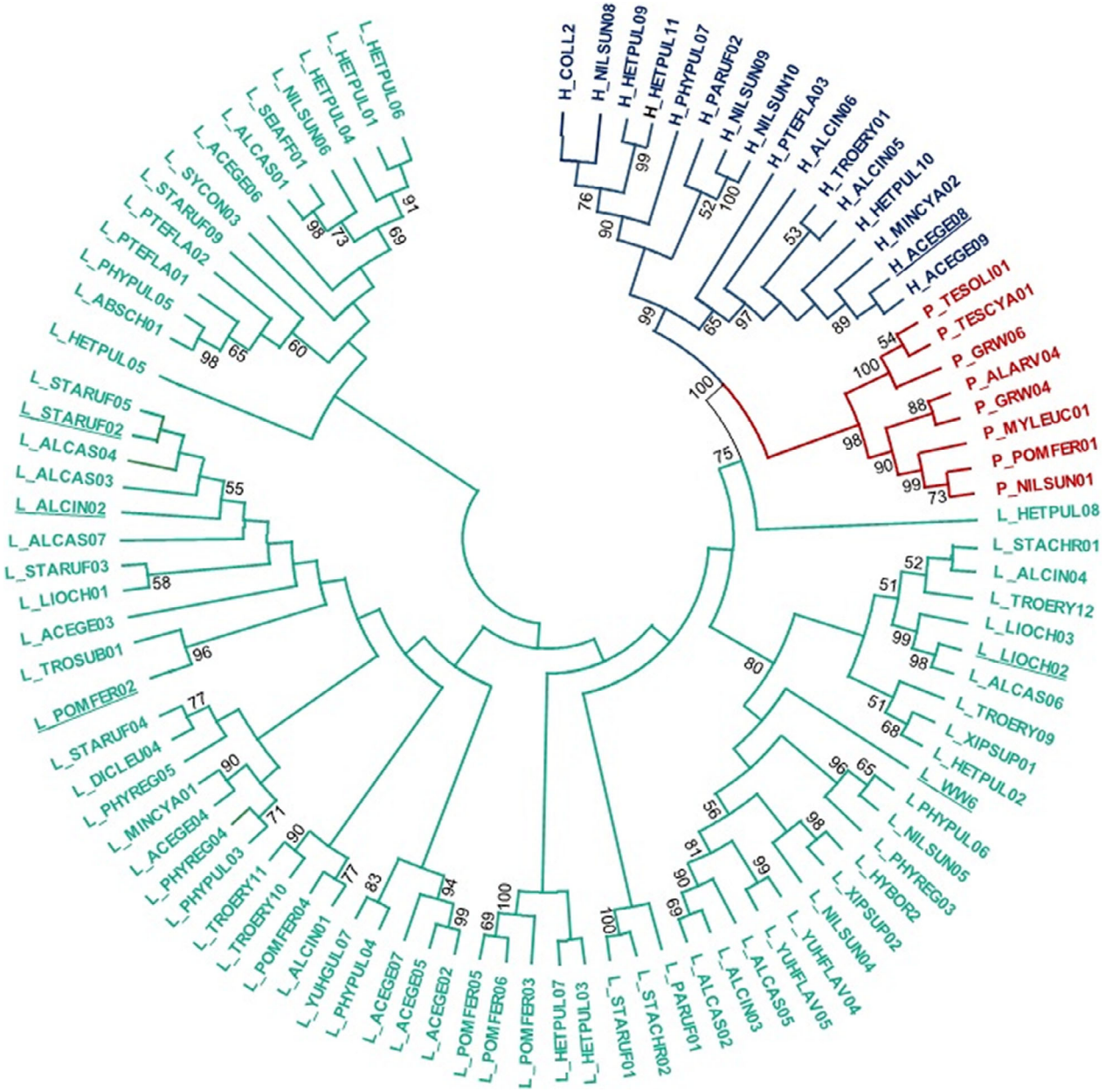

Figure 2. Phylogenetic relationships between parasite lineages retrieved from birds in Eaglenest Wildlife Sanctuary. Lineages with prefix L = *Leucocytozoon*, H = *Haemoproteus* and P = *Plasmodium*. Bootstrap support > 50% is shown at nodes. Underlined lineages are host-specific. See Table S1 for the full host species list and prevalence details by logging status.

