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Cite this article: Costa APL, Gawecka KA, Winck GR, D'Andrea PS, Andreazzi CS. 2026 From dilution effect to dilution landscapes: effects of natural vegetation cover and fragmentation on host–parasite eco-evolutionary dynamics. *Proc. R. Soc. B* **293**: 20260912.
https://doi.org/10.1098/rspb.2026.0912

Received: 8 April 2026
Accepted: 24 June 2026

Subject Category:
Ecology

Subject Areas:
ecology, evolution

Keywords:
landscape conversion, zoonotic risk, metacommunity model, ecological networks, habitat loss

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Supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8570623.

THE ROYAL SOCIETY PUBLISHING

From dilution effect to dilution landscapes: effects of natural vegetation cover and fragmentation on host–parasite eco-evolutionary dynamics

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The degradation of natural landscapes is a key driver of biodiversity loss and the erosion of ecosystem services, including disease regulation. Although 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 to examine how landscape configuration shapes ecological and coevolutionary outcomes. We found that: (i) landscapes with more natural cover and lower fragmentation level dilute the distribution of parasites throughout the host community and lead to more homogeneous coevolutionary trajectories; (ii) highly degraded, fragmented landscapes constrain host–parasite dispersal, promoting smaller, more heterogeneous interaction networks with divergent coevolutionary dynamics, which raise the risk of new parasite variants emerging; and (iii) loss of habitat reduces diversity, reducing 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 increased zoonotic transmission risk and stronger parasite–host interactions in degraded landscapes. Hence, conservation actions should focus on maintaining forest core integrity to mitigate the effects of landscape conversion on host–parasite dynamics and to promote the disease-regulation service of natural ecosystems.

1. Introduction

Ecological and evolutionary processes are tied together through the interplay of species interactions [1,2]. Ecological aspects like the composition of local communities and dispersal patterns affect the strength and direction of selection imposed by species interactions, driving genetic and phenotypic evolution within communities [3–5]. In turn, evolutionary changes can influence ecological dynamics by altering local colonization and extinction rates and diversity patterns, ultimately affecting regional-scale processes [6]. The composition and configuration of landscapes also affect diversity patterns and, hence, species interactions. In this sense, human-caused landscape changes due to the removal and fragmentation of natural areas may have profound effects on the eco-evolutionary dynamics of species interactions, generating divergence in evolutionary trajectories across landscapes [3,4]. An

open challenge is understanding when and how landscape changes affect species' eco-evolutionary dynamics, particularly of intricate and complex systems, such as host–parasite interactions [7].

Eco-evolutionary feedback loops drive phenotypic selection arising from host immune responses and parasite infection strategies, thereby shaping infection dynamics [8]. Thus, the effect of habitat fragmentation on eco-evolutionary dynamics of host–parasite interactions is crucial for managing pathogen spread and anticipating the conditions that favour zoonotic spillover [8,9]. Moreover, hosts and parasites may differ in the strength of the selection pressures they experience and in the rates at which they evolve, potentially creating asymmetric selection dynamics within host–parasite systems [9]. These selective dynamics can change depending on the community diversity patterns and environmental conditions [9,10], with ecological and evolutionary processes happening on the same timescale [11,12]. Specifically, extinction and colonization events determine species composition locally, creating a regional mosaic of selection pressures that leads to divergent coevolutionary trajectories among populations [2]. In this sense, habitat fragmentation can increase the isolation of local host populations, reducing gene flow and limiting the influx of genetic diversity, thereby constraining their capacity to respond to selection (reducing their evolutionary potential) [13,14].

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 [15]. 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 parasite transmission risk within the community through a set of mechanisms, including regulating the density of competent hosts [16]. Amplification occurs when conditions increase the opportunities for infection and raise the prevalence of a specific parasite in the community, for example, by increasing the abundance of its competent hosts or vectors [16,17]. To integrate these processes with an evolutionary perspective, the coevolution effect hypothesis proposes that habitat fragmentation isolates host–parasite interactions, promoting genetic or phenotypic divergence among fragments [3]. This divergence can increase parasite genetic variability across the landscape by strengthening local coevolutionary interactions and increasing the likelihood of new variants arising.

In disturbed landscapes, reduced host adaptive capacity favours the emergence of parasite variants with higher transmissibility and virulence, ultimately increasing infection risk [14,18]. Although the coevolution effect 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. To address the gap in how species coevolve in response to different landscape configurations, we integrated a simulation-based coevolutionary framework into a spatially explicit metacommunity model. Host–parasite interactions were parameterized with known associations between mammal host species and virus genotypes, as well as bacteria species, from the Brazilian Atlantic Forest. This region is recognized as one of the world's most diverse yet also most degraded ecosystems [19,20].

