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Predicting Landscape Conversion Impact on Small Mammal Occurrence and the Transmission of Parasites in the Atlantic Forest

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ABSTRACT

Aim: Changes in landscape configuration significantly impact ecosystems and the services they provide, including disease regulation for both humans and wildlife. Land use conversion usually favors disturbed-adapted species, which are often known reservoirs of zoonotic parasites, thereby potentially escalating spillover events (i.e., the transmission of parasites to new hosts, including humans). Here we aimed to investigate how alterations in landscape use and configuration influence the distribution and co-occurrence of potential hosts of zoonotic and epizootic parasites.

Location: Brazilian Atlantic Forest.

Time Period: Data collection spanned from 1997 to 2019.

Major taxa studied small mammals.

Methods: We integrated ecological network metrics and joint distribution models while accounting for phylogenetic relationships and functional traits to answer two main questions: (1) do small mammal species considered central hosts in the transmission of parasites exhibit a higher probability of occurrence in landscapes with reduced native vegetation areas? (2) Do small mammal hosts that share a higher number of parasites have higher co-occurrence probabilities?

Results: Our results demonstrated that species identified as significant hosts in our centrality network analysis displayed an increased probability of occurrence in landscapes that are both more fragmented and have a higher proportion of farming areas, hence fewer native vegetation areas. Regarding the relationship between species co-occurrence and parasite sharing, our findings indicated that most strong co-occurrences were prevalent within groups with higher parasite fauna similarity, but not all species sharing parasites had a higher probability of co-occurring.

Conclusions: Here we highlight the effects of landscape conversion on small mammal species, including how different configurations of land use can influence both central and non-central host occurrences. Besides, our results also indicate that parasite transmission may be overestimated when the co-occurrence probability of potential host species is not considered. We highly recommend incorporating co-occurrence data to estimate zoonotic risk.

1 | Introduction

Changes in natural landscapes due to deforestation cause multiple impacts on biodiversity, leading to a pervasive loss of species worldwide (Young et al. 2016). The conversion of forests into cropland, pastures, or urban areas disrupts fundamental ecosystem services essential for human and animal health regulation. In particular, deforestation amplifies the presence of disturbed-adapted species, which may act as potential hosts of zoonotic and epizootic parasites (Gibb et al. 2020). The increase in host species abundance associated with higher contact rates favors spillover events, where parasites infect new hosts, including humans (e.g. Gibb et al. 2020; Keesing and Ostfeld 2021). However, the occurrence of such events relies on the transmission opportunity and infection success (Araujo et al. 2015). While the link between habitat loss and the transmission of zoonotic and epizootic parasites is recognized (Andreazzi et al. 2023), the specific landscape use and configurations fostering crucial hosts remain elusive. Furthermore, the role of the co-occurrence of hosts in the opportunity of transmission that can lead to new successful parasite infections has not yet been analyzed.

Global studies predicting spillover risk often rely on broad host–parasite association data, overlooking the fine-scale co-occurrence of different host species. These predictions are usually based on centrality metrics (the role of species in connecting the network), parasite richness, and overlapping geographical ranges (Wardeh, Sharkey, and Baylis 2020). The ones investigating the effect of land use change on parasite transmission generally conclude that habitat loss correlates positively with spillover (Gibb et al. 2020; Keesing and Ostfeld 2021). Although illuminating, these analyses often miss subtle characteristics defining parasite transmission in specific contexts. On smaller spatial scales, studies revealed diverse effects of landscape changes on parasite transmission, highlighting the need for a more contextual understanding (Andreazzi et al. 2023). Thus, the response of host–parasite interaction to different land use and configurations could vary, affecting parasite transmission risks.

Spillover likelihood rises where there is transmission opportunity and host compatibility (Araujo et al. 2015), particularly in closely related hosts with shared behaviors and morphophysiological traits (Salkeld, Padgett, and Jones 2013). Successful parasite spillover is expected to be higher between hosts that share more parasites and occupy the same habitat (McKee et al. 2019; Stephens et al. 2019). In this sense, the co-occurrence of different generalist and host-competent species could escalate spillover risks, emphasizing the complexity of disease emergence phenomena. Therefore, understanding the relationship between co-occurrence and parasite sharing is crucial in predicting spillover events. Here, we delve into the co-occurrence importance of parasite sharing and the effect of landscape use and configuration on the distribution of competent hosts by focusing on the small mammal assemblages in the Brazilian Atlantic Forest (herein BAF). This biome, home to most of the Brazilian human population, has been devastated since European colonization (Scarano and Ceotto 2015). Despite increasing efforts to restore vegetation, urbanization, and agriculture continues to alter the landscape (Rezende et al. 2018). The BAF houses a high small mammal diversity (i.e., rodents and marsupials), and spillover risk is a major concern since several species harbor zoonotic parasites like Orthohantavirus (De Oliveira et al. 2014), *Bartonella* spp., and *Borrelia* spp. (Gonçalves-Oliveira et al. 2020).

We used data on small mammal occurrences across the BAF and their associations with different parasite groups (viruses, bacteria, protozoa, and helminths) based on a dataset of all possible associations (Cruz et al. 2023) to unravel the impact of landscape use on the distribution and co-occurrence of small mammals. Our approach integrates network analysis and a spatially explicit joint species distribution model (Marjakangas et al. 2020). We focused on two relevant network metrics related to parasite transmission: centrality and modularity. Host centrality identifies highly connected hosts within the network that act as bridges between different interacting groups, providing a key measure of host competence in parasite transmission (Gómez, Nunn, and Verdú 2013; Romano et al. 2016). Network modularity, quantified by the Q metric (proposed by Newman and Girvan 2004 and later refined by Barber 2007), measures the degree to which a network is divided into distinct clusters or modules. In a modular network, species within the same module are more densely connected, while connections between different modules are sparser. It offers insights into parasite sharing, which is used here as a proxy for spillover risk. These metrics were related to occurrence and co-occurrence probabilities generated by the Hierarchical Modeling of Species Communities (HSMC), which computes species' response to landscape use while accounting for the influence of their traits and phylogenetic-relatedness (Ovaskainen and Abrego 2020). Incorporating trait information and phylogeny enhances the model's confidence and robustness, ensuring a comprehensive understanding of landscape impact on host co-occurrence and spillover risk.

Here, we used node centrality to classify small mammals into central and non-central hosts based on their parasite faunas, to address the first issue: (1) Do central host species have a higher probability of occurrence in landscapes with reduced native vegetation areas? We hypothesize that central host species succeed in a wider range of environmental conditions (habitat generalist) than other species from the same community, leading to higher occurrence in heterogeneous landscapes with reduced forest cover. We then analyzed small mammal co-occurrences, modeling them as a function of their clustering pattern (measured by modularity) to address the second issue: (2) Do small mammals sharing a higher number of parasites have higher co-occurrence probabilities? We expect that host species more prone to co-occur also share more parasites and belong to the same network modules. As evolutionary factors affect parasite sharing, we hypothesize that species inside each module are more phylogenetically related to each other than to species in different modules. Our study not only bridges critical knowledge gaps but also lays the groundwork for understanding the intricate interplay between host co-occurrence, parasite sharing, and changing environments.

2 | Methods

2.1 | Data Collection and Compilation

The BAF is mainly distributed along the eastern coast of Brazil. Although highly endangered (with only 12.4% of its original vegetation cover), it comprises several phytophysiognomies, being the forest with the greatest diversity of trees per hectare globally and holding countless endemic species, characterizing it as a biodiversity hotspot (Mittermeier et al. 2011).