Using the Shannon–Wiener index, both parasite diversity (Primary = 3.66, CI = 3.22–3.59; Logged = 3.69, CI = 3.24–3.60) and bird diversity (Primary = 3.30, CI = 3.10–3.32; Logged = 3.31, CI = 3.10–3.33) did not vary with logging status.

Effect of logging status, host diversity and life-history traits on parasite prevalence

All explanatory variables used in mixed models to predict haemosporidian infections had VIFs below 3,

indicating the absence of collinearity among them. We found that among many ecologically relevant parameters driving host–parasite interactions, feeding stratum and social behaviour were the most important predictors of infection status with haemosporidian genera in understorey birds. In *Leucocytozoon* models, infection probability was significantly higher in upper canopy than in understorey foraging birds (Fig. 3a, Table S3). However, midstorey foraging birds exhibited a significantly higher probability of *Haemoproteus* infection. We found no influence of feeding stratum on the infection probability with *Plasmodium*. The probability of parasitism by *Leucocytozoon* varied significantly by social behaviour. Expected rates of *Leucocytozoon* infection were lowest in solitary species but nearly tripled in both mixed-species and intraspecific flocks. Social behaviour had no effects on infection with *Haemoproteus*. We found that solitary bird species had a significantly higher prevalence of *Plasmodium* compared with flocking species (Fig. 3b, Table S3).

Effect of host abundance and logging status on parasite diversity

The 12 most abundant species ($n = 314$) were Yellow-throated Fulvetta *Schoeniparus cinereus*, Rufous-capped Babbler *Cyanoderma ruficeps*, Rufous-winged Fulvetta *Schoeniparus castaneceps*, Golden-breasted Fulvetta *Lioparus chrysotis*, Snowy-browed Flycatcher *Ficedula hyperythra*, Golden Babbler *Cyanoderma chrysaeum*, Black-faced Warbler *Abroscopus schisticeps*, Large Niltava *Niltava grandis*, Black-throated Parrotbill *Suthora nipalensis*, Blyth's Leaf Warbler *Phylloscopus reguloides*, White-spectacled Warbler *Phylloscopus intermedius* and Grey-cheeked Warbler *Phylloscopus poliogenys*. Host abundance showed a positive association with parasite diversity ($b = 0.06$, $t = 2.29$, $P < 0.001$) and primary forest plots showed lower parasite diversity than logged plots ($b = –0.11$, $t = –3.81$, $P < 0.001$; Fig. 4).

Phylospecificity by host species and habitat quality

We considered 18 *Leucocytozoon*, four *Haemoproteus* and three *Plasmodium* lineages infecting ≥ 2 host species to understand phylogenetic host specificity (Table 1). At the host level, phylogenetic host specificity analyses (based on significant SES.MPD values) revealed that *Leucocytozoon* and *Haemoproteus* lineages were relatively more host-

