Title: Moving from the Dilution Effect to Dilution Landscapes: Effects of Natural Vegetation Cover and Fragmentation on Host-parasite Eco-evolutionary Dynamics

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ABSTRACT

The conversion and fragmentation of natural landscapes are key drivers of biodiversity loss and the erosion of ecosystem services, including disease regulation. Although habitat degradation is linked to higher zoonotic disease risk, the mechanisms by which landscape structure shapes host-parasite eco-evolutionary dynamics remain poorly understood. Here, we combine a spatially explicit metacommunity and coevolutionary model with empirical host-parasite interactions data to examine how landscape cover and configuration shape ecological and coevolutionary outcomes. We find that (1) landscapes with a higher amount of natural cover and lower fragmentation level dilute the distribution of parasites throughout the host community and lead to more homogenous coevolutionary trajectories; (2) highly degraded, fragmented landscapes constrains host-parasite dispersal, promoting smaller, more heterogeneous interaction networks with divergent coevolutionary dynamics, which rise the risk of new parasite variants emerging; and (3) loss of habitat reduces host diversity, impacting parasite host range. These results extend the dilution effect hypothesis by incorporating the structure of the interaction networks and the coevolutionary dynamics. Our findings suggest an increased risk of zoonotic transmission and strength of parasite-host interactions in a degraded landscape. Hence, conservation actions should focus on maintaining functional connectivity to mitigate the effect of landscape conversion on host-parasite dynamics and promote the disease regulation service of natural ecosystems.

Keywords: landscape conversion, zoonotic diseases, metacommunity model, ecological networks

INTRODUCTION

Ecological and evolutionary dynamics are tied together through the interplay of species interactions (Thompson, 1999, 2005). Species distribution affects the coevolutionary forces imposed by interspecific interactions, as varying dispersal opportunities create new community assemblies and drive divergent evolutionary paths (Urban et al., 2008). In turn, coevolution may influence community dynamics by altering local extinction rates and diversity patterns, ultimately affecting regional-scale processes (Fernandes et al., 2019). Species interactions act as pathways of evolutionary selection, driving genetic and phenotypic evolution within communities (Andreazzi et al., 2017; Guimarães et al., 2017). Changes in the landscape configuration, due to the loss and fragmentation of natural vegetation cover, may potentiate the eco-evolutionary feedback dynamics, generating divergence in phenotypic distribution patterns and consequently, in species interactions (Laine, 2009; Legrand et al., 2017). An open challenge is understanding which factors and landscape scenarios affect species eco-evolutionary dynamics, particularly of intricate and complex systems, such as host-parasite interactions (Hagen et al., 2012).

Understanding how rapidly changing natural landscapes affect host-parasite eco-evolutionary dynamics is crucial for managing disease spread, zoonosis spillover, and outbreaks (Deshpande et al., 2025; Penczykowski et al., 2016). Host-parasite interactions vary widely in selection forces and evolutionary potential (Gandon et al., 2008), with evolutionary and ecological changes taking place simultaneously (Castledine et al., 2020; Frickel et al., 2016; Pilosof et al., 2020). For instance, traits related to host immunological responses and parasite infection may determine the probability of successful interaction, which can change depending on the species diversity patterns and environmental selection forces (Andreazzi et al., 2017; Cosmo et al., 2023). In a broader spatial context, varying environmental pressures can create a mosaic of selection forces, driving a higher intensity of coevolution in some areas. Extinction events and genetic drift contribute to feedback loops characterised by arms race dynamics, where parasite evolution drives directional selection in hosts to resist parasitic effects. This, in turn, is amplified by landscape fragmentation (Gandon et al., 2008; Gawecka et al., 2022).

From an ecological perspective, habitat loss and fragmentation are key drivers of biodiversity decline, leading to changes in host-parasite dynamics and, consequently, in the regulation of infectious diseases (Guégan et al., 2020). The two main hypotheses concerning the role of biodiversity in these changes are the dilution and amplification effects. The dilution effect posits that higher species richness decreases the likelihood of infecting competent hosts, thereby reducing parasite prevalence and disease risk within the community (Keesing et al., 2006). An amplification occurs when a competent host increases its abundance in the area, thereby increasing the opportunity for infection and consequently its prevalence (Keesing et al., 2006; Keesing & Ostfeld, 2021b). To integrate these hypotheses with the evolutionary perspective, the coevolution effect proposes that habitat fragmentation isolates host-parasite interactions, resulting in genetic or phenotypic divergence among the fragments. This increases genetic variability across the landscape and the probability of new variants arising, with a higher transmissibility and virulence capacity, which results in higher infection risk in disturbed areas (Zohdy et al., 2019).

Although the coevolution hypothesis offers essential insights into disease emergence and zoonotic outbreaks, it has not been explored in a spatially explicit context: on a landscape scale where metacommunity dynamics shape species distributions. Besides, the loss of natural habitats and the level of fragmentation may have varied local effects on the dynamics of host-parasite interactions, changing their spatial eco-evolutionary outcomes. Here, we integrate a dataset of mammal-parasite interactions from the Brazilian Atlantic Forest—one of the most diverse yet degraded ecosystems globally (Cruz et al., 2023; Rezende et al., 2018) —with a spatially explicit eco-evolutionary metacommunity model. We investigate how various aspects of host-parasite eco-evolutionary dynamics respond to changes in landscape configuration, specifically in terms of the amount and fragmentation level of natural habitats. Specifically, we answer the following questions: (1) How does landscape configuration affect ecological and evolutionary outcomes behind host-parasite interactions? (2) What are the main spatial and ecological factors driving the ecological and evolutionary outcomes? We expect changes in local interaction patterns across different landscapes and eco-evolutionary trajectories, indicating aspects of the dilution and coevolution hypothesis. By elucidating the processes behind these outcomes, we shed light on the risk of zoonotic transmission and its relation to the management and conservation of natural landscapes.

METHODS

Host-parasite data organisation

We built a network of all possible associations between mammal species and their virus and bacterial parasites registered for the Atlantic Forest Biome and gathered in Cruz et al. (2023) dataset. Mammals from the Rodentia, Didelphimorphia, Primates, Cingulata, Carnivora, Pilosa, Perissodactyla, and Lagomorpha orders were included, summarising only wildlife mammal species. Viruses and Bacteria were filtered to account for their finest taxonomic level possible, including only species and serotypes records. The so-called metanetwork is represented by a binary matrix A_{ij}, where $A_{ij}=1$ indicates an interaction between a virus or bacteria i and a mammal species j.