Our dataset on small mammal occurrences was compiled from medium- and long-term community studies conducted by two prominent Brazilian research groups: (i) the Laboratory of Biology and Parasitology of Wild Mammal Reservoirs at the Oswaldo Cruz Foundation (D'Andrea et al. 2021); and (ii) the SES-MA database (Synthesis in Atlantic Forest Ecology and Sustainability Group) (Püttker et al. 2020). Data collection spanned from 1997 to 2019, totaling 2476 records of 69 species of small mammals across 604 sampling sites within the BAF. This dataset incorporated geographical data, sampling efforts, capture methods, and sampling timelines. To build our association network between small mammals and their parasites, we used data from Cruz et al. (2023) database, where we compiled bacteria, viruses, fungi, protozoa, and helminth parasite infections registered at the BAF region for each small mammal species in this study. Parasites used were in the finest taxon level registered in the database, mainly genus and species level (Table S5). We built a bipartite matrix A_{mn} where m is the host species (rows) and n is the parasite (columns); thus, mn represents the presence/absence of the host–parasite interaction. While we acknowledge that the parasite richness of each host species is correlated with the number of studies (Figure S4), we also recognize a biological pattern: more abundant species are sampled more frequently, and their abundance is positively correlated with parasite diversity (Kamiya et al. 2014). Additionally, parasites of greater public health importance (zoonotic parasites) are more frequently found in abundant hosts (Dallas, Han, et al. 2019), and many studies contain redundant information on parasite composition (Gibb et al. 2020; Cardoso et al. 2020). Therefore, we accounted for this sampling bias by using host centrality categories rather than raw measurements and adding the number of studies as a covariate in our analysis.

2.2 | Species Occurrences and Landscape Delimitation

To create our small mammal occurrence matrix (presence/absence), we compiled the data from all 604 sampling sites, identifying the centroid of the entire sampled area from each study. Using an 800-m radius, we defined 212 landscapes within which we assessed the community composition based on the species sampled and measured landscape use and configuration metrics (see below). Buffer radius length was based on the dispersal abilities of non-volant small mammals and previous research examining the influence of landscape configuration on small mammals' distribution (Bovendorp et al. 2019; Muylaert et al. 2019). We then excluded landscapes with fewer than four species and species occurring in fewer than five landscapes, resulting in a final matrix comprising 52 species occurring in 136 landscapes (Figure 1).

2.3 | Land Use Classification and Landscape Metrics

The land use classification relied on the 7.0 collection of the Brazilian Annual Land Use and Land Cover Mapping Project (MapBiomas) (Souza et al. 2020). For each landscape, we used shapefiles relative to the median year of the sampling period, since changes in the land use and configuration between the end and start years of the studies were negligible (see Table S2). MapBiomas project generates classifications through Landsat 8 satellite imagery with a pixel resolution of 30×30m (Souza et al. 2020). In our study, we reclassified MapBiomas 7.0 collection classes into native forest formation (forest, savanna, and mangrove), native non-forest formation (grassland and wetland), pasture, agriculture (temporary and perennial crops), forest plantation (silviculture), undefined farming (mosaic of farming areas where it was not possible to distinguish between pasture and agriculture), non-vegetated areas (e.g., mining and urban areas), and water areas. Elevation data were gathered from the Topodata project (http://www.dsr.inpe.br/topodata/index.php).

Our selection of landscape metrics was based on previous research on small mammal distribution (Bovendorp et al. 2019; Muylaert et al. 2019). For each landscape (an 800m radius buffer), we calculated the percentage of land use for all classes, mean elevation, landscape Shannon diversity and evenness, and the number of patches (a measure of landscape granularity that considers the amount of land that differs from its surroundings, taking all classes into account). Specifically for the native forest class, we also estimated the number of native forest patches, edge density, and Euclidean nearest neighbor distance. All metrics were calculated using the packages "landscapemetrics" (Hesselbarth et al. 2019) and "landscapetools" (Sciaini et al. 2018) in R software (R Core Team 2023). Detailed metric definitions can be found in Table S1. We used preliminary correlation analysis to exclude highly autocorrelated metrics (r between |0.6| and |0.8|, see Figure S1 for more details) and to diminish collinearity between variables in the final model.

2.4 | Network Analysis

The BAF metanetwork accounted for the 52 small mammal species in the final occurrence matrix. As our main goal was to identify central hosts related to potential spillover events, we focused on parasite-shared associations within taxa found to infect multiple host species. Out of the 52 mammals, we identified 36 host species associated with 133 parasite taxa, including helminths, protozoa, bacteria, and viruses (Tables S4 and S5).

To identify central host species, we estimated betweenness centrality and node degree (Rushmore, Bisanzio, and Gillespie 2017; Wardeh, Sharkey, and Baylis 2020). Betweenness centrality measures all the shortest paths passing through a node (Jordan, Liu and Davis 2006; Rushmore, Bisanzio, and Gillespie 2017). When accounting for parasite sharing, species with higher betweenness are identified as critical hosts because they are more likely to become infected and spread parasites. In contrast, species degree counts the number of links inside the network, indicating highly connected hosts (Dallas, Han, et al. 2019). Centrality and degree values were calculated using "igraph" (Csardi and Nepusz 2006).

To analyze small mammal group formations based on parasite associations, we calculated metanetwork modularity (Costa,

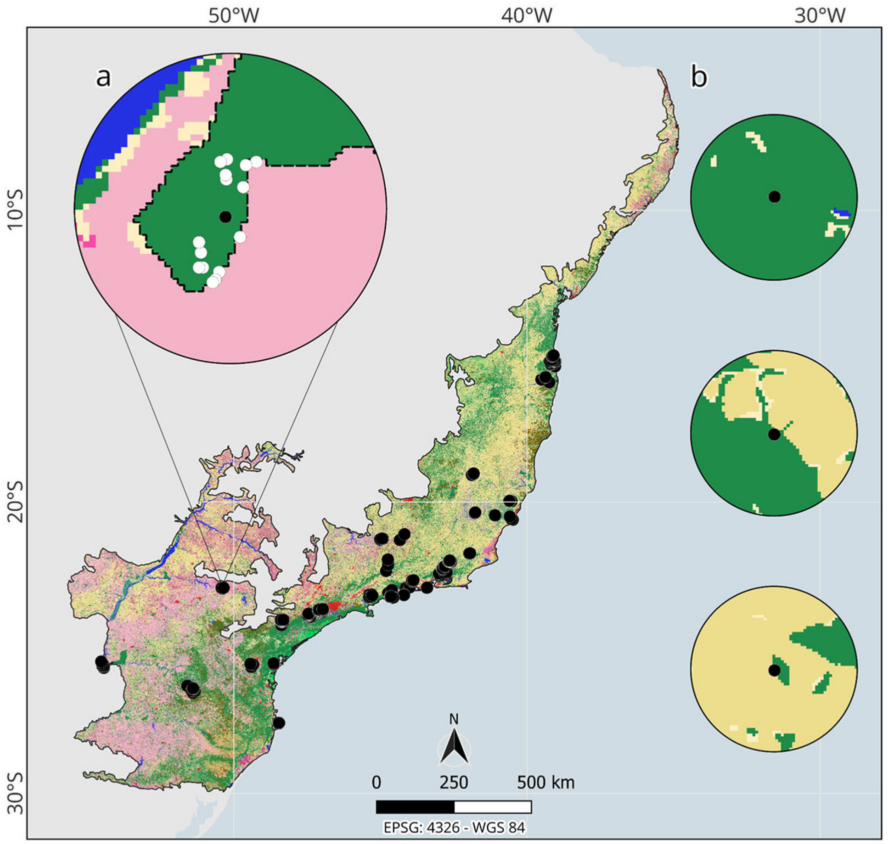

FIGURE 1 | Distribution of small mammal communities in the Brazilian Atlantic Forest used in this study. The black dots on the map represent the landscape centroids used to calculate the land-use metrics. Figure (a) shows the 800-m radius buffer, considered a landscape in this study. White dots are the sample points aggregated in the buffer to assemble the small mammal community. The colors on the map represent the different land use classes. The green polygon outlined in black shows what is considered a forest patch in the landscape metrics calculation. (b) Examples of different landscape configurations sampled in this study. Here the landscapes differ in the percentage of forest (green color) and agriculture (yellow color).

Bascompte, and Andrian Padial 2023). Modularity measures the tendency for cluster formation in a network, identifying groups of host species highly interconnected due to shared parasites (Newman and Girvan 2004). We measured modularity using Barber's modularity metric for bipartite networks (Q_b) with MODULAR software (Marquitti et al. 2014). Significance was estimated through 999 null model simulations (Bascompte et al. 2003), wherein the probability of a pair being connected to an edge is proportional to the number of edges of each node. To confirm convergence in the module's configuration between iterations, we ran the modularity analysis 10 times. We focus on the configuration with the highest modularity value, ensuring the robustness of our results.