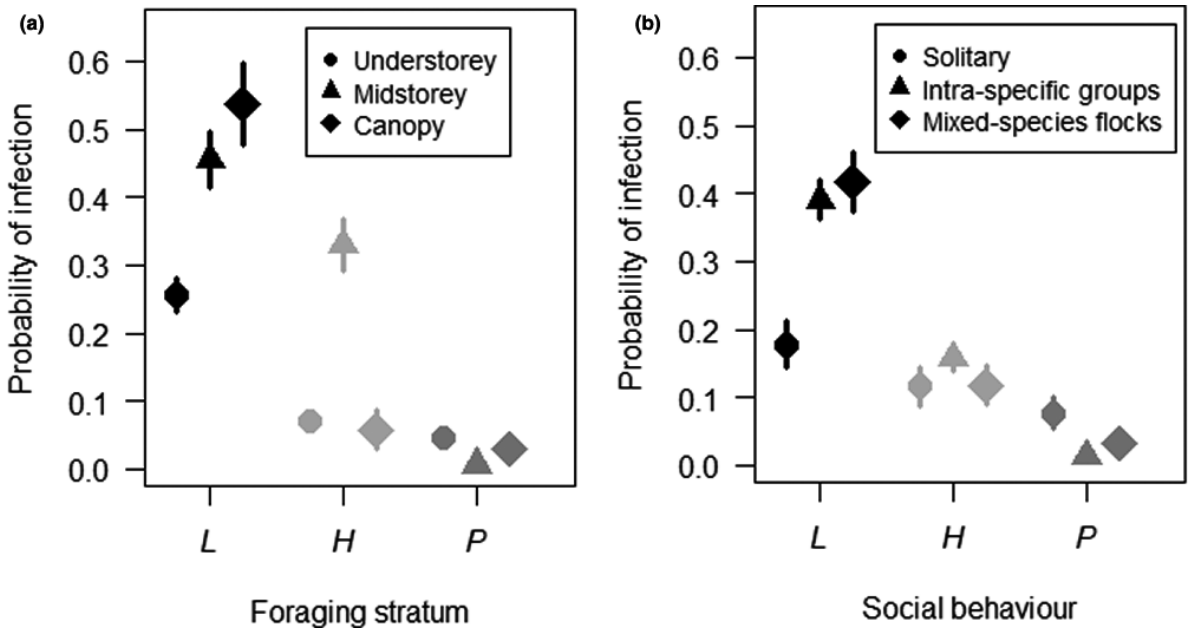

Figure 3. Effect of species-specific life-history traits as top predictors: (a) foraging stratum and (b) social behaviour on the probability of infection with *Leucocytozoon* (L), *Haemoproteus* (H) and *Plasmodium* (P).

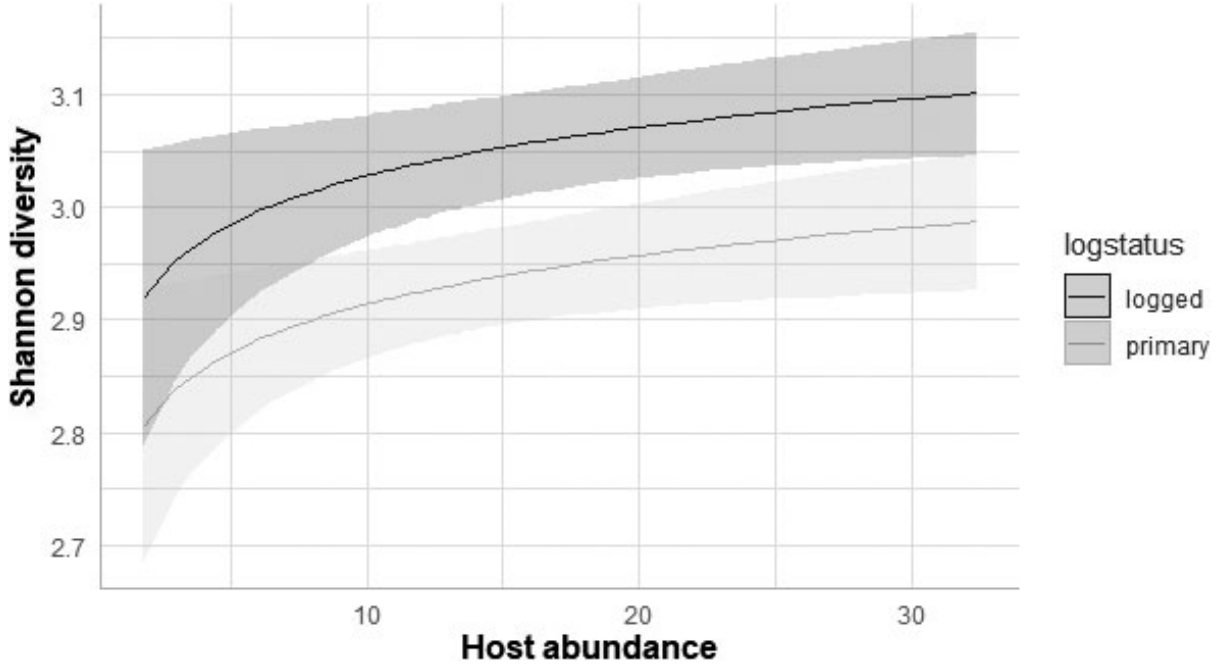

Figure 4. Effect of host abundance and logging status on parasite diversity.