We also gathered data on the frequency of occurrence of mammal species in forested areas. To achieve this, we utilised data on wildlife mammal occurrences in Brazil, provided by SALVE-ICMBio (Biodiversity Extinction Risk Assessment System). Occurrence data were juxtaposed with land cover and land use classification maps developed by the MapBiomas Project (Souza et al., 2020). We extracted MapBiomas data for each species occurrence point within the Atlantic Forest Biome between 1985 and 2022 (the period covered by MapBiomas 8th collection). Land use data were subsequently summarised into two main categories: forest areas, encompassing all natural forest formations, and the non-forest regions, which include agricultural, urban, mining, and natural open areas (more information is available in the Supplementary Information (SI)). We calculated the occurrence frequency (*f*) for each mammal species in forest and non-forest areas (the proportion of SALVE occurrences in forest areas and disturbed areas, ranging between 0 and 1). This information was used to parametrise the probabilities of host species extinction and colonisation, as described in the section below.

Coevolutionary metacommunity model

We employed a cellular automaton-based model for spatial metacommunity dynamics, coupled with a coevolutionary model for ecological networks (Gawecka et al., 2022), to simulate host-parasite eco-evolutionary dynamics in landscapes with varying levels of forest cover and fragmentation. We generated landscapes with 50 by 50 grid cells, where each grid cell represents a habitat patch. We classified patches as "disturbed", "forest core" - forest patches with all four neighbouring patches being forest, and "forest edge" - forest patches with up to three adjacent forest patches (Figure 1). Landscapes varied in the amount of forest cover - 10, 30, 50 and 70%, and forest fragmentation level - low, medium and high, resulting in 12 distinct scenarios (Figure 1). We generated the landscapes using the package NLMR (Sciaini et al., 2018) in the R environment (R Core Team, 2023). We adopted the metanetwork of interactions between mammals and their viral and bacterial parasites, with a total of 51 host species and 103 infectious agents, as the initial regional community composition.

Spatial ecological dynamics

The metacommunity dynamics in our model followed a patch-dynamic perspective (Leibold, 2004). Each patch can be either occupied or unoccupied by a species. Patch colonisations and extinctions are stochastic processes with probabilities shaped by the local species composition and trait-matching. Here, we defined trait-matching, T_{ij}^{t}, between species *i* and *j* in a given patch at time *t* as:

$$T_{ij}^{t} = e^{-\alpha(Z_i^t - Z_j^t)^2} \tag{1}$$

Where Z_i^t is the mean trait value of the population of species *i* in a given patch at time *t*, and α is a constant controlling how sensitive T_{ij}^{t} is to differences between the trait values of species *i* and species *j*.

If a certain species is present in a patch, it has an intrinsic probability of becoming locally extinct in the next step. Extinction probabilities differ between hosts and parasites. For hosts (*j*), extinction depends on their occurrence frequency in forests (*f*) and the composition of the surrounding patch neighbourhood. This probability varies linearly from $p_{e,j} = f_j$ in a disturbed patch to $p_{e,j} = 1 - f_j$ in a patch entirely surrounded by forest (forest core), according to:

$$p_{e,j} = \left(\frac{p_s}{5} - f_j\left(\frac{2}{5}p_s - 1\right)\right) \tag{2}$$

where p_s is the patch habitat type. For a destroyed patch $p_s = 0$. For a forest patch, p_s varies between 1 and 5 according to the number of forest patches in the neighbourhood (assuming von Neumann neighbourhood), such that $p_s = 1$ for a forest patch surrounded by destroyed patches and $p_s = 5$ for a core forest patch surrounded only by forest patches.

For parasites, extinction ${p^t}_{e,i}$ depends on the presence of hosts and trait matching, decreasing with matching between traits of parasite *i* and hosts *j* and the number of host species present in a given patch:

$${p^t}_{e,i} = \prod_{j=1}^{N}(1 - \frac{e_i}{j})(1 - e_i T_{ij}^{t}) \tag{3}$$

where e_i is the intrinsic extinction probability of the parasite, and *N* is the number of hosts present in the patch. If none of its hosts are present in the patch, the parasite becomes locally extinct at time t.

Species can also colonise patches where they are currently absent from one of their four nearest neighbouring patches. Colonisation events from different patches are independent of each other, and colonisation probabilities vary between hosts and parasites. For hosts, colonisation probabilities $p_{c,j}$ depend on their occurrence frequency in forest (*f*) and on the habitat type (p_s) in the patch they aim to colonise:

$$p_{c,j} = \left(f_j\left(\frac{2}{5}p_s - 1\right) - \frac{p_s}{5} + 1\right) \tag{4}$$

Thus, colonisation probability varies linearly from $p_{c,j} = 1 - f_j$ in a destroyed patch to $p_{c,j} = f_j$ in a forest core patch.

Parasites can colonise a patch where at least one of their hosts is present, with the probability increasing with the number of hosts and the degree of trait matching, following a saturating function:

$$p^t{}_{c,i} = 1 - \prod_{j=1}^{N}\left(1 - \frac{c_i}{j}\right)\left(1 - c_i T_{ij}^t\right) \tag{5}$$

where c_i is the intrinsic colonisation probability of the parasite, and *N* is the number of hosts present in the patch to be colonised at time t. Once the assemblages of hosts and parasites are established for each time step, interactions are assigned based on the potential links defined by the regional metanetwork; that is, each parasite is assumed to interact with all its potential host species present within a given patch.