2.5 | Joint Species Distribution Modeling and Spatial Analysis

To analyze the small mammal community's response to environmental covariates, we used Hierarchical Modeling of Species Communities (HMSC) (Tikhonov et al. 2020). HMSC integrates species-level models within a hierarchical structure, allowing us to explore communities' responses to environmental covariates taking into account their traits and phylogenetic similarity. Another critical aspect incorporated into the HMSC framework is spatial autocorrelation, which describes how the similarity in species occurrences decays with increasing spatial distance (Tikhonov et al. 2020). HMSC was incorporated using a probit distribution for presence-absence data (Marjakangas et al. 2020). Landscape centroid coordinates were transformed into a latent variable and incorporated as a random factor in the model. Landscape metrics, species traits, and phylogeny were included as fixed factors.

Small mammal traits were gathered from the literature, including average body mass, caudal length, body length, trophic level, food items, main guild, period of activity, home range size, locomotor habit, and age of sexual maturation (more information on Sup. material). To identify non-representative traits to be excluded and to avoid collinearity, we used correlation analysis. The phylogenetic tree, built with Genbank's molecular data, utilized cytochrome B sequences from all 52 species, aligned with Geneious software (Biomatters) (Kearse et al. 2012). The aligned sequences were imported into MEGA software (Tamura, Stecher, and Kumar 2021), for generating a maximum parsimony tree via the Bootstrap method. The methodology for the creation of the phylogenetic tree followed Bovendorp et al. (2019).

Our modeling adhered to Ovaskainen and Abrego's (2020) HMSC workflow, encompassing model structuring, fitting, posterior distribution analysis, and explanatory and predictive power assessment. Bayesian inference of Markov Chain Monte Carlo (MCMC) ensured posterior sample distribution validation through convergence diagnostics. To assess predictive performance, we employed a cross-validation procedure (Tikhonov et al. 2020), computing Tjur's R^2 and the Area Under the Curve (AUC). We computed several models (Table S3) with different sets of landscape metrics and traits to find the one that best accounted for landscape effect on species occurrences. Thus, the final HMSC model featured covariates with the best fit in the convergence diagnosis and higher explanatory and predictive power. All joint distribution analyses were conducted using the "Hmsc" R package (Tikhonov et al. 2023).

2.6 | Do Small Mammal Species That Are Central Hosts Have a Higher Probability of Occurrence in Landscapes With Lower Natural Areas?

To determine whether species occurrences are best explained by spatial structure or landscape metrics, we first partitioned variation among fixed and random factors. Then, we built a variation from the minimum to the maximum value for all landscape covariates of the model, using the function "contructGradient" of the "HMSC" package. The variations were used to build predictions of species occurrences for each landscape covariate (function "predict"). As our model relies on presence-absence data, predictions represent the occurrence probabilities of species based on each landscape metric, fitted as a covariate. We only considered predictions with a posterior probability above 0.8 for both negative and positive relationships of each species to each landscape covariate, given to us by the beta parameter of the HMSC (Figure S5). We set this confidence value to encompass all species present in our dataset. To analyze species occurrence probability, we compressed their distribution into the posterior mean prediction (Ovaskainen and Abrego 2020). Subsequently, we plot the predicted occurrence probabilities according to the classification of small mammals into central, non-central hosts and hosts with no parasite registry. We constructed generalized additive models (GAM) with beta distribution to ascertain the significance of the differences between the probabilities of occurrence grouped by small mammal centrality classification for all landscape covariates. We used integrated smoothness estimation with a factor interaction to see non-linear relationships between landscape variation as a function of host centrality classification (predictors), and the occurrence probability predicted by the HMSC model (response variable). The number of studies for each host was fitted as a smooth term with a random factor basis to account for sampling biases in our analysis. GAM analyses were conducted in "mgcv" R package (Wood 2011), and the results controlled by the number of studies were reported using the function "plot_predictions" of the "marginaleffects" R package (Arel-Bundock 2024).

2.7 | Do Small Mammals Sharing a Higher Number of Parasites Have Higher Co-Occurrence Probabilities?

To answer the second question, we employed a two-step analysis. First, we classified small mammal species based on cluster configurations derived from modularity analyses. These modules enlighten host species sharing the highest number of parasites in the BAF metanetwork, indicating a higher potential for new spillover events. Analyzing module classification alongside species co-occurrence probabilities allows us to investigate the likelihood of encounters between hosts that could result in a successful parasite exchange. For each computed module, we calculated the mean values of small mammals' residual variance–covariance matrix defined by random effects—specifically, the spatial structure of the data (Dallas, Laine, and Ovaskainen, 2019). The species-to-species residual associations were scaled in a correlation matrix and assumed to have a 0.75 posterior probability, either positive or negative, following Dallas, Laine, and Ovaskainen (2019). This step allowed us to assess correlation patterns within and between modules.

To better understand species module configuration patterns, we examined whether small mammal species inside each module were closely related phylogenetically to each other than to species in other modules. To achieve this, we calculated phylogenetic pairwise distances using cophenetic distance, comparing species pairs within the same module and those from different modules. To determine if the difference between these groups was statistically significant, we conducted a linear model with permutation tests through the "lmPerm" R package (Wheeler and Torchiano 2016).

3 | Results

3.1 | Centrality and Modularity in Small Mammal-Parasite Associations

Among the 52 host species, 16 had no registry of more than one parasite association in our database. As both betweenness and degree centralities were highly correlated, we used betweenness to classify species between central and non-central hosts (Figure S3). Among the 36 species linked to multiple parasites, 31 had centrality values above zero, ranging from 0.76 to 4246 (mean: 520.38, median 60.4). This variance may reflect differences in small mammals' competence to transmit distinct parasites to distinct hosts. We used a centrality threshold of 68 to categorize small mammals into central and non-central hosts, corresponding to the 55% quantile of centrality values. Sixteen species were classified as central (Table S4).

The BAF metanetwork was significantly modular (modularity index: 0.428, p-value: 0.01), resulting in six groups of species with stronger parasite interconnections compared to other groups. Across the 10 iterations of the modularity analysis conducted, seven consistently showed the same species configuration. An additional seventh group emerged, comprising small mammals with no registry of parasite association. Modularity clustering patterns were linked to species co-occurrence and served as a proxy for assessing parasite sharing among hosts. Further information about host and parasite module formation and their centrality values is available in Tables S4 and S5.

3.2 | HMSC Model Performance

The best-performing HMSC spatial model included seven landscape covariates and two species traits for explaining small mammal distribution. Included landscape covariates were mean elevation, percentage of native forest, agriculture, pasture, undefined farming, number of native forest patches, and Landscape Shannon's diversity. The ratio between caudal and body length and the period of activity (diurnal, nocturnal or cathemeral) were the selected traits. The model had strong explanatory power (AUC = 0.91, Tjur's $R^2 = 0.29$) and robust predictive power (AUC = 0.79, Tjur's $R^2 = 0.20$). Random effects explained 13.3% of species distribution variation. Native forest and farming areas (agriculture, pasture, and undefined farming) explained 27.9% and 29.6% of species distribution variation, respectively (Figure 2). The model convergence analyses are available in Figure S2.

Traits explained 22% of species variation in response to the landscape. Among landscape covariates, agriculture and pasture had the highest variation explained by species traits (36 and 33%), followed by Landscape diversity (31%). Regarding phylogeny, we found minimal evidence of a phylogenetic signal in species' responses to landscape covariates; with only 2.5% of species distribution showing a 19% phylogenetic explanation.

3.3 | The Occurrence Probability of Small Mammals in the Atlantic Forest

Of the 52 small mammal species included in the HMSC model, 32 were positively related to native forest areas, and 11 species were negatively related. Conversely, 17 species were related positively to farming areas (agriculture, undefined farming, and pasture), and 25 were negatively related. Only 13 species were positively related to Landscape diversity, and 28 were negatively related. The number of native forest patches was positively correlated with 14 species, while 23 had negative relationships. Finally, 34 species were positively related to mean landscape elevation, and 10 had a negative relationship. These results were based on a 0.8 posterior probability confidence (Table S6). The probability of occurrence of each species by landscape covariate metrics is in Figures S6–S10.