specific than *Plasmodium* lineages. Among 26 parasite lineages, five *Leucocytozoon* lineages and one *Haemoproteus* lineage exhibited higher phylogenetic clustering compared with *Plasmodium* lineages (Table 1, Fig. 2).

At the habitat level across logging status, parasite lineages showed no significant pattern in phylogenetic clustering ($t = –1.870$, df = 3.206, $P = 0.152$; Fig. 5a). However, the negative NRI estimates showed a significant difference ($t = –3.161$, df = 4.442, $P < 0.029$; Fig. 5b) with logging status, suggesting that parasite communities from primary forest plots are phylogenetically even (i.e. more distantly related than expected by chance; standardized effect size (SES) > 0) and communities from logged habitats are phylogenetically clustered (i.e. more closely related than expected by chance; SES < 0).

DISCUSSION

Our molecular survey of avian haemosporidians revealed a diverse parasite community influenced by species-specific ecological traits. At the habitat level, parasite lineages were clustered by logging status. We did not detect an influence of logging status of forest plots on either parasite prevalence or parasite diversity. From the 26 parasite lineages detected in two or more hosts, we found that *Leucocytozoon* were relatively host-specific compared with *Haemoproteus* and *Plasmodium* lineages. The parasite lineages were phylogenetically clustered in logged forest plots. As we predicted, host life-history traits influenced the probability of infections.

Parasite prevalence, diversity across logging status, life-history traits

The effect of habitat fragmentation on the prevalence of avian haemosporidians has remained inconclusive across regions and is largely context-dependent and difficult to generalize. For example, empirical studies show a variable pattern in parasite prevalence with forest disturbance. Bonneaud *et al.* (2009) found an increase in *Plasmodium* prevalence in intact forested areas compared with deforested areas in Cameroon. Loiseau *et al.* (2010) reported a decrease in parasite prevalence with increased forest fragmentation in Ghana. Tchoumbou *et al.* (2020b) recently found that selective logging favoured an increase in the prevalence of *Plasmodium* in insectivores. Similarly, several studies show no effect of habitat degradation on haemosporidian prevalence (e.g. Rivero de

Table 1. Mean pairwise phylogenetic distance (MPD) weighted by frequency of hosts infected and standardized effect size of the mean phylogenetic distance (SES.MPD) for haemosporidian lineages infecting two or more host species.

Lineages	Taxa	MPD	SES (MPD)	*P*
Leucocytozoon				
ALCAS01	2	17.382	−1.206	0.231
ALCAS07	4	19.516	−1.660	0.073
ALCIN01	2	17.382	−1.265	0.220
ALCIN02	2	9.289	**−1.839**	**0.022**
DICLEU04	5	68.625	1.630	0.984
HYBOR2	6	66.439	1.267	0.931
LIOCH01	3	19.899	−0.683	0.241
LIOCH02	3	13.790	**−2.120**	**0.025**
NILSUN05	3	46.554	0.187	0.579
NILSUN06	2	43.380	0.745	0.734
PHYPUL06 4		39.256	−0.942	0.169
PHYPUL04	2	35.161	0.079	0.375
PHYPUL05	5	55.657	0.493	0.669
PHYREG04	3	24.672	−1.622	0.097
POMFER02	2	12.932	**−1.645**	**0.055**
STARUF02	7	29.939	**−2.278**	**0.028**
STACHR02	2	12.932	−1.681	0.066
WW6	2	9.780	**−1.798**	**0.037**
Haemoproteus				
ALCIN05	6	21.646	−1.641	0.084
ACEGE08	2	3.678	**−1.921**	**0.022**
NILSUN09	2	43.380	0.782	0.754
PHYPUL07	2	35.161	0.114	0.411
Plasmodium				
GRW06	3	58.821	1.250	0.922
NILSUN01 4		49.624	−0.145	0.353
POMFER01 2		13.459	−1.551	0.115

Host phylogenetic tree tip labels were randomized to create null models and assess the level of significance. Statistically significant results ($P < 0.05$) are given in bold.