Trait coevolution

Following colonisation and extinction processes, species traits evolve in response to the environment and selection by interacting species (i.e., coevolution) within each patch at each time step. We computed changes in traits Z_i^t based on the model proposed by Andreazzi et al. (2017, 2020) for coevolution within antagonistic communities. This model adapts the original phenotypic evolution equation (Lande, 1976) to incorporate a selection gradient that links environmental and interaction-driven selection to the species' mean fitness. The evolution of species' mean trait is described by:

$$Z_i^{t+1} = Z_i^t + \varphi_i(S_i^t + E_i^t) \tag{6}$$

where φ is a constant that affects the slope of the selection gradient, and is proportional to the trait additive genetic variance. S_i^t and E_i^t are the partial selection differentials imposed by interactions and environment, respectively. Interaction-driven changes are described by:

$$S_i^t = m_i \sum_{j,j \neq i}^{N} q_{ij}^t I_{ij}^t \tag{7}$$

where *N* is the number of species in the local network, m_i the level of coevolutionary selection and measures the strength of the relative importance of interactions in trait evolution. I_{ij}^t the phenotype selected by the interaction between species *i* and *j*. q_{ij}^t describes the evolutionary effect of species *j* on species *i*, as:

$$q_{ij}^t = \frac{a_{ij} e^{-\alpha(Z_j^t - Z_i^t)^2}}{\sum_{k,i \neq k}^{N} a_{ik} e^{-\alpha(Z_k^t - Z_i^t)^2}} \tag{8}$$

where a_{ij} is an element of the local network adjacency matrix, a subset of the regional metanetwork. I_{ij}^t differs for hosts and parasites. We assumed that parasites' evolution favours trait matching to their hosts $I_{ij}^t = Z_j^t - Z_i^t$. Conversely, hosts evolve towards a trait mismatch, based on a fixed critical mismatch ε. Thus, if $\left|Z_i - Z_j\right| \leq \varepsilon$ we expect an increase or decrease of host trait value, and $I_{ji}^t = Z_i^t - Z_j^t + \varepsilon$ if $Z_i^t < Z_j^t$ and $I_{ji}^t = Z_i^t - Z_j^t - \varepsilon$ if $Z_i^t > Z_j^t$. Otherwise, if $\left|Z_i - Z_j\right| > \varepsilon$, parasites do not affect host fitness, then $I_{ji}^t = 0$.

The partial selection differential of the environment, E_i^t, is described as:

$$E_i^t = (1 - m_i)(\theta_i - Z_i^t) \tag{9}$$

where θ_i is the environmental optimum of species i. θ_j for hosts is the weighted average between the disturbed patches' environmental optimum mean ($\theta_d = 10$), the forest patches' environmental optimum ($\theta_f = 20$), and the host forest occurrence frequency (*f*):

$$\theta_i = f_i \theta_f + (1 - f_i)\theta_d \tag{10}$$

Parasite θ_i was calculated as the average of its host's θ_j. Environmental selection refers to the sum of the effects of factors other than interactions. The parameter m_i ($0 \leq m_i \leq 1$) plays an important role in controlling the weight of the two selection forces. At one extreme, when $m_i = 0$, trait evolution is driven exclusively by the environment. At the other extreme, when $m_i = 1$, selection is imposed solely by interacting species.

Finally, species with no interacting partners in a given patch evolve towards their environmental optimum, as described by:

$$Z_i^{t+1} = Z_i^t + \varphi_i(\theta_i - Z_i^t) \tag{11}$$

Simulations

In the first time step, every patch contained the entire metanetwork, and the initial trait values of hosts and parasites were set to their θ_i and θ_j. At each time step, simulations included local colonisation and extinction events, followed by the coevolution among species within each patch. Each model scenario was iterated for 1000 time steps, which was sufficient to reach a steady state of species' global abundances and trait distributions (Gawecka et al., 2022). We assumed that there is feedback between ecological and evolutionary processes operating on the same timescale, with distinct evolutionary forces for hosts and parasites. Hosts were equally driven by environmental and co-evolutionary selection ($m = 0.5$), while parasites responded strongly to co-evolutionary selection ($m = 0.7$). The intrinsic colonisation and extinction probabilities of the parasite were set to 0.6 and 0.5, respectively. Here we show the results with intermediate parameter values (see Supplementary Information), with $\varphi = 0.5$, $\alpha = 0.2$, $\varepsilon = 0.5$, $\theta_d = 10$ and $\theta_f = 20$. We considered other scenarios, with different extinction and colonisation values, as well as scenarios without host evolution. Their results are qualitatively similar to those presented here and are described in the SI. Simulations were performed with Julia version 1.4.2 (Bezanson et al., 2017).

Data analysis

We measured the effect of vegetation cover and landscape configuration on mammal-parasite dynamics, considering two descriptors of ecological and evolutionary patterns for each species, averaged by patch habitat type (forest core, forest edge, and disturbed patches):

1. Relative degree, quantified as the ratio between parasite degree (i.e., the number of its hosts) in local networks and their degree in the metanetwork. This ratio approaches 1 as the species degrees in the local and regional networks become more similar.
2. The mean degree of trait matching between parasites and their co-occurring hosts across all patches. (equation 1).

Additionally, for each habitat type in the landscape, we calculated the abundance of suitable hosts for each parasite as the mean proportion of patches in which any of that parasite's potential hosts were present. We also quantified the parasite extinction rate for each landscape by calculating the proportion of parasite species lost, defined as the difference between the initial parasite richness in the metanetwork and the final richness, divided by the initial metanetwork parasite richness. All data analysis was conducted using R version 4.2.3 (R Core Team, 2023).

We measured the structure of local networks using the following metrics: network size (number of host and parasite species in the network), connectance (ratio of realised interactions and all possible interactions in the network), nestedness, and modularity. Nestedness reflects a pattern where specialist species tend to interact with subsets of species that predominantly interact with generalists. This pattern was quantified using the NODF metric proposed by Almeida-Neto et al. (2008), calculated with the “nestednodf” function in the “vegan” package (Oksanen et al., 2022). Modularity quantifies the tendency of interactions to cluster within the network and was calculated using a greedy optimisation algorithm available in the “igraph” package (Csárdi et al., 2025). The four network metrics were summarised using principal component analysis (PCA) in the “vegan” package (Oksanen et al., 2022). The first axes of the PCA served as a proxy for network structure to evaluate their influence on the four community descriptors. It explained 96% of the variance and was correlated with connectance (51%), size (-50%), modularity (-51%), and nestedness (48%) (SI, Figure S1).

To assess the dissimilarities between local species interactions, we measured the β-diversity by sampling 10% of the patches of each habitat type, totalling 250 sampled patches by landscape. We calculated the dissimilarity using the Whittaker measure, partitioned into turnover (βst) and rewiring (βos) (Poisot et al., 2012). As we have no opportunity for rewiring (spillover) in our model, we analysed interaction turnover (βst) across habitat type (within and between), proportion of forest cover, and fragmentation level using generalised additive models (GAMs) with landscape identity as a random factor in the package “mgvc” (Wood, 2017).

