




It's all about scale: The landscape effect on avian haemosporidians

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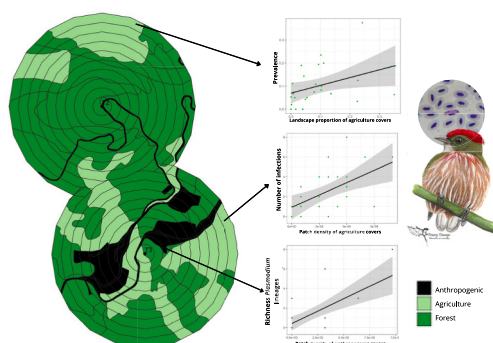
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HIGHLIGHTS

- Landscape and environmental factors determine avian haemosporidians across scales.
- Scale effects on prevalence and infections intensify at larger spatial scales.
- Agricultural land cover proportion increases parasite prevalence.
- Predicting parasite infection is hard due to unaccounted variables in host systems.

GRAPHICAL ABSTRACT



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ABSTRACT

Environmental characteristics drastically shape the host-parasite associations under natural conditions. This is the case of parasites such as avian haemosporidians which naturally infect birds and are transmitted by insect vectors. Landscape characteristics are known to determine the epidemiology of transmission of these parasites in the wild, but the strength of these factors may differ at different spatial scales. We studied the effects of the landscape structure and environmental variables on the prevalence and richness of lineages of avian haemosporidial parasites (genera *Plasmodium*, *Haemoproteus* and *Leucocytozoon*) infecting birds in a highly diverse area of Antioquia, Colombia. We screened blood samples from 678 individuals across 90 bird species for number of infections, prevalence and richness of haemosporidial lineages in sites surrounding three hydroelectric dams. We obtained environmental and landscape structure variables around the bird sampling points at different spatial scales (from 50 to 500 m radii, every 50 m) and selected the most important ones. We modelled the relationships between parasite infection variables and landscape structural and environmental characteristics. Effects of landscape structure on variables reflecting haemosporidial infections varied according to the selected scale of analyses. The scale of the effect of landscape structure was larger for the number of infections and prevalence (Average = 350 and 425 m radius) than for lineage richness (Average = *Plasmodium* 219 m, *Haemoproteus* 244 m). Agricultural patch density notably increased number of infection rates (pseudo- $R^2 = 0.68$). The number of infections and the richness of *Haemoproteus* lineages correlated with agricultural connectivity at larger scales

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(500 m). Haemosporidian prevalence was primarily linked with proportion forest and agricultural covers. *Haemoproteus* richness was influenced by connectivity and NDVI — Normalized Difference Vegetation Index (pseudo- $R^2 = 0.83$), while *Plasmodium* richness was affected by anthropogenic density, edge density, forest proportion, and temperature (pseudo- $R^2 = 0.79$). Changes in parasite infection and prevalence remain difficult to predict, as each parasite-host system is susceptible to many unaccounted variables. This study found that transformed landscapes, particularly density of anthropogenic and agricultural patches nearby increases haemosporidian parasites at different scales. These findings underscore the complex interplay between landscape structure and haemosporidian infections in avian hosts in tropical ecosystems.

1. Introduction

The impact of landscape transformation extends beyond mere effects of habitat loss on biodiversity. As habitats undergo fragmentation and degradation, landscape structure changes in its composition (type and amount of land cover) and its configuration (spatial arrangement of land cover), ultimately influencing species survival (Fahrig, 2003; Santos and Telleria, 2006). While land use changes leading to habitat loss unequivocally reduces biodiversity, the impacts of habitat fragmentation—such as the increase in habitat patches at the landscape level—are more complex (Fahrig, 2003; Fletcher et al., 2018). Fragmentation can, for example, enhance bird species richness and abundance, highlighting the intricate relationship between landscape configuration and biodiversity dynamics (Morelli et al., 2013). Moreover, landscape transformation and its effects on biodiversity could also disrupt ecological interactions such as parasitism (Bastiani et al., 2020), although the effects of landscape structure on these ecological interactions are poorly studied (Dáttilo et al., 2022), especially in the case of wild host-parasite interactions (Clark et al., 2014; Rivero de Aguilar et al., 2018). To understand the ecological determinants of transmission dynamics and relationships among species and their environment, it is crucial to identify the ecological interactions between hosts, vectors, and pathogens in heterogeneous landscapes.

Transmission patterns of vector-borne diseases are shaped by the distribution of vectors, which are related to variables such as topography, soil composition, and landscape structure (Ganser et al., 2016). Landscape structure affects the transmission dynamics of vector-borne pathogens of wild birds, including avian malaria (Sehgal, 2010; Jiménez-Peñuela et al., 2021). For instance, deforestation not only affects the fitness, distribution, and migration patterns of avian species, but also alters the feeding ecology of vectors and the infection dynamics of the pathogens they transmit (Sehgal, 2010; Chakarov et al., 2020). Landscape transformation may also have an impact on habitat quality. The normalized difference vegetation index (NDVI), an indirect measure of vegetation quality and cover, has been proven as a good predictor of parasite transmission dynamics (Foley et al., 2003; Omumbo et al., 2005; Sehgal, 2015; Altamiranda-Saavedra et al., 2017). Higher NDVI values may be related to the availability of breeding and roosting habitats for both mosquitoes and birds (Reisen et al., 1990; Lillesand et al., 1994), nevertheless the radius or scale may vary depending on the mosquito species considered and the time of the year (Roiz et al., 2015). A comprehensive review by Ferraguti et al. (2023) found that intensity of land use or land cover transformation due to anthropogenic activities affects the prevalence of vector-borne infections. The role of landscape in heterogeneous disease dynamics highlights the necessity of incorporating landscape structure into ecological studies of host-parasite systems (Wood et al., 2007).