Aguilar *et al.* 2018, Sebaio *et al.* 2010). We found no effect of logging status on the prevalence of any parasite genus. However, parasite diversity decreased in primary forest plots, and host species showed differential patterns in the transmission dynamics of three parasite genera. Furthermore, the sampled plots have not been disturbed since 2002, which probably allowed sufficient time for accumulation of generalist parasite lineages and lower rates of parasite extinction.

Previous research has mainly analysed forest plots which were several kilometres apart (Bonneaud *et al.* 2009, Chasar *et al.* 2009, Laurance *et al.* 2013), although a few studies (e.g. Wood *et al.* 2007) have looked at parasitic infection patterns on a small spatial scale. Wood *et al.* (2007) found that *Plasmodium* prevalence in a single-species population could vary up to six-fold at a small spatial scale in temperate woodland. However, the likelihood of malaria infection may depend on the natal site, as young birds are more prone to infection, and the choice of breeding site could determine infection risk (Wood *et al.* 2007). Our study was conducted in the early breeding season, when adults hold breeding territories and young birds are hard to capture in mist-nets. Furthermore, unlike in the Neotropics, 'transient' individuals passing through the landscape are rare (Srinivasan, 2019). Therefore, the overwhelming majority of sampled birds are highly likely to have been caught on their breeding territories, inside arbitrarily delineated plot boundaries representing primary and logged forest in a continuous landscape (< 1% of individuals were captured on multiple plots within the same session; Srinivasan *et al.* 2015). Although it is possible that the similarity in parasite prevalence in primary and logged forests could arise simply from the proximity of sampled plots, we think this is unlikely in our study area, and over a 7-year period with yearly sampling (2011–2017), 3.4% of individuals captured in one habitat type were subsequently recaptured in the other habitat type (Srinivasan 2019). Even allowing for a capture probability of roughly 0.3 (U. Srinivasan unpubl. data), only ~ 11% of individuals would have moved between habitat types, strongly indicating that the vast majority of sampled birds were indeed representative of their habitat (i.e. either primary or logged forest plots). For our abundant focal species in logged habitat, parasite diversity showed a positive association with host abundance, which further implies that logged habitat is supporting higher local densities of several insectivorous bird species as well as high parasite diversity. Anthropogenic habitat alteration may increase parasite diversity by altering host characteristics (home-range, abundance, inter- and intraspecific contacts), thereby increasing overlap among host species and an increase in parasite diversity (Gillespie & Chapman 2008, Chakraborty *et al.* 2019). However, the small ranges and limited dispersal ability of these forest specialist bird species are unlikely to overcome the true effects of habitat quality on parasite prevalence.

Feeding stratum and social structure were the main ecological traits which appeared to have influenced variation in prevalence. We found that birds foraging in the upper canopy and midstorey were more likely to be infected with *Leucocytozoon*