To understand which factors contribute to the descriptors patterns found in our simulations, we built generalized linear mixed models fitted within piecewise structural equation models (pSEM), using the following explaining factors: proportion of forest cover, forest fragmentation level, patch habitat type (core, edge, or disturbed), parasite group (bacteria or virus), zoonotic category, parasite extinction rate, and network structure. Models were constructed with random effects that accounted for the hierarchical structure of the data, with species, habitat type, and landscape level. Response variables were scaled by dividing the values by their standard deviations using the function “scale” of the “Base” package in R.

The modelling process followed several steps. First, we created a global model that included all potential predictors for the two eco-evolutionary descriptors (relative degree and mean trait-matching), one explaining network structure, and one for parasite extinction rate. Model residuals were then analysed using the "DHARMa" package and the "testResiduals" function (Hartig, 2022). If necessary, outliers were removed based on regression deletion diagnostics using the “cooks.distance” function. Next, we performed an automated model selection with the “MuMIn” package (Bartoń, 2023) to identify the best-fitting model for our response variables. Finally, if the selected model for each eco-evolutionary descriptor included the network structure or the extinction rate as explanatory factors, we developed a piecewise structural equation model. The pSEM was used to explore possible indirect effects that occurred through the network topology and/or the parasite extinction rate. Models were created using the “piecewiseSEM” package (Lefcheck, 2016).

RESULTS

Effect of vegetation cover and landscape configuration on local species interaction networks

The structure of mammal-parasite interaction networks is strongly influenced by local landscape factors, particularly the type of patch habitat (R2 = 0.93; F = -4.93; $p < 0.001$) (Figure 2). Forest core patches tend to support large, poorly connected and modular networks, whereas forest edge patches are associated with more nested structures (SI- figure S1 and table S4). In contrast, disturbed patches are characterised by small, yet more connected and nested networks (Figure 2a, SI- table S4). As a result, highly fragmented landscapes with low forest cover generally harbour smaller, more interconnected and nested networks than landscapes with high forest cover and low fragmentation (Figure 2b, SI- table S4).

The dissimilarity among local networks is highly affected by habitat type, with different aspects of the landscape affecting the dissimilarity within and between habitats. Fragmentation level has no effect on interaction dissimilarity within habitats (R2 = 0.28; F =

26.29; $p < 0.001$) (Figure 3a), whereas dissimilarity between habitats is affected by forest cover and fragmentation (R2 = 0.45; F =159.16; $p < 0.001$) (Figure 3b). Local networks in disturbed habitats are more heterogeneous than those in forest habitats, with a tendency for dissimilarity to increase with the proportion of forest cover. In contrast, heterogeneity between forest edge networks decreases with increasing forest cover (Figure 3a, SI - Table S6). Notably, interaction dissimilarity is highest between forest core and disturbed patches. Forest edge networks are more similar to forest core networks than to disturbed networks. Generally, network dissimilarity between habitat types tends to reduce with increasing forest cover and fragmentation (Figure 3b, SI - Table S7).

Descriptors of host-parasite eco-evolutionary dynamics

Parasite relative degree serves as an indicator of the landscape's dilution effect: the more similar the local degree is to the metanetwork, the more diluted the parasite's impact on the host community. This is due to the realisation of the parasite’s potential interactions, including a great diversity in the degrees of trait matching. On the other hand, when the parasite's relative degree is low, it indicates that the parasite is interacting with only a subset of its potential host species, most probably with the highly competent ones. Our results show that the relative degree of zoonotic parasite species is the most affected by variation in habitat type and the abundance of suitable hosts. Specifically, zoonotic parasites exhibit lower relative degrees than non-zoonotic parasites, a pattern most evident in disturbed patches (Figure 4a and c).

At the landscape scale, the relative degree declines as parasite extinction rates increase ($\beta = -0.04$)(Figure 4a and c). The structural equation model (pSEM) accounted for 26% of the variation in relative degree, 65% of the suitable host's abundance, and 83% of the parasite extinction rate (Fisher’s C = 18.5, P-value = 0.18, df = 14). Zoonotic parasites show a consistent decline in relative degree compared to non-zoonotic ones ($\beta = -0.36$), with the greatest reduction observed in disturbed patches (β = -0.13)(Figure 4a and c). In contrast, parasites in core forest patches exhibit higher relative local degrees than those in disturbed or edge habitats (β = 0.06). Suitable host abundance also varies between habitat types, with the forest core having a higher mean host abundance (β = 0.32)(Figure 4a). As expected, parasite relative degree increases with host abundance (β = 0.15)(Figure 4a and b). In summary, landscapes with high forest cover and low fragmentation exhibit a high abundance of suitable hosts, high parasite relative degrees, and a strong resemblance between local and regional interaction networks, which are indicators of diluted landscapes.

Trait matching between parasite and host species—used here as a proxy for interaction strength —further supports this pattern. Interactions in disturbed patches show higher trait matching than in other habitat types, mirroring the trend observed in relative degree. In all habitats, higher host abundance is associated with higher trait matching. The pSEM explained 44% of the variation in trait-matching, 66% of the suitable host's abundance and 89% of network structure (Fisher’s C = 8.4, P-value = 0.39, df = 8), with the strongest effects attributed to the abundance of suitable hosts (β = 0.99) and habitat type—particularly disturbed patches (β = 0.67)(Figure 5a and c). Smaller, more connected and nested networks achieve higher trait matching than larger, sparsely connected and modular networks (β = 0.36)(Figure 5a and b). This aligns with findings at the landscape level: trait matching slightly decreases in landscapes with higher forest cover (β = -0.08)(Figure 5a). In summary, landscapes that are more fragmented and have less forest cover lead to the isolation of interactions, increasing the trait-matching and consequently the strength of interactions among the remaining species.