Vector-borne pathogens are shaped by environmental factors, which affect both the vectors and their vertebrate hosts (Reisen, 2010; Ferraguti et al., 2018, 2024). However, insects and birds respond differentially to changing environments, with insects being more sensitive to changes in temperature and precipitation, while birds tend to be mainly affected by changes in forest patch size, shape, isolation, and other landscape features (Carrara et al., 2015; Santiago-Alarcon and Marzal, 2020). Water availability is a crucial determinant of the distribution

patterns of vectors (e.g. mosquitoes), as it is necessary for larvae development (Loaiza and Miller, 2013; Okanga et al., 2013a; Krama et al., 2015; Padilla et al., 2017) and have been associated with avian malaria infection patterns in mosquitoes (Ferraguti et al., 2024). However, the vectors involved in the transmission of the different genera of avian haemosporidians, such as mosquitoes, *Culicoides* biting midges and blackflies, differ in their environmental requirements (e.g. breeding sites). Furthermore, environmental conditions can affect parasite reproduction and development rates in both vectors and hosts, with temperature and precipitation being the most important predictors of prevalence across environmental gradients (Zamora-Vilchis et al., 2012; Padilla et al., 2017; Martínez-Alvarado, 2019). Furthermore, Wood et al. (2007) found that parasite prevalence fluctuated significantly depending on the lineage assessed and distance from the river, suggesting considerable variation in infection risk among birds of the same population.

To elucidate the effects of landscape structure on ecological processes, it is important to detect the scale of effect of the landscape characteristics on the response variables. Therefore, landscape effects need to be assessed across several spatial scales to identify the most relevant scale to a given ecological pattern or process (“scale of effect” (Jackson and Fahrig, 2012, 2015; Miguet et al., 2016; San-José et al., 2019)). Different studies relating landscape and vector-borne haemosporidian parasites yield contrasting results depending on the scale of analysis, with landscape variables partially explaining malaria transmission at the smaller scales (Wood et al., 2007; Cosgrove et al., 2008), as well as precipitation (Martínez-Alvarado, 2019; McNew et al., 2021). However, at a regional or broader scale, host community turnover exerts a greater influence on haemosporidian infections (Illera et al., 2017; Mcnew et al., 2021). Wood et al. (2007) found marked and complex associations between avian *Plasmodium* infections and landscape at the smaller scale within a single blue tit (*Cyanistes caeruleus*) population. Estimating the most relevant scale at which landscape characteristics should be incorporated into infection risk assessments is a challenge (Ostfeld et al., 2005), particularly given the differential impact of spatial structure on species with varying dispersal capabilities (Wood et al., 2007). According to Weeks et al. (2023), the fragmentation sensitivity is strongly predicted by dispersal limitation in Neotropical birds, since the extent to which bird wings are designed for crossing habitat patches affects their ability to survive fragmentation. Consequently, connectivity between patches and size of patches could be a key factor in parasite-host interactions, especially considering that the habitat use for hosts and vectors occurs on a small scale (up to 500 m) (Thompson, 1976; Finn et al., 2006; Morelli et al., 2013; Morante-Filho et al., 2021; Juárez-Fragoso et al., 2024). Moreover, landscape connectivity and diversity of plants and patches facilitates the occurrence of interactions. A landscape characterized by high complexity, connected by a network of corridors and linear elements, can enhance dispersal and survival of many insect species (Overgaard et al., 2003) and birds (Weeks et al., 2023).

The avian haemosporidian parasites including *Plasmodium* and the related *Haemoproteus* and *Leucocytozoon* provide a compelling study system for the research of the transmission dynamics of vector borne pathogens in the wild. This study model offers valuable parallels for understanding human malaria and related pathogens, thus enabling the investigation of ecological determinants of transmission dynamics under

natural conditions (Clark et al., 2014; Rivero de Aguilar et al., 2018). In a previous study, we screened blood parasites in wild birds to identify the impact of biodiversity on the infection patterns (Tamayo-Quintero et al., 2023). Here, using the information of parasite infections from this study, we aim to evaluate the relationship between the prevalence (number of infections over the total number of samples evaluated at each site for all bird community), total number of infections and lineage richness (*Plasmodium* and *Haemoproteus* each independently) of the avian haemosporidians in relation to environmental and landscape structural variables at different scales. To identify the variables that better explain haemosporidian infection variables, a set of 27 variables encompassing environment (temperature and precipitation), landscape (composition and configuration), and other geographic and vegetation quality variables were employed as predictors. These predictors were reduced using Random Forest and were subsequently incorporated into generalized linear models to determine at which scale and how they affect the number of infections, prevalence, and richness per parasite genus.

2. Methods

2.1. Study area and bird sampling

This study was conducted in forested areas around three artificial hydroelectric dams (Playas, Porce II, and Porce III) in Antioquia, Colombia (Fig. 1). The study area is a tropical rainforest, with an

average annual temperature of 22.1 °C (range = 13.9 °C–33.4 °C). The average annual relative humidity is 83.3 % and annual precipitation ranges between 2300 and 3300 mm. The three areas surrounding the hydroelectric dams are characterized by a highly diverse avian community, with similar species richness (Playas = 158 species, Porce II = 186 species, and Porce III = 212 species), diversity and dominance (Tamayo-Quintero et al., 2023).