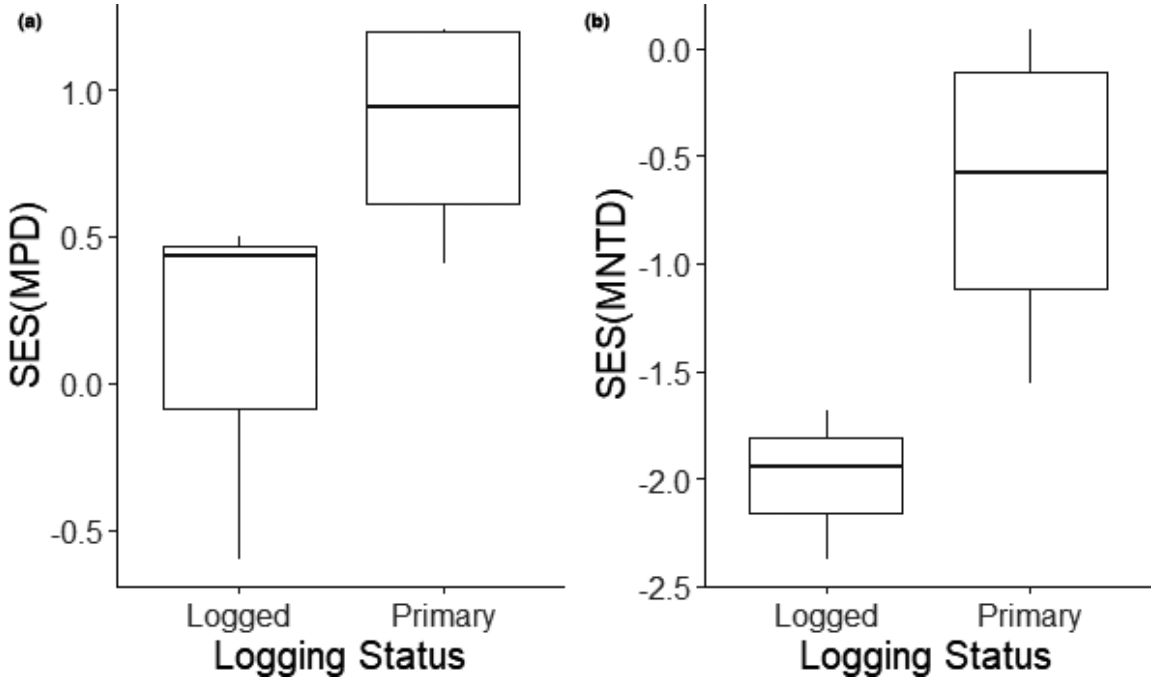

Figure 5. Comparison of parasite community diversity using standardized effect size (SES) of: (a) the mean pairwise distance (SES (MPD)) and (b) the mean nearest taxon distance (SES(MNTD)) in selectively logged vs. primary forest plots.

and *Haemoproteus*, respectively. Contrary to our prediction, we found high *Leucocytozoon* prevalence in species foraging in mixed-species flocks and intraspecific groups, whereas solitary foragers had a low prevalence of *Leucocytozoon* and high *Plasmodium* infections. Our sampling is primarily biased towards foliage gleaners, which feed in mixed-species flocks in the upper canopy and are more exposed to swarms of blackflies, and could explain the high prevalence of *Leucocytozoon* in this group. Our results are consistent with vertical stratification in a vector community where biting midges and black flies occupied the canopy and C*ulex* mosquitoes are mainly restricted to ground-level habitats (Černý *et al.* 2011). Despite the diurnal nature of black flies, which must feed on active birds or in the nest, as opposed to a few ornithophilic nocturnal vectors such as mosquitoes and biting midges (Fecchio *et al.* 2020), the *Leucocytozoon* infections were significantly higher in our avian community. We found a very low prevalence of *Plasmodium*, which could be due to an elevational effect (2000 m asl). Elsewhere, both *Haemoproteus* and *Plasmodium* infections show a negative relationship with elevation (LaPointe *et al.* 2010, but see González *et al.* 2014). Temperature drives the vector and parasite ecology, which determines parasite transmission. Ishtiaq and Barve (2018) found a negative association in *Plasmodium* prevalence and intensity with an increase in elevation in wild birds in the western Himalaya. Nonetheless, the relatively high prevalence of *Leucocytozoon* and *Haemoproteus* indicates that vectors and parasites are not restricted by thermal constraints in this habitat. Changing climate is shifting the range of *Plasmodium* spp. in this landscape but to predict this change, we need more fine-scale data on host–parasite–vector interactions.