DISCUSSION

Species coevolution shapes complex interactions, such as parasitism, and is influenced by ecological processes at the population and community levels (Thompson, 2013). Changes in colonisation and extinction processes mediated by deforestation alter species spatial distributions across the landscape, which can drive distinct trajectories of local rapid coevolution (Hairston et al., 2005; Koch et al., 2014; Pelletier et al., 2009; Post & Palkovacs, 2009). Here, we demonstrate that local forces drive the coevolution and metacommunity dynamics of hosts and parasites. However, the regional landscape configuration scales up these patterns, influencing parasite persistence and distribution dynamics, which sets the theoretical basis for understanding the dilution and coevolution effect hypothesis (Zohdy et al., 2019). The dilution effect hypothesis relates host biodiversity to the prevalence of parasites on host populations (Keesing et al., 2006). Here, we argue that, in addition to host diversity, the structure of the interaction network and the coevolutionary dynamics are key for regulating parasite transmission.

The network's eco-evolutionary dynamics varied between the different landscape configurations. We found that landscapes with a high proportion of forest core habitats supported larger and more modular interaction networks. These landscapes also exhibited a tendency towards more homogeneous local interactions between and within different habitats, enabling them to sustain higher parasite richness. Modular networks can buffer the spread of perturbations (Gilarranz et al., 2017), such as the spread and spillover of parasites (Lula Costa et al., 2023). For instance, the transmission of a parasite to a new host is more likely to occur inside an interaction module than over the entire network, slowing the spread of a new infection (Evans et al., 2021; Proesmans et al., 2021). In contrast, more nested and connected structures, which we found in highly disturbed habitats, facilitate the transmission of parasites (Graham et al., 2009). Our findings suggest that highly degraded landscapes compromise the property of core habitats to regulate disease spread by changing the structure and distribution of interactions (Höckerstedt et al., 2022; Toorians et al., 2025). Consequently, these landscapes increase the risk of zoonotic transmission and divergent coevolutionary trajectories in edge and disturbed habitats.

Moreover, the loss of forest cover and its fragmentation increased the environmental filtering imposed by edge and disturbed habitats. This led to the persistence of generalist interactions, as evidenced by the increase in the abundance of what we may call “super-spreader hosts”- species with a higher diversity of parasite fauna (Streicker et al., 2013). In addition, the presence of different fragments across the landscape increased trait divergence among host populations, indicating distinct coevolutionary trajectories. Functional connectivity, i.e., the ease with which organisms, genes, or interactions move across the landscape, likely plays a key role in shaping these patterns (Fahrig, 2017). In degraded landscapes, reduced connectivity can constrain host and parasite movement, limiting gene flow and interaction opportunities, which in turn promotes localised coevolutionary dynamics and increases the probability that new parasite variants emerge (Fahrig, 2017; Gilarranz et al., 2015).

Trait divergence is reflected in the positive relationship between the presence of more abundant suitable hosts and trait-matching, which is exceptionally high in disturbed areas. As generalist hosts became more abundant and host diversity declined (reflected in reduced parasite relative degree), coevolutionary dynamics intensified. This process likely transformed generalist parasite populations into a mosaic of locally specialised populations. This is evidenced by the higher interaction dissimilarity observed in disturbed patches. Network heterogeneity in disturbed habitat indicates an isolation of specific interactions, which can be represented by units of coevolutionary engines (Zohdy et al., 2019). These units result in mosaics of evolution, increasing parasite trait variability across the landscape, leading to a higher probability of new variants arising and the capacity of successfully infecting new hosts (Zohdy et al., 2019). Isolated populations tend to be more susceptible to new infections due to a decrease in the diversity of resistant phenotypes in host populations (Höckerstedt et al., 2022). The isolation and, consequently, the increase in interaction strength found in highly degraded landscapes lead to a perfect storm of disease emergence.

From a species-level perspective, the outcomes of our model varied according to the parasite's zoonotic status, with zoonotic parasites showing the most significant loss in host diversity in disturbed habitats. Although some studies support a stronger dilution effect for zoonotic parasites in more preserved landscapes, the evidence remains mixed (Civitello et al., 2015; Keesing & Ostfeld, 2021a). These parasites tend to be more generalist, and the diversity of their hosts includes species with varying transmission competencies, which can influence disease dynamics in complex ways. The transmission of parasite species within a more diverse host community is modulated by the presence of both highly and poorly competent hosts (Ostfeld & LoGiudice, 2003). The loss of suitable but low-competence hosts is a key factor driving increased parasite prevalence among the remaining hosts (Streicker et al., 2013). This result, aligned with the increase in their interaction strength, suggests the potential of zoonotic spillover to humans in highly fragmented units. This calls for the need to improve surveillance and evidence-based conservation actions based on a transdisciplinary approach (Plowright et al., 2017).

While previous models focus on either spatial structure or coevolution in isolation (Barbier, 2021; Faust et al., 2018; Guégan et al., 2020), this is the first to account for eco-evolutionary feedbacks and habitat-specific dynamics using empirical data. Thus, our model incorporates ecological realism by adopting real occurrence data to model host-parasite dynamics. Related model approaches have already emphasised the influence of landscape and environmental change on different ecological interactions (Cosmo et al., 2023; Gawecka et al., 2022). A coevolving metacommunity framework enables us to understand the interplay between species dispersion and adaptation to the persistence of communities in a constantly changing world (Urban et al., 2008). Despite its contributions, our model has limitations that should be acknowledged. First, it assumes a single evolving trait per species and does not account for multivariate or context-dependent coevolution (Poisot et al., 2011; Zilio et al., 2024). Second, while we used empirical data on species distributions and interactions, the coevolutionary dynamics are simulated under simplified assumptions, and spillover among new hosts was not explicitly modelled (Plowright et al., 2017; Zohdy et al., 2019). Third, the model does not include pathogen-specific traits such as transmission mode or latency, which could influence eco-evolutionary feedbacks (Bolnick et al., 2011; Makau et al., 2022). These complex processes should be handled carefully in multi-host models, as they can alter the outcomes of local network structure and global extinction rates. Future studies should aim to integrate more detailed trait-based models and explore dynamic spillover processes in multi-host systems, particularly under scenarios of climate and land-use change.