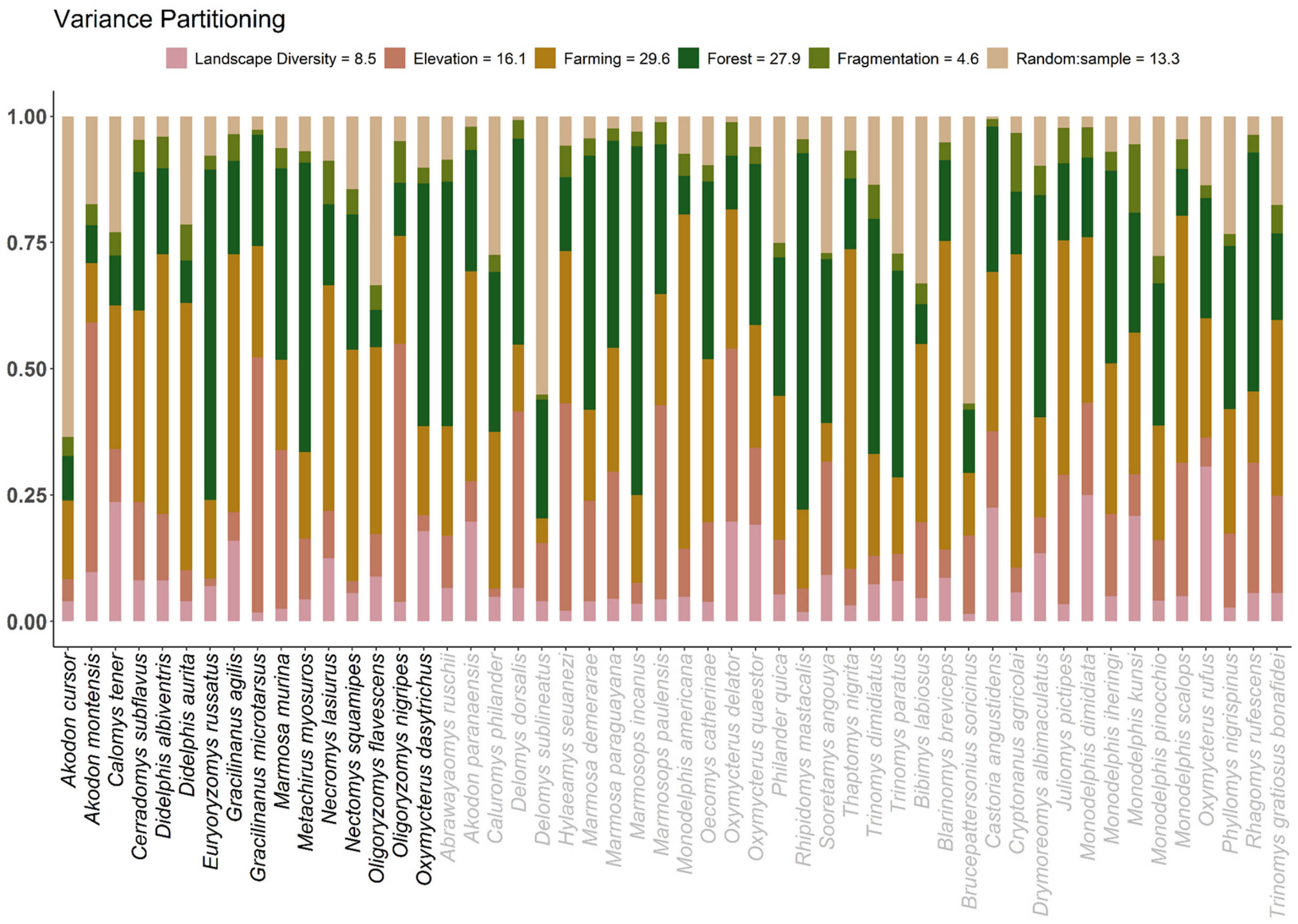

FIGURE 2 | Variation partition of each landscape covariate explanation for small mammals' occurrence in the Atlantic Forest The *x*-axis shows small mammal species, where black denotes central hosts, grey represents non-central hosts and species without a parasite association registry. The *Y*-axis shows the percentage of explanation. Each color corresponds to a specific landscape covariate, as indicated in the legend: Light pink = Landscape diversity; Coral = Elevation; Brownish orange = Farming; Green = Forest; Light green = Fragmentation; Light brown = Random (spatial). The values described in the legend show the mean rate of explanation for each covariate.

Although sample size accounted for a large part of the variance in GAM analysis, summarizing the occurrence probabilities in each landscape covariate variation by host centrality categorization, and species with no parasite registries revealed significant patterns. Central hosts showed significantly higher occurrence probabilities in landscapes with higher mean elevation, amount of farming areas, and number of forest patches (Figure 31B–D, Table 1). Non-central hosts tended to occur in landscapes with a higher proportion of forests, besides higher mean elevations (Figure 31A,B, Table 1), and decrease their occurrence probability with the higher number of forest patches and landscape diversity (Figure 31D,E, Table 1). Small mammals with no parasite association recorded in the Cruz et al. (2023) dataset increased their occurrence probability with increasing forest, mean elevation, amount of farming areas and number of forest patches (Figure 31A–D, Table 1), although they tended to present a relatively lower probability for all landscape predictions (Figure 32A–E, Table 1). GAM results indicated significant differences among non-central and central hosts probability of occurrence concerning forest and mean elevation predictions (Figure 32A,B, Table 1).

3.4 | Co-Occurrence of Small Mammals as a Function of Host–Parasite Modularity Association

The small mammal co-occurrence matrix was obtained from the HMSC model and shows expected co-occurrence patterns based on the model's spatial structure (random factor). By analyzing species mean co-occurrence within modularity clustering (Figure 4), the results showed that within the same module, species share more parasites than with species in different modules. Surprisingly, our results revealed that not all species have significantly high co-occurrence correlation within or between modules. Examining the correlation between the modules (Figure 4), it is evident that the fourth and sixth modules exhibit negative or weak correlations with all other modules, including themselves. Species with no registry of parasite associations had a positive correlation with only the second and third modules and a weak or negative correlation with the species in the other modules.

To better understand this pattern, we analyzed the phylogenetic proximity of species within module clusters. As expected, small mammals had higher phylogenetic proximity to species inside their modules compared to species in other modules ($F=48.37$, d.f. $=6$, $p<0.0001$; Figure S11). Notably, the first and most of the fourth modules (except for two rodent species) comprised marsupial species, whereas other modules consisted of rodent species.

Considering zoonotic parasites, all modules contained reservoir hosts for zoonotic pathogens. For example, reservoir species for Orthohantavirus were present in the second, third, and fifth modules. Species transmitting *Borrelia* spp., rabies viruses, and *Leishmania* spp. (causing visceral leishmaniasis) were mainly in the first module, whereas those that are reservoirs for cutaneous leishmaniasis, schistosomiasis, and spotted fever were in the sixth module. The fourth module encompassed hosts of infectious agents causing toxoplasmosis and leptospirosis, some shared with the first module. Detailed information is available in Table S5.

4 | Discussion

Our results showed that agricultural and deforestation activities favor the occurrence of species acting as central hosts for parasite transmission within the small mammal community of the BAF. Conversely, non-central species showed an increased occurrence probability in areas with a higher mean elevation and forest areas. Species with no registry of parasite associations showed a generally lower probability of occurrence, highlighting the need for increasing studies on these rare and less abundant species. These findings support other studies on spillover risk, demonstrating central hosts as potential key species for parasite transmission to humans as they share a high diversity of parasites with other species and occupy anthropogenic areas, favoring contact with human populations (Gibb et al. 2020; Gómez, Nunn, and Verdú 2013; Wardeh, Sharkey, and Baylis 2020). The network module clustering shows that small mammals sharing more parasites are more closely related phylogenetically, although they do not always co-occur locally. The lack of strong spatial correlation within modules and the negative spatial correlation between different modules shows the importance of considering host species co-occurrences when estimating spillover risk to avoid overestimating spillover probability. This is especially significant when compiling parasite–host relationships from secondary data, as these often lack precise geolocation information, requiring researchers to set a larger spatial scale for local communities.