Bird sampling was carried out between February and June 2018 in Playas and between March and October 2019 in Porce II and Porce III. We located mist nets in sites near the monitoring sites of permanent plots of vegetation and took the mean coordinate between the sets of mist nets in each transect, ensuring spatial independence between the sampled areas by having, at least, 500 m between transects. We obtained a blood sample (~20 µl) via brachial venipuncture from each captured bird. Blood samples were stored in Queen lysis buffer during the field-work and maintained at room temperature in the laboratory until DNA extraction and molecular diagnosis of haemosporidians. For details of the molecular analyses methodology used, see Tamayo-Quintero et al. (2023).

2.2. Landscape analysis

Landscape variables were computed with a high-resolution raster (10 × 10 m) for circular areas spanning radii from 50 to 500 m (10 at intervals of 50 m) centered on the mean coordinates of the net sets within the transects (Fig. 1). These areas were deemed comparable due

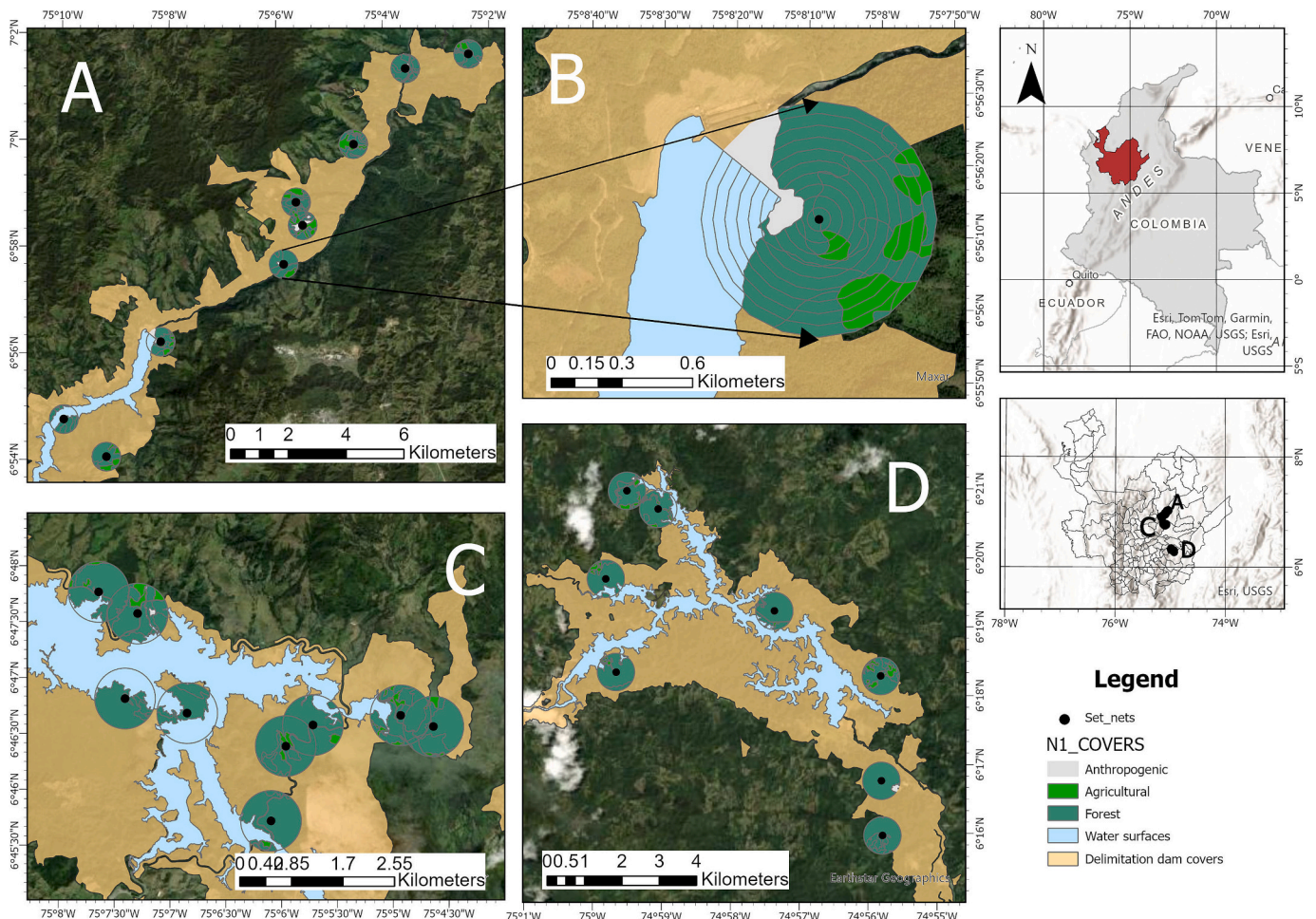


Fig. 1. Study areas in the department of Antioquia — Colombia, South America. Three different areas were studied around three artificial hydroelectric dams: Porce III (A, B), Porce II (C), and Playas (D). Fig. B corresponds to a zoom of fig. A showing the scales in one of the evaluated landscapes. Landscape metrics were computed for each of the circular areas spanning radii from 50 to 500 m (10 radii at intervals of 50 m) around the mean coordinates of the net sets.

to their identical sampling efforts. To obtain the landscape structure metrics for each dam, we used the land cover maps elaborated by Empresas Públicas de Medellín (EPM) in March 2017 for Playas, and September 2019 for Porce II and Porce III. The land covers were grouped at the N1 level according to the Corine Land Cover for Colombia methodology (IDEAM, 2010) and categorized as: 1) artificial or anthropogenic surfaces, 2) agricultural areas, 3) forests and semi-natural areas, and 4) water bodies (5, in Corine Land Cover) (Table S1, Supporting information). Then, we selected non-correlated and ecologically significant metrics from LeCos tool (Jung, 2013) within QGIS v 3.8.3-Zanzibar software (QGIS.org, 2019), resulting in three configuration metrics and one composition metric. These metrics were deemed relevant both for avian populations and haemosporidians, in alignment with existing literature (see Table 1).