Enhancing functional connectivity may mitigate biodiversity loss at edges between habitat patches. Which, in turn, could mitigate some of the fragmentation effects observed, consequently increasing interaction similarity between the forest core and edge networks (Faust et al., 2018). Hence, conservation and restoration actions should not only focus on diminishing fragmentation per se, but on preserving the integrity of forest core habitats (Faust et al., 2018; Prist et al., 2023; Roberts et al., 2021). For example, decision makers should aim to maintain or restore ecological corridors and manage edge zones (Hilty et al., 2020). Corridors can enhance functional connectivity, facilitating movement of hosts and their associated parasites, and promoting more stable interaction networks (Martensen et al., 2012). Likewise, managing edge habitats to reduce abrupt transitions may help maintain interaction continuity and buffer against the isolation effects that drive divergent coevolutionary processes and increased zoonotic risk. Our results suggest that landscapes that account for the integrity of their natural core habitats “dilute” the distribution of parasites throughout the host community. Hence, maintaining the connectivity between forest fragments also leads to more homogeneous coevolutionary trajectories. Furthermore, host abundance acts as a driver for the interaction and coevolutionary patterns regulating the opportunity of parasite infection and impacting the persistence of parasite species throughout the landscape. By this, we demonstrate potential outcomes of habitat loss and fragmentation on the risk of zoonotic diseases and the ways to manage and conserve natural areas to mitigate this risk.

Data availability statement

Data and code for model construction and analysis can be found in the Zenodo repository [link will be added].

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FIGURES

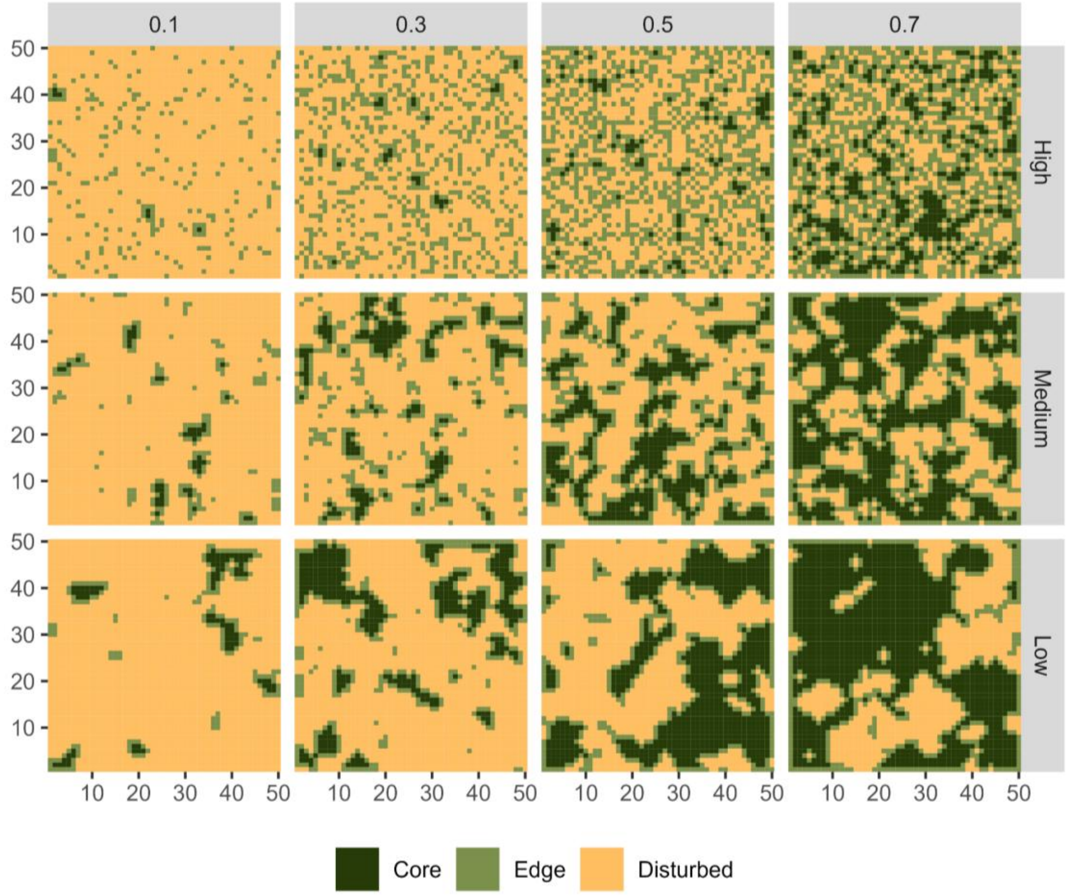

Figure 1: Landscapes used as input for the coevolutionary metacommunity model. Landscapes vary in the proportion of forest patches (0.1, 0.3, 0.5, and 0.7) and the level of fragmentation (High, Medium, and Low).

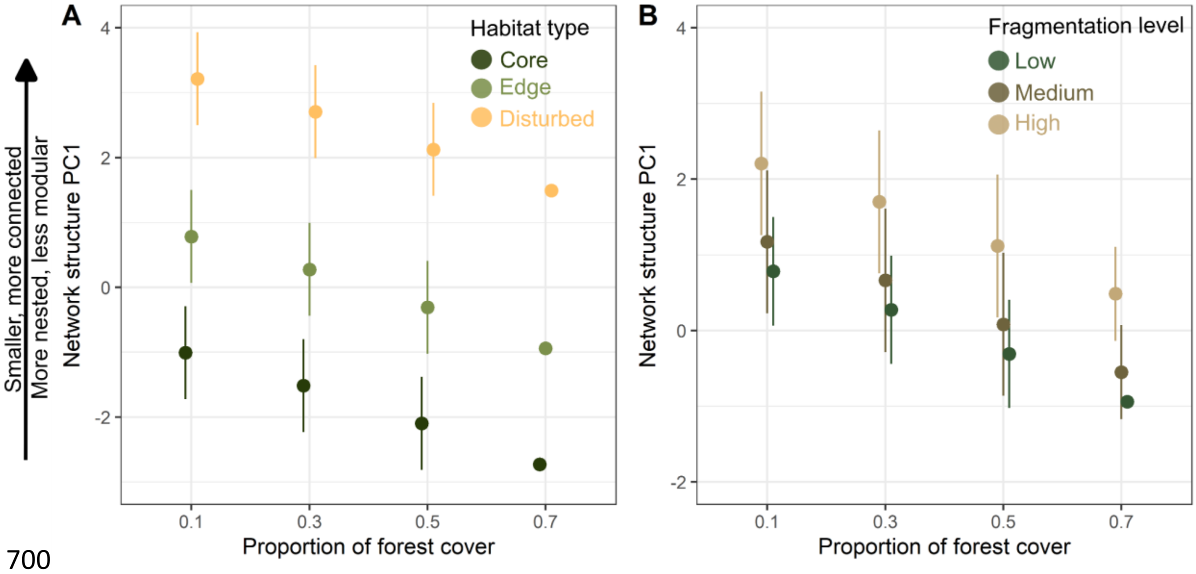

Figure 2: Relationship between network structure (First axis of the PCA – PC1) and the different landscape aspects. A. Local network structure by habitat types (dark green: forest core, light green: forest edge, yellow: disturbed patch) and landscapes with different proportions of forest cover (x-axis). B. Local network structure in landscapes with different

proportions of forest cover (x-axis) and fragmentation level (dark green: low level, dark brown: medium level, light brown: high level).