Our findings highlighted the predominant influence of landscape covariates on small mammal occurrence probability, with limited impact from species traits and phylogeny. However, species traits may interact with environmental conditions and other factors since they are associated with the species' ability to explore and use different habitats (Hannibal et al. 2020). Overall, natural habitats favor specific small mammal species, whereas forest fragmentation and expansion of farming areas positively affect others (e.g., Paise, Vieira, and Prado 2020). Understanding these relationships is essential for informed conservation decisions integrated with public health policies, especially in the BAF, a biodiversity hotspot (*sensu* Mittermeier et al. 2011) characterized by several land uses promoting wildlife-human contact (e.g., agriculture).

The percentage of agricultural areas significantly influenced the occurrence and distribution of small mammals and was positively related to central hosts. Different crops may promote different small mammal diversity due to varying resource availability (Heroldová et al. 2007). Intensive agroecosystems can markedly impact small mammal richness and abundance (Fischer and Schröder 2014), whereas complex and sustainable landscapes favor richness (Serafini, Priotto, and Gomez 2019). Our findings support these findings, as non-central hosts had a significant positive relationship with native forest areas. Thus, integrating larger, interconnected forest patches into diverse crop productions (e.g., agroforestry) can sustain diverse and equitable communities (Serafini, Priotto, and Gomez 2019; Perrin

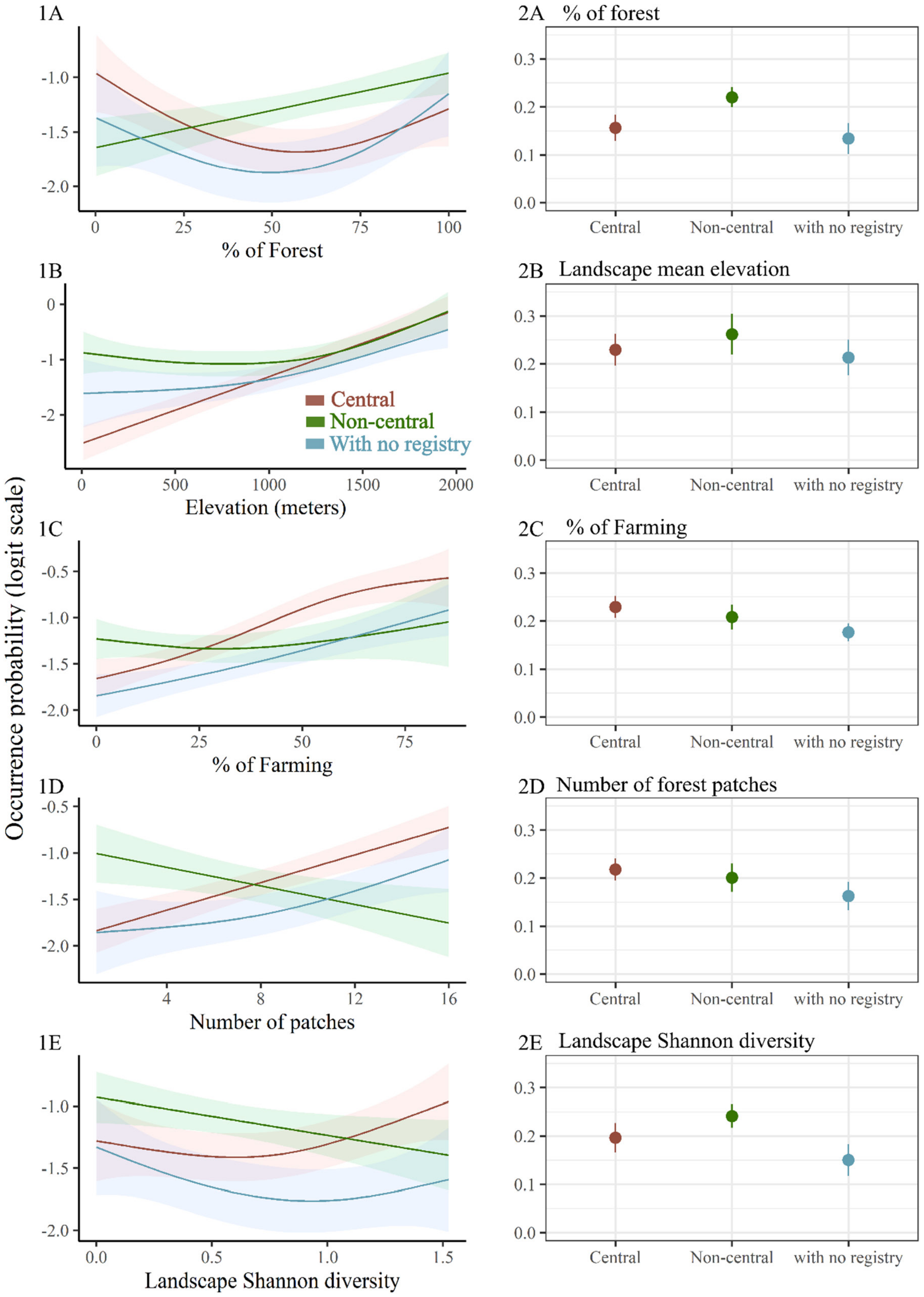

FIGURE 3 | Legend on next page.

FIGURE 3 | Marginal effects of the relationship between the probability of small mammal occurrence based and specific landscape metrics variation. Graphics on the right relate to the probability of occurrence (response scale) and species centrality classification, whereas those on the left relate the probability of occurrence on a logit link scale and the factor smooth interaction of the variation of the metric and the host centrality. Small mammal species are grouped as central hosts, non-central hosts, and species with no registry of parasite association. (1A and 2A) % of Forest variation = percentage of forest areas; (1B and 2B) Elevation variation = mean elevation values of the landscape. (1C and 2C) % of Farming variation = probability of occurrence based on the percentage of agricultural areas, mosaic of agriculture and pasture uses, and percentage of pasture areas; (1D and 2D) Number of forest patches variation; (1E and 2E) Landscape diversity variation = Landscape Shannon diversity index.

TABLE 1 | Generalized Additive Models (GAM) summary results showing the differences in the probability of occurrence among small mammal species classified as central hosts, non-central hosts, and those with no registry of associated parasites and the landscape predicted variation as a function of host centrality s(Variation: Centrality).

Response variable	Predictors	Coefficient	SE	EDF	Chi-sq	*p*-value	DE
Probability of occurring due to % of Forest	Intercept	−1.91	0.09			0.00	0.55
	Central spp.—Non-central spp.	0.20	0.11			0.06	
	Central Spp.—Spp. with no registry	−0.15	0.12			0.21	
	s(Variation: Central)			2.61	13.67	< 0.01	
	s(Variation: Non-Central)			1.00	12.15	< 0.001	
	s(Variation: With no registry)			2.45	8.89	0.03	
	s(number of studies)			0.99	297.97	< 0.001	
Probability of occurring due to Landscape elevation	Intercept	−1.57	0.12			< 0.001	0.45
	Central spp.—Non-central spp.	0.40	0.13			< 0.01	
	Central Spp.—Spp. with no registry	0.04	0.14			0.78	
	s(Variation: Central)			1.00	92.95	< 0.001	
	s(Variation: Non-Central)			2.59	20.69	< 0.001	
	s(Variation: With no registry)			1.92	22.76	< 0.001	
	s(number of studies)			0.99	145.39	< 0.001	
Probability of occurring due to % of Farming	Intercept	−1.56	0.00		0.46	< 0.001	0.46
	Central spp.—Non-central spp.	−0.07	0.41		—	0.41	
	Central Spp.—Spp. with no registry	−0.32	0.00		—	< 0.001	
	s(Variation: Central)			2.38	69.09	< 0.001	
	s(Variation: Non-Central)			1.74	1.76	0.46	
	s(Variation: With no registry)			1.33	24.95	< 0.001	
	s(number of studies)			0.99	302.69	< 0.001	
Probability of occurring due to Number of forest patches	Intercept	−1.88	0.09		0.70	< 0.001	0.70
	Central spp.—Non-central spp.	−0.10	0.12		—	0.40	
	Central Spp.—Spp. with no registry	−0.29	0.12		—	0.02	
	s(Variation: Central)			1.00	32.92	< 0.001	
	s(Variation: Non-Central)			1.00	6.50	0.01	
	s(Variation: With no registry)			1.58	8.79	< 0.01	
	s(number of studies)			0.99	408.00	< 0.001	

(Continues)

TABLE 1 | (Continued)

Response variable	Predictors	Coefficient	SE	EDF	Chi-sq	*p*-value	DE
Probability of occurring due to Landscape Shannon diversity	Intercept	−1.68	0.09			< 0.001	0.48
	Central spp.—Non-central spp.	0.14	0.11			0.19	
	Central Spp.—Spp. with no registry	−0.33	0.13			< 0.01	
	s(Variation: Central)			2.05	6.36	0.07	
	s(Variation: Non-Central)			1.00	4.97	0.02	
	s(Variation: With no registry)			1.82	3.12	0.23	
	s(number of studies)			0.99	201.21	< 0.001	

Note: The number of studies was fitted as a smooth term with a random factor basis.
Abbreviations: Chi-sq = chi-square statistic for the smooth term; DE = deviation explained; EDF = estimated degrees of freedom for the smooth term; SE = standard error.