To select the scale of effect for each landscape metric and response variables, we used Generalized Linear Models (GLMs) following San José et al. (2019). Count-type variables such as the number of infections (including hosts positive for any genus) or richness per genus (*Haemoproteus* and *Plasmodium*, excluding *Leucocytozoon* due to limited number of infections) were analyzed using a Poisson-type error distribution. Meanwhile, the prevalence (number of infections over the total number of samples evaluated at each site, a continuous variable of proportion type) was tested with the betareg error distribution. These models were carried out across all buffer sizes (ranging from 50 to 500 m at intervals of 50 m; 10 buffers, Fig. 1B). Then, the percentage of explained deviance as a measure of goodness-of-fit for each model referred to as pseudo-R² (Crawley, 2013), was plotted to identify the radius (landscape size) that makes response-landscape relationships the strongest (i.e. the scale of effect), selecting the scale with the largest value of the explained deviance.

To characterize environmental conditions, we assessed climatic variables, elevation, and vegetation quality. Climatic variables included: temperature seasonality (standard deviation of monthly temperature × 100), annual temperature range, isothermality, maximum temperature of the warmest month, precipitation of the driest quarter, and precipitation of the warmest quarter. We obtained this information from WorldClim images with 1 km² resolution (Fick and Hijmans, 2017). Also, the distance to freshwater sources, including the water surface of the dam and to rivers or streams, were obtained with the NNJoin tool within QGIS (QGIS.org, 2019). A digital elevation model (DEM) was used to identify the elevation at each net set. To assess vegetation quality (NDVI), we used the Sentinel 2 satellite images from the 2 years of bird sampling (2018 and 2019), offering a resolution of 10 × 10 m. We computed the normalized difference vegetation index (NDVI), a metric derived from the ratio between red and near-red wavelength bands, that is indicative of photosynthetically active radiation (Tucker et al., 1985). To obtain the NDVI values for individual landscapes (500 m radius), the average was calculated across various points within each landscape. Furthermore, plant diversity (quantified using Shannon diversity index: H') of previously established plots (plant sampling was carried out simultaneously with this research (Universidad de Antioquia, 2018, 2020a, 2020b)), close to the sampling sites was incorporated into the analysis.

For each of the response variables, comprising the total number of infections and parasite prevalence for all the three genera and richness of *Haemoproteus* (only infections for *Haemoproteus* subgenus *Parahaemoproteus* were found) and *Plasmodium* lineages (due to the low number of *Leucocytozoon* lineages, this genus was not included in this analysis), a subset of four landscape metrics (four for each cover type) was measured, focusing on the scales of effect selected. Regarding the climate variables, a selection with a correlation analysis on pairs of predictors with $r > 0.7$ was conducted. This selection encompassed six variables: temperature seasonality, annual temperature range, isothermality, maximum temperature of the warmest month, precipitation of the driest quarter, and precipitation of the warmest quarter. Additional variables encompassed plant diversity (H_Veg), NDVI, elevation,

Table 1

Description and ecological significance of landscape metrics used to assess the effect of landscape structure on the prevalence, number of infections and lineage richness of the avian haemosporidians (*Plasmodium* and *Haemoproteus* genera). *Leucocytozoon* was not included as an independent variable in the analyses due to the low prevalence found in sampled birds.

Landscape metric	Units	Description	References
Landscape proportion (LP)	Proportion (0 to 1)	A landscape composition metric that quantifies the relative extent of a particular cover within the surrounding landscape. Provides information about the dominance and distribution of different habitat types, which can influence species preferences and interactions.	(Overgaard et al., 2003; Reiter and LaPointe, 2007; Morante-Filho et al., 2021)
Edge density (ED)	meters per hectare	A landscape configuration metric that calculates the sum of all forest edges per unit area and is expressed in meters per hectare. Ecological edges are boundaries or transition zones between two adjacent landscape patches or land cover types and can influence species distributions and interactions.	(Hargis et al., 1998; Morelli et al., 2013; Watts, 2015; Morante-Filho et al., 2021).
Patch density (PD)	Number of patches per 100 ha	A landscape configuration metric that measures the number of patches in the landscape relative to the total landscape area, and it can be used as an index to express the degree of landscape fragmentation if only the number of forest patches is considered and not their areas or spatial distribution. Ecologically, this variable provides information about the availability of suitable habitats and potential movement corridors for species.	(Okanga et al., 2013b; Watts, 2015).
Patch cohesion index (PCI)	Index (0 to 10)	The class-level patch cohesion index is a landscape configuration metric that measures the physical connection of the corresponding land cover type. Values closer to 0 mean than the patches belonging to a particular category are very scattered. Values closer to 10 indicate that they are tightly clustered. It provides insights into habitat connectivity, which is crucial for the movement, dispersal, and survival of the species such as birds or vectors.	(Hargis et al., 1998; Overgaard et al., 2003; Okanga et al., 2013b; Watts, 2015; Weeks et al., 2023)

distance to rivers, and distance to dams. In total, 27 variables were procured and subjected to a Random Forest model (Liaw and Wiener, 2002), to determine the relative importance of each variable across the various models (Table S2, Supporting information).