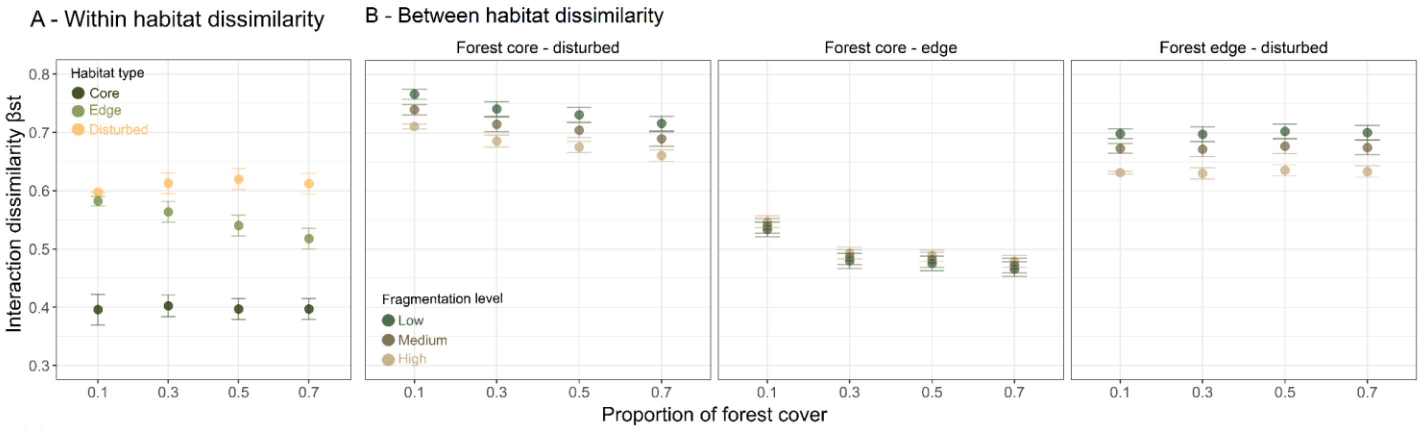

Figure 3: Beta diversity due to interaction turnover (βst) calculated between local networks within and between habitat types. A. Pairwise comparisons between local networks in the same habitat types and their relationship with the proportion of forest cover. Colours indicate patches' habitat type (dark green: forest core, light green: forest edge, yellow: disturbed patch). B. Pairwise comparisons between local networks in different habitat types and their relationship with the proportion of forest cover. Colours indicate the fragmentation level (dark green: low level, dark brown: medium level, light brown: high level).