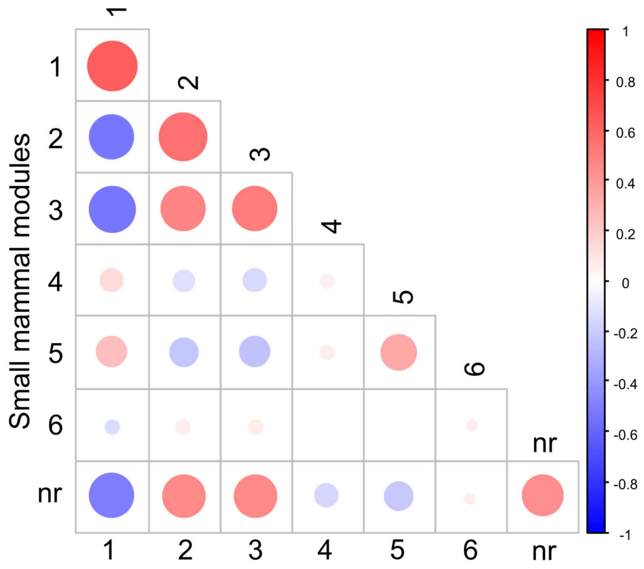

FIGURE 4 | Mean co-occurrence pattern of small mammals based on species modules calculated by the modularity metric. The x-axis represents each one of the six small mammal modules computed in the host–parasite association metanetwork, and the nr module represents the small mammal species with no registry of parasite association. In this context, species within the same module share more parasites with each other than with species in different modules. Associations depicted in red indicate a higher probability of co-occurrence, signifying a positive relationship. Associations in blue indicate spatially negative relationships, meaning that species in these modules tend not to co-occur.

et al. 2023). Balancing agricultural production and native ecosystem conservation is a complex challenge.

In our model, species assemblages varied based on elevation, with both central and non-central species increasing their occurrence probability in higher elevations. The BAF comprises native forest patches stretching from coastal regions to mountains and spans elevations from sea level to over 2000 m (Ferreguetti et al. 2021). Mid-elevation areas have higher small mammal diversity, while high-elevation regions may harbor more endemism (Sakane, Percequillo, and Setz 2019; Ferreguetti et al. 2021). Most remaining natural areas in the BAF are in the mountains or comprise secondary vegetation, with a notable proportion outside conservation areas (Rezende et al. 2018). Therefore, we should expect a higher proportion of species that are not disturbed-adapted to have a higher probability of occurrence at higher elevations, representing the more conserved regions in the BAF.

Although we demonstrate that central host species are by lower percentages of native forest, their occurrence probability was highly variable across all metrics. Central hosts were mainly generalist ones, which tolerate different conditions and types of habitats (Püttker et al. 2020). Their heterogeneous response to landscape metrics shows how idiosyncratic host–parasite interactions are (Salkeld, Padgett, and Jones 2013). Different hosts harbor distinct parasites, and the ecological processes related to their transmission and infection will depend on the host traits, parasite transmission strategies, their life cycle, and the local environment (Marcogliese 2004). The occurrence of central host species in all landscapes indicates a potential for host–parasite interactions (including spillover) independent of landscape features (Gómez, Nunn, and Verdú 2013). However, forest loss may favor only certain central species, increasing their abundance and potentially reducing host diversity while increasing the prevalence of specific parasites (Gómez, Nunn, and Verdú 2013). The potential abundance increases of certain parasite faunas and the dominance of select central hosts may hold an increased risk of spillover to humans.

Additionally, we emphasize the lack of information regarding the parasite fauna of rare and less abundant small mammal species (those without recorded parasite associations). The number of studies was strongly correlated to host centrality, accounting for a large part of the variation. While we recognize that more extensively studied hosts are typically of greater public health importance, this knowledge gap may obscure interactions with novel pathogens that have zoonotic potential. Consequently, understanding the probabilities of species co-occurrence is crucial for more accurately predicting parasite transmission dynamics in these areas and, thus, the spillover risk to wildlife and human populations. While exercising caution in interpreting co-occurrences as a proxy for direct interactions, their integration enhances prediction accuracy when estimating spillover risk at a broader scale (Blanchet, Cazelles, and Gravel 2020; Dormann et al. 2018). The spatial structure of host communities is a key factor for predicting parasite transmission (Muylaert et al. 2019), also evident in our study. We identified specific host groups that are unlikely to share parasites, along with a non-uniform distribution of zoonotic parasites across metanetwork modules. By discerning modules with higher co-occurrence probabilities, we identified zoonotic parasites with a higher probability of spilling over species belonging to those modules. For example, hosts with no registry of parasite association are more prone to be infected by parasites presented in the second and third modules. With the understanding that hosts tend to share parasites with phylogenetically related species and in closer spatial proximity, we may predict the unknown parasite fauna of these hosts (Romano et al. 2016). In fragmented landscapes, it is crucial to identify host pairs more likely to exchange parasites and what parasites they harbor (Perrin et al. 2023).

4.1 | Final Remarks and Future Directions

Identifying central hosts and species prone to parasite sharing is crucial for predicting spillover risk. Prioritizing these species enhances surveillance and boosts public health readiness. Analyzing landscape covariates and small mammal occurrence probabilities underscore the pivotal role of habitat preservation in both biodiversity conservation and disease risk reduction. The positive relationship of non-central species to native forest and elevation areas (most conserved ones) highlights the importance of increasing forest patch connectivity. Conversely, the association of central host species with fragmentation and farming areas emphasizes the need for a balanced approach to land use that harmonizes agricultural production, ecosystem conservation, and public health.

Comprehending the geographic distribution of host–parasite metanetwork modules facilitates proactive disease outbreak anticipation, enabling tailored and efficient surveillance and intervention strategies. This approach optimizes resource allocation and response efforts for effective disease control. Additionally, our results have relevance for conservation strategies in the BAF, emphasizing the importance of monitoring programs focused on diagnosing parasites and their phylogenetic diversity, using central hosts related to each module as indicators of parasite diversity.

However, our study has limitations. While our data set is spatially accurate for predicting co-occurrence, our sampling points were mostly aggregated in the southeast part of the BAF, limiting our ability to predict biome diversity distribution. Additionally, future studies should examine the temporal effects on species assemblages. The literature-based network of all possible associations used to measure host centrality and module configuration offers insights into host–parasite interaction patterns but is highly dependent on the number of studies and lacks precision at a local scale. Although we used the finest parasite scale in the data set, high taxa records may inflate the sharing of interactions. Still, our study provides valuable insights into important processes shaping small mammal distribution and its relationship to parasite sharing and spillover risk. Despite the limitations, we built a robust model with high predictive and explanatory power.

Moving forward, future research should focus on the fine-scale habitat preferences of small mammal species and the presence of zoonotic pathogens within these populations. We strongly advise intensifying efforts to collect parasite samples from small mammal species lacking parasite infection data, diminishing the impact of sampling efforts in the analysis of their interactions. Also, increasing parasite data information on rare and less abundant species may support our predictions that parasite spillover is related to small mammal co-occurrence. Additionally, we support monitoring programs including the interactions among small mammals and parasites and potential changes due to forest area loss and connectivity. Studies investigating the occurrence of zoonotic pathogens in small mammal populations within these landscapes can further elucidate the potential risks to human health. Such investigations will refine our ability to design targeted conservation and public health strategies, ensuring a resilient coexistence between humans and the natural environment. Finally, this study emphasizes the interconnectedness of biodiversity conservation and public health, calling for integrated approaches to address zoonotic diseases in an era of environmental change.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code are available from the Figshare Repository: https://doi.org/10.6084/m9.figshare.24435034.v3.