To assess the impact of landscape structure and environmental variables on the prevalence, number of infections and lineage richness of avian haemosporidians, we used generalized linear models (GLMs). Within these models, prevalence was included with betareg distribution, while number of infections and the richness of lineages (for *Plasmodium* and *Haemoproteus*) were analyzed using a Poisson distribution. We evaluated each of the predictors chosen by Random Forest, as well as a model selected from a stepwise selection of models from the stepAIC function of package “MASS” in R (Venables and Ripley, 2002). The most plausible models were selected based on AIC criteria ($\Delta AIC \leq 2$). These analyses were performed with the R statistical packages “lmer4” (Bates et al., 2015), “betareg” (Cribari-Neto and Zeileis, 2010) and “MuMIn” (Bartón, 2023). The R “performance” package was used to evaluate the quality of the models (Lüdecke et al., 2021), and the “sjPlot” package was used to observe the coefficient estimates that represent the relationship between the response variable and the predictor variables in the model and providing the significance level of each variable (Lüdecke, 2023).

3. Results

3.1. Haemosporidian infections

Blood samples from 678 individuals corresponding to 90 bird species were screened for haemosporidian infection. Detailed information on parasite-infected birds is found in Tamayo-Quintero et al. (2023). We found a parasite prevalence of 9.73 % (66 infected birds), spanning 29 different bird species. Most infections corresponded to *Haemoproteus* ($n = 30$ birds) and *Plasmodium* ($n = 27$ birds) parasites, while only 9 birds were infected by *Leucocytozoon*. Overall, we identified 14 *Haemoproteus* lineages, 17 lineages of *Plasmodium* and 8 lineages of *Leucocytozoon*. We did not find significant differences between the number of infections and the prevalence of haemosporidians in birds from the three dams

(Kruskal-Wallis $p > 0.05$).

3.2. The scale of effect of landscape structure on avian haemosporidian parasites

The scale of effect of landscape structure on prevalence, number of infections, and richness of *Haemoproteus* and *Plasmodium* lineages was variable according to the land cover, landscape metric and response variable evaluated (Fig. 2). Water amount and configuration poorly explained most of the response variables (DE < 20 %) but prevalence (DE > 20 %); meanwhile forest, agricultural and anthropogenic covers explained over 20 % of the variance of all response variables (Table S3, Supporting information). Landscape structure was more related to prevalence of Haemosporidians and richness of *Plasmodium* lineages than to infections or richness of *Haemoproteus* lineages. The latter two variables were only related to connectivity of agricultural areas at larger scales (500 m radius). Prevalence (Average = 425 m) and number of infections (Average = 350 m) showed on average larger scales than richness for each genus (*Plasmodium* Average = 219 m, *Haemoproteus* Average = 244 m).

3.3. Effects of landscape and environmental variables on avian haemosporidian parasites

The stepwise selection models built with the environmental and landscape predictors for each response variable (hereafter full models) as well as the relative importance or weight of each climatic and landscape metric (measured at their scale of effect) on response variables are shown in Table S4, Supporting information. Except for the number of infections, the full models performed better than singled-predictor models (pseudo- $R^2 > 0.49$). The number of infections was better explained by only the agricultural patches density, where more patches increased the number of infections (estimate = 0.43, pseudo- $R^2 = 0.68$; Figs. 3, 4a). Prevalence and lineage richness were related to different environmental and landscape predictors (Fig. 3). Prevalence mostly increased with the proportion of agricultural areas (Fig. 4b), and to a lesser extent was explained by the proportion and connectivity of