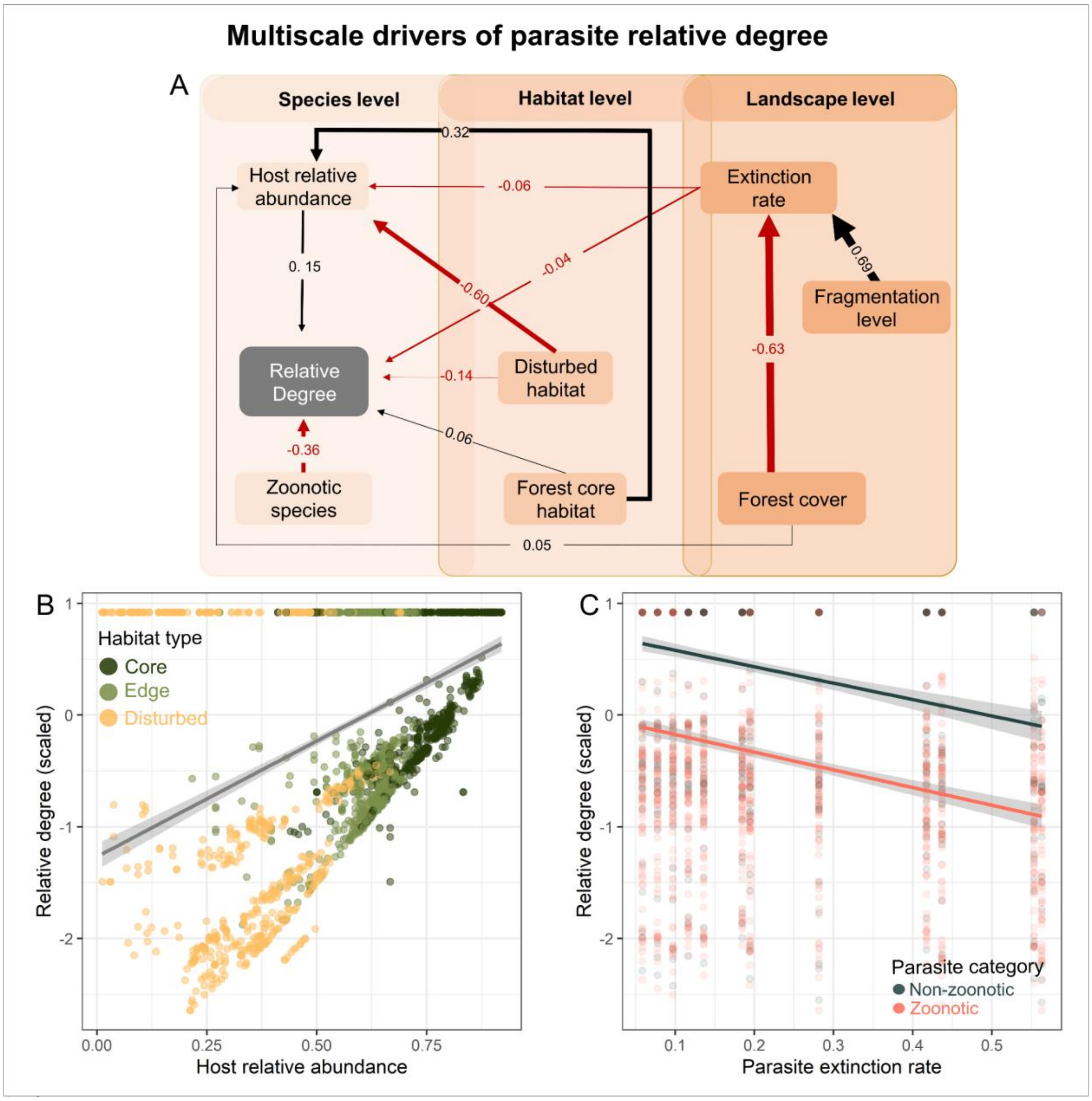

Figure 4: A. Piecewise structural equation model (PSEM) diagram describing the effects of landscape level (proportion of forest cover, fragmentation, and parasite extinction rate), habitat level (forest core and disturbed patches), and species level (zoonotic species and host abundance) variables on the relative degree of parasites. Only significant relationships are shown ($p < 0.05$). Positive and negative pathways are indicated by black and red lines, respectively. The thickness of the arrows indicates the relative strength of the effects, and each line displays the standardised coefficients. B. Relationship between parasite relative degree and their host abundances in the landscape. Colours indicate patches' habitat type (dark green: forest core, light green: forest edge, yellow: disturbed patch). C. Relationship between parasite relative degree and their global extinction rate in the landscape. Colours indicate the parasite zoonotic category (non-zoonotic parasites: dark blue; zoonotic parasites: red).

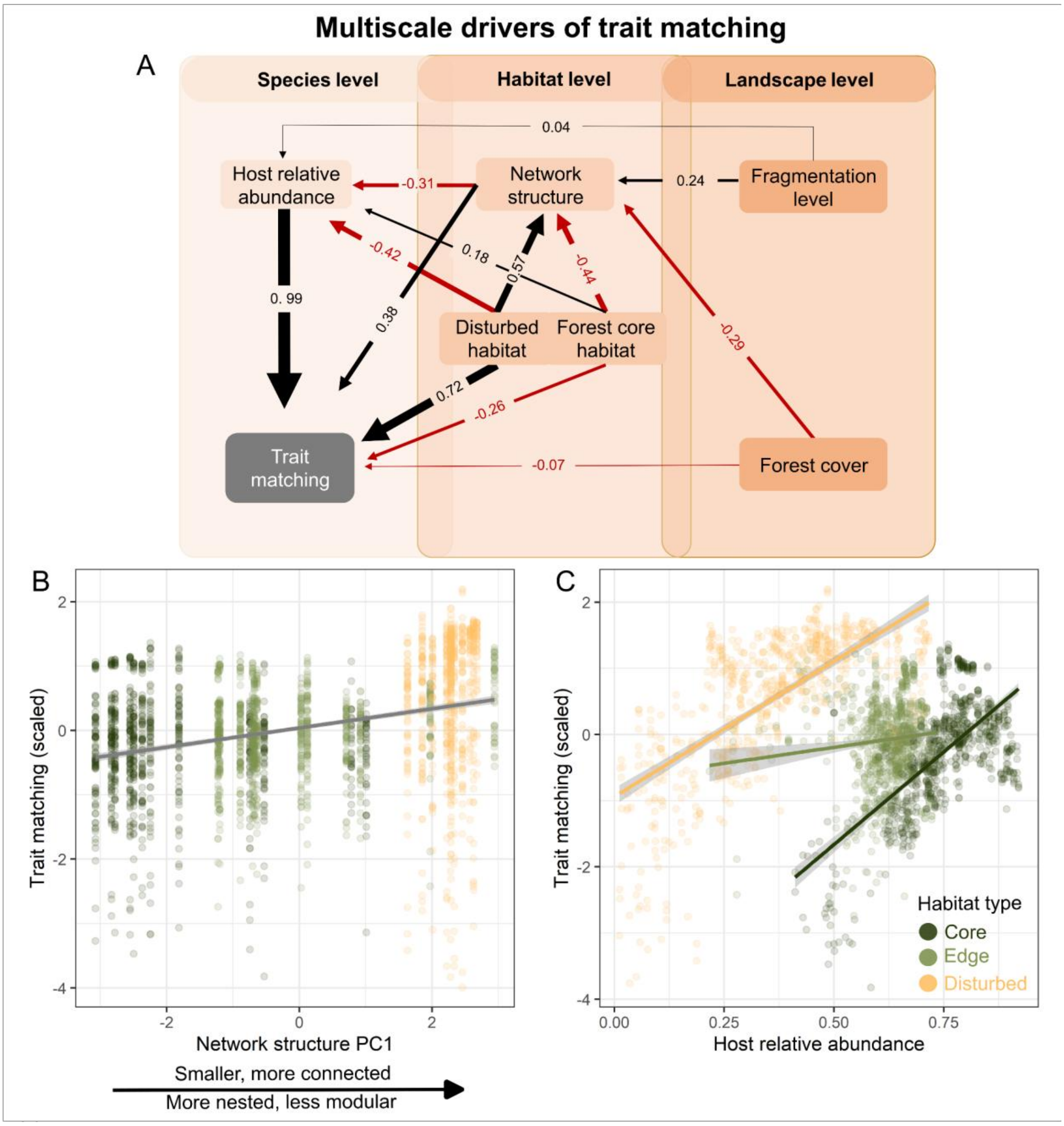

Figure 5: A. Piecewise structural equation model (PSEM) diagram describing the effects of landscape level (proportion of forest cover, and fragmentation), habitat level (network structure, forest core and disturbed patches) and species level (host relative abundance) variables on the trait matching between parasite and host species. Only significant relationships are shown ($p < 0.05$). Positive and negative pathways are indicated by black and red lines, respectively. The thickness of the arrows indicates the relative strength of the effects, and each line displays the standardised coefficients. B. Relationship between host-parasite trait matching and network structure - PC1. Colours indicate the proportion of forest cover. C. Relationship between host-parasite trait matching and host abundance in the landscape. Colours indicate patches' habitat type (dark green: forest core, light green: forest edge, yellow: disturbed patch).