References

Andreazzi, C. S., L. A. Martinez-Vaquero, G. R. Winck, et al. 2023. “Vegetation Cover and Biodiversity Reduce Parasite Infection in Wild Hosts Across Ecological Levels and Scales.” *Ecography* 5: e06579. https://doi.org/10.1111/ecog.06579.

Araujo, S. B. L., M. P. Braga, D. R. Brooks, et al. 2015. “Understanding Host-Switching by Ecological Fitting.” *PLoS One* 10: e0139225. https://doi.org/10.1371/journal.pone.0139225.

Arel-Bundock, V. 2024. “_marginaleffects: Predictions, Comparisons, Slopes, Marginal Means, and Hypothesis Tests_.” R Package Version 0.19.0. https://CRAN.R-project.org/package=marginaleffects.

Barber, M. J. 2007. “Modularity and Community Detection in Bipartite Networks.” *Physical Review E* 76, no. 6: 066102.

Bascompte, J., P. Jordano, C. J. Melián, and J. M. Olesen. 2003. "The Nested Assembly of Plant–Animal Mutualistic Networks." *Proceedings of the National Academy of Sciences* 100, no. 16: 9383–9387. https://doi.org/10.1073/pnas.1633576100.

Blanchet, F. G., K. Cazelles, and D. Gravel. 2020. "Co-Occurrence Is Not Evidence of Ecological Interactions." *Ecology Letters* 23, no. 7: 1050–1063. https://doi.org/10.1111/ele.13525.

Bovendorp, R. S., F. T. Brum, R. A. McCleery, et al. 2019. "Defaunation and Fragmentation Erode Small Mammal Diversity Dimensions in Tropical Forests." *Ecography* 42, no. 1: 23–35. https://doi.org/10.1111/ecog.03504.

Cardoso, T. S., S. F. Costa-Neto, C. Braga, et al. 2020. "Helminth Metacommunity of Small Mammals in a Brazilian Reserve: The Contribution of Environmental Variables, Host Attributes and Spatial Variables in Parasite Species Abundance." *Community Ecology* 21, no. 2: 159–170. https://doi.org/10.1007/s42974-020-00016-5.

Costa, A. P. L., J. Bascompte, and A. Andrian Padial. 2023. "Modularity in Host-Parasite Mixed Networks: Interaction Configuration Shifts Based on Human Perturbation and Parasitism Form." *International Journal for Parasitology* 10: 585–594. https://doi.org/10.1016/j.ijpara.2023.04.004.

Cruz, G. L. T., G. R. Winck, P. S. D'Andrea, E. Krempser, M. M. Vidal, and C. S. Andreazzi. 2023. "Integrating Databases for Spatial Analysis of Parasite-Host Associations and the Novel Brazilian Dataset." *Scientific Data* 10, no. 1: 757.

Csardi, G., and T. Nepusz. 2006. "The Igraph Software Package for Complex Network Research." _InterJournal_, *Complex Systems. https://igraph.org.

Dallas, T. A., B. A. Han, C. L. Nunn, A. W. Park, P. R. Stephens, and J. M. Drake. 2019. "Host Traits Associated With Species Roles in Parasite Sharing Networks." *Oikos* 128, no. 1: 23–32. https://doi.org/10.1111/oik.05602.

Dallas, T. A., A.-L. Laine, and O. Ovaskainen. 2019. "Detecting Parasite Associations Within Multi-Species Host and Parasite Communities." *Proceedings of the Royal Society B: Biological Sciences* 286: 1471–2954. https://doi.org/10.1098/rspb.2019.1109.

D'Andrea, P. S., B. R. Teixeira, J. Gonçalves-Oliveira, et al. 2021. "The Mammal Collection of the Laboratory of Biology and Parasitology of Reservoir Wild Mammals–Oswaldo Cruz Foundation." *Brazilian Journal of Mammalogy* e90: e90202119.

De Oliveira, R., A. Guterres, J. Fernandes, P. D'Andrea, C. Bonvicino, and E. De Lemos. 2014. "Hantavirus Reservoirs: Current Status With an Emphasis on Data From Brazil." *Viruses* 6, no. 5: 1929–1973. https://doi.org/10.3390/v6051929.

Dormann, C. F., M. Bobrowski, D. M. Dehling, et al. 2018. "Biotic Interactions in Species Distribution Modelling: 10 Questions to Guide Interpretation and Avoid False Conclusions." *Global Ecology and Biogeography* 27, no. 9: 1004–1016. https://doi.org/10.1111/geb.12759.

Ferreguetti, Á. C., M. B. de Menezes, J. Pereira-Ribeiro, C. F. D. Rocha, and H. G. Bergallo. 2021. "Influence of Altitude and Climate on Species Richness and Endemism: A Study Case With Non-volant Small Mammals in the Atlantic Forest, Brazil." *Austral Ecology* 46, no. 4: 603–612. https://doi.org/10.1111/aec.13010.

Fischer, C., and B. Schröder. 2014. "Predicting Spatial and Temporal Habitat Use of Rodents in a Highly Intensive Agricultural Area." *Agriculture, Ecosystems & Environment* 189: 145–153. https://doi.org/10.1016/j.agee.2014.03.039.

Gibb, R., D. W. Redding, K. Q. Chin, et al. 2020. "Zoonotic Host Diversity Increases in Human-Dominated Ecosystems." *Nature* 584, no. 7821: 398–402. https://doi.org/10.1038/s41586-020-2562-8.

Gómez, J. M., C. L. Nunn, and M. Verdú. 2013. "Centrality in Primate–Parasite Networks Reveals the Potential for the Transmission of Emerging Infectious Diseases to Humans." *Proceedings of the National Academy of Sciences* 110, no. 19: 7738–7741. https://doi.org/10.1073/pnas.1220716110.

Gonçalves-Oliveira, J., T. Rozental, A. Guterres, et al. 2020. "Investigation of *Bartonella* Spp. in Brazilian Mammals With Emphasis on Rodents and Bats From the Atlantic Forest." *International Journal for Parasitology: Parasites and Wildlife* 13: 80–89. https://doi.org/10.1016/j.ijppaw.2020.07.004.

Hannibal, W., N. L. D. Cunha, V. V. Figueiredo, F. B. Teresa, and V. L. Ferreira. 2020. "Traits Reveal How Habitat-Quality Gradients Structure Small Mammal Communities in a Fragmented Tropical Landscape." *Austral Ecology* 45, no. 1: 79–88. https://doi.org/10.1111/aec.12831.

Heroldová, M., J. Bryja, J. Zejda, and E. Tkadlec. 2007. "Structure and Diversity of Small Mammal Communities in Agriculture Landscape." *Agriculture, Ecosystems & Environment* 120, no. 2: 206–210. https://doi.org/10.1016/j.agee.2006.09.007.

Hesselbarth, M. H. K., M. Sciaini, K. A. With, K. Wiegand, and J. Nowosad. 2019. "Landscapemetrics: An Open-Source R Tool to Calculate Landscape Metrics." *Ecography* 42: 1648–1657.

Jordán, F., W. Liu, and A. J. Davis. 2006. "Topological Keystone Species: Measures of Positional Importance in Food Webs." *Oikos* 112, no. 3: 535–546. https://doi.org/10.1111/j.0030-1299.2006.13724.x.

Kamiya, T., N. Mideo, S. Alizon, and R. Poulin. 2014. "Host Diversity Drives Parasite Diversity: Meta-Analytical Insights Into Patterns and Causal Mechanisms." *Ecography* 37, no. 7: 689–697. https://doi.org/10.1111/j.1600-0587.2013.00571.x.

Kearse, M., R. Moir, A. Wilson, et al. 2012. "Geneious Basic: An Integrated and Extendable Desktop Software Platform for the Organization and Analysis of Sequence Data." *Bioinformatics* 28, no. 12: 1647–1649. https://doi.org/10.1093/bioinformatics/bts199.

Keesing, F., and R. S. Ostfeld. 2021. "Impacts of Biodiversity and Biodiversity Loss on Zoonotic Diseases." *Proceedings of the National Academy of Sciences* 118, no. 17: e2023540118. https://doi.org/10.1073/pnas.2023540118.