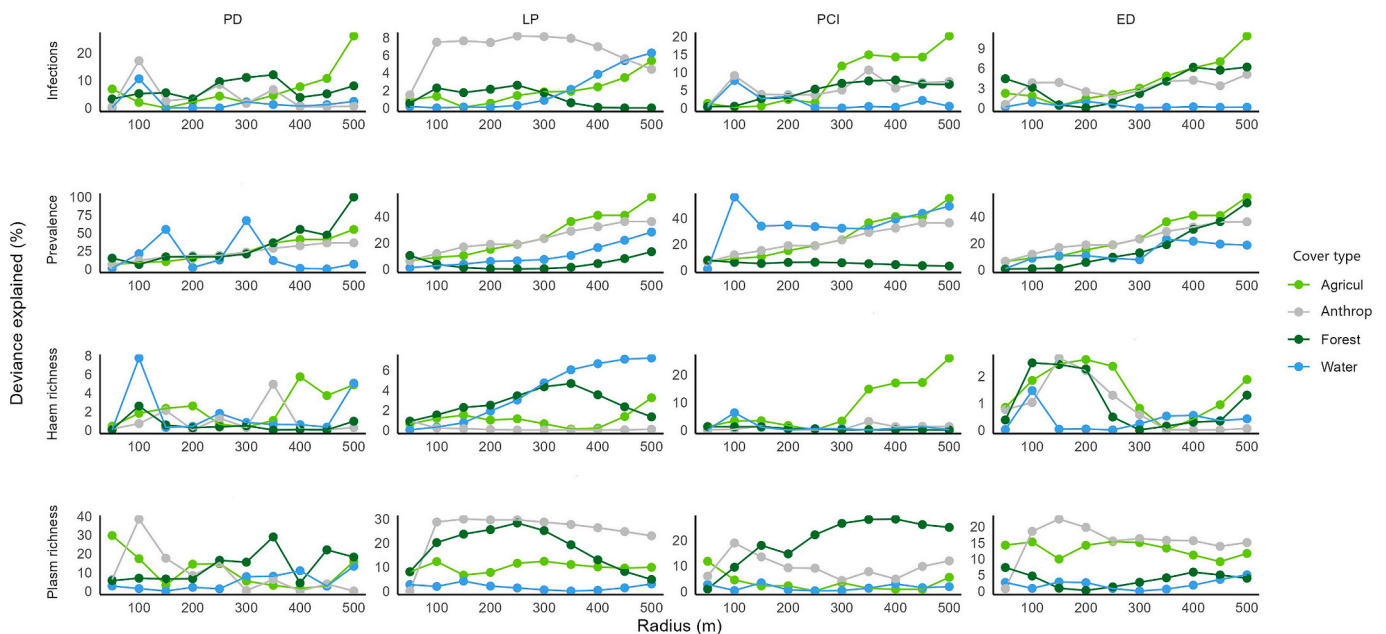


Fig. 2. The scale of effect of the landscape structure on the number of infections and prevalence by haemosporidians, and lineage richness of *Plasmodium* and *Haemoproteus*. We plotted the percentage of deviance explained (DE) by each landscape metric at each of ten radii (50 to 500 m, 50 m interval) for each response variable. We assessed three configuration metrics (patch density — PD, patch cohesion index — PCI and edge density — ED) and one composition metric (landscape proportion — LP) obtained for each cover type: anthropogenic (Anthrop, grey), agricultural (Agricul, light green), forest (drank green) and water (blue) cover.

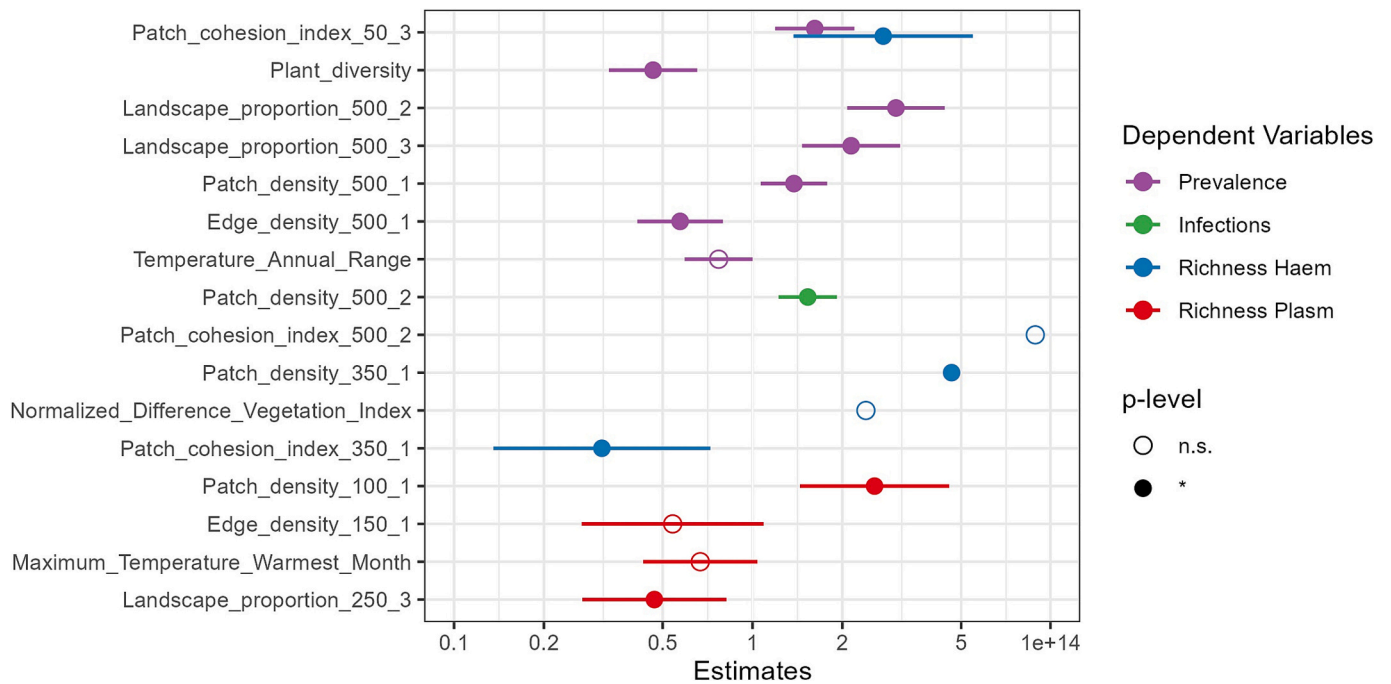


Fig. 3. Landscape and climatic variables selected from GLMs for prevalence, number of infections, and richness of *Plasmodium* and *Haemoproteus* lineages. The coefficient estimates represent the relationship between the response variable and the predictor variable in each model, along with the significance value of each variable. The line indicates the SE 95 % CI. The number after the landscape metrics indicates the scale of effect detected, followed by the number of the land cover: anthropogenic (1), agricultural (2) and forest (3).

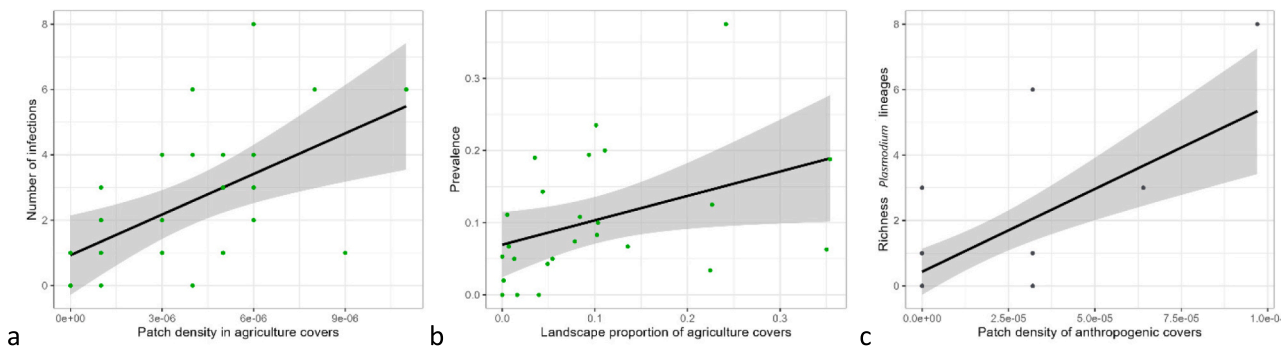


Fig. 4. Effects of the most important landscape metrics explaining the number of avian haemosporidian infections (a), prevalence (b) and richness of *Plasmodium* lineages (c). The grey area corresponds to the standard error.

forested areas and fragmentation of anthropogenic areas. However, prevalence decreased with annual temperature range, plant diversity (H_Veg) and anthropogenic edge density at 500 m (pseudo-R² = 0.49).