Phylospecificity by host species and habitat quality

Both *Leucocytozoon* spp. and *Haemoproteus* spp. showed phylogenetic host specificity by infecting closely related bird species more than expected by chance. By contrast, *Plasmodium* spp. were phylogenetic generalists with a large proportion of lineages with broad host and geographical distributions. The negative NRI estimates between logged habitat and parasite communities suggest phylogenetic clustering at the base of the tree,

leading to species assemblages of related species. Our findings further imply that disturbed habitats support host-specific lineages, and opportunities for parasites to shift to distantly related hosts are probably low and constrained by the limited niche. In contrast, undisturbed habitats support a broad community of host species which allows for parasite switching – the high avian diversity in undisturbed habitats could contribute to a dilution effect (Keesing *et al.* 2006). We lack entomological and epidemiological data, which are integral to understanding how habitat changes (e.g. logging) influence arthropod vectors and in turn impact disease risk. Furthermore, we considered tree density as the only parameter to define forest characteristics – openness of the forest canopy governs penetration of sunlight and larval habitats and could be more relevant for vector biology and malaria risk (Hahn *et al.* 2014). Nonetheless, we observed a pattern in clustering in parasite lineages and reduced infection risk in mixed flocks and understorey-dwelling host species.

CONCLUSIONS

Our study highlights the influence of avian life-history traits and habitat disturbance on parasite diversity, whereas a small home-range and proximity of sampled plots showed no effect on infection status with haemosporidian parasites in Eastern Himalayan birds. We showed that feeding stratum and social behaviour were the top ecological parameters in predicting infection by haemosporidians. In addition, we revealed a vertical stratification in genera-specific infections driven by vector group – upper canopy foragers in mixed-species flocks showed an increased infection risk with *Leucocytozoon* and midstorey foragers exhibited an increased infection risk with *Haemoproteus* parasites, whereas the solitary foragers had a high prevalence of *Plasmodium*. In addition, we found a high abundance of edge specialist bird species in logged forest which harboured high parasite diversity and a host-specific parasite assemblage. Further research with a focus on parasite intensity and vector abundance will help to understand anthropogenic impacts on parasite transmission dynamics in Eastern Himalayan birds.

The study was funded by the Wellcome Trust/DBT India Alliance (IA/I(S)/12/2/500629) to F.I. in 2013–2019. Birds were captured and sampled with ethical approval and permission from the Arunachal Pradesh State Forest Department (Permit No. CWL/G/13(95)/2011-12/Pt/382-383). The field experiments comply with the current laws of India where the study was performed. We thank the field assistants and volunteers at Eaglenest Wildlife Sanctuary for helping with data collection. We thank three anonymous reviewers and the Associate Editor Dr Sarah Burthe and Editor Rauri Bowie for their constructive comments, which helped to improve the manuscript.

AUTHOR CONTRIBUTION

Rohan K. Menzies: Data curation (supporting); Writing-original draft (supporting); Writing-review & editing (supporting). **Joli Rumi Borah:** Resources (supporting); Writing-review & editing (supporting). **Umesh Srinivasan:** Formal analysis (equal); Methodology (equal); Project administration (equal); Resources (equal); Writing-review & editing (equal). **Farah Ishtiaq:** Conceptualization (lead); Formal analysis (equal); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Supervision (lead); Writing-review & editing (equal).

Data Availability Statement

All data are available in Table S1. DNA sequences with GenBank accession numbers MW023106–MW023200 have been submitted to the GenBank database.

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Received 15 May 2020;
Revision 4 November 2020;
revision accepted 8 January 2021.
Associate Editor: Sarah Burthe

SUPPORTING INFORMATION

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

Figure S1. Summary of total birds sampled by species-specific life-history trait across primary and logged forest plots: (a) feeding stratum, (b) social behaviour, (c) nest height, (d) migratory status.

Figure S2. Rarefaction curves for the bird community and haemosporidian lineages by logging status.

Table S1. Host, life-history traits and parasite lineage associations. DS= Double sequence; R= Resident; EM: elevational migrant.

Table S2. Details of top models with AICc < 7 predicting the odds *Haemoproteus* infections in birds.

Table S3. Summary of parameter estimates for top models with AICc <7 predicting the odds of infections in birds.