Marcogliese, D. J. 2004. "Parasites: Small Players With Crucial Roles in the Ecological Theater." *EcoHealth* 1, no. 2: 151–164. https://doi.org/10.1007/s10393-004-0028-3.

Marjakangas, E., N. Abrego, V. Grøtan, et al. 2020. "Fragmented Tropical Forests Lose Mutualistic Plant–Animal Interactions." *Diversity and Distributions* 26, no. 2: 154–168. https://doi.org/10.1111/ddi.13010.

Marquitti, F. M. D., P. R. Guimarães, M. M. Pires, and L. F. Bittencourt. 2014. "MODULAR: Software for the Autonomous Computation of Modularity in Large Network Sets." *Ecography* 37, no. 3: 221–224. https://doi.org/10.1111/j.1600-0587.2013.00506.x.

McKee, C. D., A. I. Krawczyk, A. D. Sándor, et al. 2019. "Host Phylogeny, Geographic Overlap, and Roost Sharing Shape Parasite Communities in European Bats." *Frontiers in Ecology and Evolution* 7, no. 69: 1–21. https://doi.org/10.3389/fevo.2019.00069.

Mittermeier, R. A., W. R. Turner, F. W. Larsen, T. M. Brooks, and C. Gascon. 2011. "Global Biodiversity Conservation: The Critical Role of Hotspots." In *Biodiversity Hotspots*, edited by F. Zachos and J. Habel. Berlin, Heidelberg: Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-20992-5_1.

Muylaert, R. L., R. S. Bovendorp, G. Sabino-Santos, et al. 2019. "Hantavirus Host Assemblages and Human Disease in the Atlantic Forest." *PLoS Neglected Tropical Diseases* 13, no. 8: 1–19. https://doi.org/10.1371/journal.pntd.0007655.

Newman, M. E. J., and M. Girvan. 2004. "Finding and Evaluating Community Structure in Networks." *Physical Review E* 69, no. 2: 026113.

Ovaskainen, O., and N. Abrego. 2020. *Joint Species Distribution Modelling*. (Cambridge, UK: Cambridge University Press, 2020). https://doi.org/10.1017/9781108591720.

Paise, G., E. M. Vieira, and P. I. Prado. 2020. "Small Mammals Respond to Extreme Habitat Fragmentation in the Brazilian Atlantic Forest According to the Landscape Continuum Model." *Mammal Research* 65, no. 2: 309–322. https://doi.org/10.1007/s13364-019-00464-z.

Perrin, A., A. Khimoun, A. Ollivier, et al. 2023. "Habitat Fragmentation Matters More Than Habitat Loss: The Case of Host–Parasite Interactions." *Molecular Ecology* 32, no. 4: 951–969. https://doi.org/10.1111/mec.16807.

Püttker, T., R. Crouzeilles, M. Almeida-Gomes, et al. 2020. "Indirect Effects of Habitat Loss via Habitat Fragmentation: A Cross-Taxa Analysis of Forest-Dependent Species." *Biological Conservation* 241: 108368. https://doi.org/10.1016/j.biocon.2019.108368.

R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Rezende, C. L., F. R. Scarano, E. D. Assad, et al. 2018. "From Hotspot to Hopespot: An Opportunity for the Brazilian Atlantic Forest." *Perspectives in Ecology and Conservation* 16, no. 4: 208–214. https://doi.org/10.1016/j.pecon.2018.10.002.

Romano, V., J. Duboscq, C. Sarabian, E. Thomas, C. Sueur, and A. J. J. MacIntosh. 2016. "Modeling Infection Transmission in Primate Networks to Predict Centrality-Based Risk: Individual Centrality and Infection Flow." *American Journal of Primatology* 78, no. 7: 767–779. https://doi.org/10.1002/ajp.22542.

Rushmore, J., D. Bisanzio, and T. R. Gillespie. 2017. "Making New Connections: Insights From Primate–Parasite Networks." *Trends in Parasitology* 33, no. 7: 547–560. https://doi.org/10.1016/j.pt.2017.01.013.

Sakane, K. K., A. R. Percequillo, and E. Z. F. Setz. 2019. "Community of Small Mammals Along an Elevational Gradient in Biological Reserve of Serra Do Japi, Municipality of Jundiaí- SP, Brazil." *Austral Ecology* 44, no. 7: 1236–1244. https://doi.org/10.1111/aec.12801.

Salkeld, D. J., K. A. Padgett, and J. H. Jones. 2013. "A Meta-Analysis Suggesting That the Relationship Between Biodiversity and Risk of Zoonotic Pathogen Transmission Is Idiosyncratic." *Ecology Letters* 16, no. 5: 679–686. https://doi.org/10.1111/ele.12101.

Scarano, F. R., and P. Ceotto. 2015. "Brazilian Atlantic Forest: Impact, Vulnerability, and Adaptation to Climate Change." *Biodiversity and Conservation* 24, no. 9: 2319–2331. https://doi.org/10.1007/s10531-015-0972-y.

Sciaini, M., M. Fritsch, C. Scherer, and C. E. Simpkins. 2018. "NLMR and Landscapetools: An Integrated Environment for Simulating and Modifying Neutral Landscape Models in R." *Methods in Ecology and Evolution* 9: 2240–2248.

Serafini, V. N., J. W. Priotto, and M. D. Gomez. 2019. "Effects of Agroecosystem Landscape Complexity on Small Mammals: A Multi-Species Approach at Different Spatial Scales." *Landscape Ecology* 34, no. 5: 1117–1129. https://doi.org/10.1007/s10980-019-00825-8.

Souza, C. M., J. Z. Shimbo, M. R. Rosa, et al. 2020. "Reconstructing Three Decades of Land Use and Land Cover Changes in Brazilian Biomes With Landsat Archive and Earth Engine." *Remote Sensing* 12, no. 17: 1–27. https://doi.org/10.3390/rs12172735.

Stephens, P. R., S. Altizer, V. O. Ezenwa, et al. 2019. "Parasite Sharing in Wild Ungulates and Their Predators: Effects of Phylogeny, Range Overlap, and Trophic Links." *Journal of Animal Ecology* 88, no. 7: 1017–1028. https://doi.org/10.1111/1365-2656.12987.

Tamura, K., G. Stecher, and S. Kumar. 2021. "MEGA11: Molecular Evolutionary Genetics Analysis Version 11." *Molecular Biology and Evolution* 38, no. 7: 3022–3027. https://doi.org/10.1093/molbev/msab120.

Tikhonov, G., Ø. H. Opedal, N. Abrego, et al. 2020. "Joint Species Distribution Modelling With the -Package Hmsc." *Methods in Ecology and Evolution* 11, no. 3: 442–447. https://doi.org/10.1111/2041-210X.13345.

Tikhonov, G., O. Ovaskainen, J. Oksanen, M. de Jonge, O. Opedal, and T. Dallas. 2023. "_Hmsc: Hierarchical Model of Species Communities_." R Package Version 3.0-14. https://www.helsinki.fi/en/researchgroups/statistical-ecology/software/hmsc.

Wardeh, M., K. J. Sharkey, and M. Baylis. 2020. "Integration of Shared-Pathogen Networks and Machine Learning Reveals the Key Aspects of Zoonoses and Predicts Mammalian Reservoirs." *Proceedings of the Royal Society B: Biological Sciences* 287: 20192882. https://doi.org/10.1098/rspb.2019.2882.

Wheeler, B., and M. Torchiano. 2016. "_lmPerm: Permutation Tests for Linear Models_." R Package Version 2.1.0. https://CRAN.R-project.org/package=lmPerm.

Wood, S. N. 2011. "Fast Stable Restricted Maximum Likelihood and Marginal Likelihood Estimation of Semiparametric Generalized Linear Models." *Journal of the Royal Statistical Society (B)* 73, no. 1: 3–36.

Young, H. S., D. J. McCauley, M. Galetti, and R. Dirzo. 2016. "Patterns, Causes, and Consequences of Anthropocene Defaunation." *Annual Review of Ecology, Evolution, and Systematics* 47, no. 1: 333–358. https://doi.org/10.1146/annurev-ecolsys-112414-054142.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.