For the richness of *Haemoproteus* lineages, the best model corresponded to the full model including several connectivity variables and NDVI (pseudo-R² = 0.83). A positive relationship was observed with the connectivity of agricultural (at 500 m) and forest (at 50 m) cover, anthropogenic patch density at 350 m, and NDVI (Table S4, Supporting information). Conversely, *Haemoproteus* richness was negatively associated with the anthropogenic land cover connectivity at 350 m. Finally, the richness of *Plasmodium* lineages increased with anthropogenic patch density at 100 m (Fig. 4c) and decreased with anthropogenic edge density at 150 m, forest proportion in the landscape at 250 m, and maximum temperature of warmest month (pseudo-R² = 0.79).

4. Discussion

Here, we assess the effect of 27 environmental and landscape structure variables on the number of infections, prevalence and richness

of avian haemosporidian lineages infecting birds in the Neotropics. Forest, agricultural, and anthropogenic cover's proportion and connectivity, as well as vegetation quality and diversity were more important predictors of the prevalence and richness of the haemosporidian lineages than geographic and climatic variables. The scale of effect of landscape metrics depended on the response variable, land cover, and landscape metric assessed, and different landscape metrics explained the number of infections, prevalence and lineage richness of avian haemosporidians.

4.1. Scale of landscape effects on avian haemosporidians

Although we assessed the landscape optimal scale of habitat use for avian haemosporidians based on previous studies on birds and vectors (Morante-Filho et al., 2021; Morelli et al., 2013), the scale of effect was the largest radius tested in this study (i.e. 500 m) in 38 % of the land cover metrics evaluated, highlighting the possibility that the scale of landscape effect on infections and prevalence of avian haemosporidians might occur at larger scales. For the number of infections, the scale of effect of agricultural patch density was 500 m; for prevalence, the same

scale of effect was observed for almost all metrics and coverages, except for edge and patch density and connectivity in water surfaces. Fuller et al. (1994) suggested that the optimal spatial scale for deriving landscape metrics, for bird species richness, is at 125 m radius. Furthermore, given that we generally worked with passerine birds, which also have variable habitat ranges, the optimal spatial extent ranges from a 125 to 600 m radius around the sampled site (Juárez-Fragoso et al., 2024; Morante-Filho et al., 2021; Morelli et al., 2013). The 250 m scale is likely to reflect the habitat requirements for vector development within their dispersal potential (Finn et al., 2006; Thompson, 1976). Here, prevalence (425 m radius) and number of infections (350 m) showed on average larger scales than the specific response variables, especially for richness of *Plasmodium* lineages (219 m). This supports that the scale of effect on avian haemosporidians depends also on the group of species involved, which may respond differentially at each scale (Bhakti et al., 2018), highlighting the need to include the range of habitat in which vector, parasite, and bird communities are able to interact in the ecosystems.

Understanding the spatial nature of parasite-host interactions can become a complex task, considering that they can interact synergistically with other processes at different spatial scales (Miguet et al., 2016; Moreira-Arce et al., 2021). When analyzing the scale of the effect of landscape metrics on species interactions, different studies have found that the effect is larger at smaller spatial scales. For example, when evaluating the scale of the effect on different taxa, Schindler et al. (2013) found that the scale affected the performance of landscape metrics as indicators of biodiversity, also affecting, the performance of metrics for modeling the richness of small land birds, improving the predictive capacity in smaller extensions of the landscape. This hypothesis was recently confirmed by Juárez-Fragoso et al. (2024), who evaluated the scale of effect on the bird community in tropical landscapes and found that, in a range of 250 to 470 m, the shape and size of habitat patches determined alpha diversity. Furthermore, landscape variables can drive avian malaria transmission at much smaller spatial scales than previously recognized (Lachish et al., 2011). This could be related to the vector's dispersal capacity, which usually does not exceed 250 m (Finn et al., 2006; Thompson, 1976), although this may vary between species and sites. Therefore, integrating vectors into this type of analysis may better elucidate this pattern, where both infection and prevalence of avian haemosporidians are similar in scale of effect to their hosts as this study suggests. This pattern has been demonstrated in different studies reporting a positive association between the diversity of parasite lineages and mosquito and host species richness (Ferraguti et al., 2024; Tamayo-Quintero et al., 2023).

4.2. Landscape structure and environmental effects on avian haemosporidians

Although different landscape metrics explained the response variables, agricultural and anthropogenic covers played an important role as avian haemosporidian predictors. The density and edge of anthropogenic patches and the proportion of forest and agricultural patches explained the prevalence of infection by haemosporidians in the different landscapes, while only the density of agricultural patches explains the number of infections. These results indicate that transformed and natural covers are good predictors of haemosporidian prevalence and number of infections in birds (Ferraguti et al., 2023). For example, some bird species have been found to experience high prevalence rates in urban areas compared to non-urban areas (Santiago-Alarcon et al., 2015). Furthermore, the most severe malaria infections have been found in agricultural landscapes (Okanga et al., 2013b). This result could be due to the effect of vectors and their dispersal capacity at this small spatial scale which may be directly related to the prevalence found in birds in the studied areas.

Forest proportion, connectivity and plant diversity were also related to avian haemosporidians. Although paradoxical, forest proportion had

a positive effect and plant diversity had a negative effect on the number of infections and prevalence. This is possible considering that high landscape complexity caused by a network of corridors and linear elements can promote dispersal and survival of many insect species (Overgaard et al., 2003). In addition, many of these landscapes are relatively homogeneous in their plant community composition, as is the case of areas destined for restoration and conservation processes (Universidad de Antioquia, 2018), which may allow a lower richness of vector species. The proximity to the edge of the forest is another important variable explaining the parasitemia of avian Haemosporidians, where parasitemia increases as birds are closer to the edge (Knowles et al., 2010). In this sense, near the edge of the forest, food resources become scarce, and predation increases, both inducing stress in birds (Knowles et al., 2010). As stress negatively impacts the host immune response (Loiseau et al., 2008), it may lead to a higher probability of a bird acquiring an infection, presenting high parasitemia, and even dying from the infection (Santiago-Alarcon and Marzal, 2020).

When evaluating the richness of each parasite genus separately, we found that richness of *Plasmodium* and *Haemoproteus* lineages in birds are favored in areas with high density of anthropogenic patches, which may provide suitable environments for both vector and bird species. Jiménez-Peñuela et al. (2021) found a higher richness of *Haemoproteus* lineages in rural habitats than in natural and urbanized ones during one of the two study years. In another study, the richness of *Haemoproteus* was significantly related to environmental variables such as altitude, forest cover, and host richness (Illera et al., 2017). However, the effects of these variables may differ according to the parasite studied. For example, Martínez-Alvarado (2019) found a higher prevalence and diversity of *Plasmodium* parasites related to low vegetation cover expressed as low NDVI values and in areas far from water bodies, but high NDVI values seem to be associated with a higher richness of *Haemoproteus* lineages. Illera et al. (2017) found that infections by parasites of the genus *Plasmodium* were more common in open and warm habitats, while *Haemoproteus* and *Leucocytozoon* showed affinities for forested areas. Even in temperate zones, when assessing the bird community in urban forests in Germany, Santiago-Alarcon et al. (2015) also found a significant positive effect on the probability of *Plasmodium* infection. Contrasting results could be due to the different requirements of the different vectors involved in the transmission of these two parasite genera. Pérez-Rodríguez et al. (2013) found that different models emerged for each parasite genus, although all parasites were studied in the same host species, which implies that a model used to develop one parasite distribution can probably not be applied identically even to the most similar host-parasite systems.

5. Conclusion

Our study reveals that landscape structure, particularly the proportion and connectivity of forest, agricultural, and anthropogenic covers, alongside vegetation quality and diversity, are key predictors of avian haemosporidian prevalence and lineage richness in the study area. The scale of landscape effects varied depending on the specific response variable, with agricultural and anthropogenic patch density notably influencing infection rates and prevalence. Studying the parasite community infecting wild birds in this hyperdiverse area, we found that changes in parasite distribution and prevalence remain difficult to predict with spatial heterogeneity, as each parasite-host system is susceptible to many unaccounted variables (Loiseau et al., 2010). Complex interactions between temperature, water availability, vector and host abundance, and community composition at the local scale partially explain the variability in haemosporidian prevalence (Ferraguti et al., 2018; Pulgarín-R et al., 2018). These findings underscore that landscape transformation plays a critical role in shaping haemosporidian infections in birds, with forest and agricultural covers facilitating different aspects of haemosporidian diversity and transmission. These results highlight the complex interplay between landscape structure and

haemosporidian-host dynamics, suggesting that effective conservation strategies must consider the spatial scales relevant to both hosts and vectors. Understanding these interactions at appropriate scales is essential for managing haemosporidian infections and improving our understanding of host-parasite dynamics in changing landscapes.

Declarations

All experiments and protocols were approved for the committee of ethics of the University of Antioquia and the resolution 0524 of ANLA (National Environmental Licensing Authority) and the University of Antioquia. The study was performed under proper legislation of the Colombian law and following the Code of Ethics of the Animal Behavior Society, and the ABS/ASAB Guidelines for the use of animals in research and teaching. Only blood samples were collected, and all birds were returned to their natural environment. Animals were not kept in captivity and were not exposed to any experimental treatment. The capture/collection of biological samples and specimens is covered by a permit for the collection of wild specimens for non-commercial purposes, issued by the National Environmental Licensing Authority (ANLA) through resolution 0524 to the University of Antioquia, which includes the Ecology and Evolution research group. Moreover, the export of samples of biodiversity in Colombia for genetic (phylogenetic) analysis, is regulated by the ANLA, which grants an export permit for Scientific Research purposes. Since Universidad de Antioquia holds a collection permit, all research activities with wild specimens or biological samples are performed under Colombian law.

All the authors complied with the ARRIVE guidelines and the submission guidelines for manuscript.

CRediT authorship contribution statement

Juliana Tamayo-Quintero: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Miriam San-José:** Writing – review & editing, Supervision, Methodology. **Josué Martínez-de la Puente:** Writing – review & editing, Supervision. **Catalina González-Quevedo:** Writing – review & editing, Supervision. **Héctor F. Rivera-Gutierrez:** Writing – review & editing, Supervision, Funding acquisition.

Declaration of Generative AI and AI-assisted technologies in the writing process

After writing the manuscript, author(s) used ChatGPT to improve the English grammar of the document. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2025.178426>.

Data availability

Data will be made available on request.

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