We studied eco-evolutionary host–parasite dynamics across static simulated landscapes that varied in the amount of natural habitat cover and in fragmentation levels, allowing host and parasite colonization and extinction as well as phenotypic adaptation to take place at the same timescale. Specifically, we answered the following questions. (i) How does landscape configuration affect the ecological and evolutionary outcomes of host–parasite interactions? (ii) What are the main spatial and ecological factors driving the ecological and evolutionary outcomes? We expected changes in species richness, composition and eco-evolutionary trajectories, with a reduction of host and parasite richness favouring generalist species in degraded landscapes, which may increase network cohesion and connectivity, consistent with expectations from 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 habitats.

2. Methods

(a) Host–parasite input data

We used literature and empirical data to parameterize host–parasite interactions and the host species' probabilities of colonization and extinction. Data were gathered from two main sources: the BMPO dataset [21] and the SALVE-ICMBio (Biodiversity Extinction Risk Assessment System) dataset (https://salve.icmbio.gov.br). We considered all possible associations between mammal species and their viral and bacterial parasites registered in BMPO for the Atlantic Forest Biome. Mammals from the Rodentia, Didelphimorphia, Primates, Cingulata, Carnivora, Pilosa, Perissodactyla and Lagomorpha orders were included, summarizing only wildlife mammal species. Viruses and Bacteria were filtered to the finest possible taxonomic level, including only species and serotype records. The BMPO dataset also summarized mammal and parasite traits gathered from the literature. Here, we used previously published information on parasite zoonotic classification [21]. The so-called metanetwork, which encompasses all interactions in the system, was represented by a binary matrix A_{ij}, where $A_{ij} = 1$ indicates an interaction between a virus or bacterium i and a mammal species j.

We utilized data on wildlife mammal occurrences in Brazil, provided by SALVE-ICMBio, to calculate the frequency of mammal species occurrence in forested areas. Occurrence data were juxtaposed with land cover and land use classification maps developed by the MapBiomas Project (8th Collection) [19]. We extracted landscape data for each species occurrence point within the Atlantic Forest Biome between 1985 and 2022. Land use data were subsequently summarized 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 electronic supplementary material). We calculated the occurrence frequency (f) for each mammal species in forest and non-forest areas as the proportion of SALVE occurrences in

forest areas and disturbed areas, ranging between 0 and 1. This information was used to parametrize host species metacommunity dynamics, as described in the section below.

(b) Coevolutionary metacommunity model

We employed a cellular automaton-based model for spatial metacommunity dynamics with a coevolutionary model for ecological networks [20] to simulate host–parasite eco-evolutionary dynamics in generated landscapes with varying levels of forest cover and fragmentation (figure 1). This model couples the coevolutionary model proposed by [9,22] and patch occupancy models proposed by [23,24] and was adapted from [20]. We built landscapes with 50 by 50 grid cells, where each grid cell represents a habitat patch. We classified patches as 'disturbed', 'forest core' (i.e. forest patches with all four neighbouring patches being forest) and 'forest edge' (i.e. forest patches with up to three adjacent forest patches). Landscapes varied in the amount of forest cover (10, 30, 50 and 70%) and the forest fragmentation level (low, medium and high), resulting in 12 distinct scenarios (figure 1). We generated the landscapes using the package NLMR [25] in the R environment [26]. 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.

(i) Spatial ecological dynamics

We adopted a patch-dynamic perspective for the metacommunity dynamics [20,27], in line with previously established models [23,24]. Each patch can be either occupied or unoccupied by a species. Patch colonizations 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:

$$T_{ij}^t = e^{-\alpha\left(Z_i^t - Z_j^t\right)^2}, \tag{2.1}$$

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 $p_{e,i} = f_i$ in a disturbed patch to $p_{e,i} = 1 - f_i$ in a patch entirely surrounded by forest (forest core), according to:

$$p_{e,i} = \left(\frac{p_s}{5} - f_i\left(\frac{2}{5}p_s - 1\right)\right), \tag{2.2}$$

where p_s is the patch habitat type. For a disturbed 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 disturbed patches and $p_s = 5$ for a core forest patch surrounded only by forest patches.

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

$$p_{e,i}^t = \prod_{j=1}^{N}\left(1 - \frac{e_i}{j}\right)\left(1 - e_i T_{ij}^t\right), \tag{2.3}$$

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 is present in the patch, the parasite becomes locally extinct at time t.

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

$$p_{c,i} = \left(f_i\left(\frac{2}{5}p_s - 1\right) - \frac{p_s}{5} + 1\right). \tag{2.4}$$

Thus, colonization probability varies linearly from $p_{c,i} = 1 - f_i$ in a disturbed patch to $p_{c,i} = f_i$ in a forest core patch.

Parasites can colonize a patch where at least one of their hosts is present, being a proxy of infection, that is, a parasite will automatically infect all suitable hosts present in the patch it has colonized. The probability of colonization increases with the number of hosts and the degree of trait matching, following a saturating function:

$$p_{c,i}^t = 1 - \prod_{j=1}^{N}\left(1 - \frac{c_i}{j}\right)\left(1 - c_i T_{ij}^t\right), \tag{2.5}$$

where c_i is the intrinsic colonization probability of the parasite, and N is the number of hosts present in the patch to be colonized 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 metanetwork; that is, each parasite is assumed to interact with all of its potential host species present within a given patch.

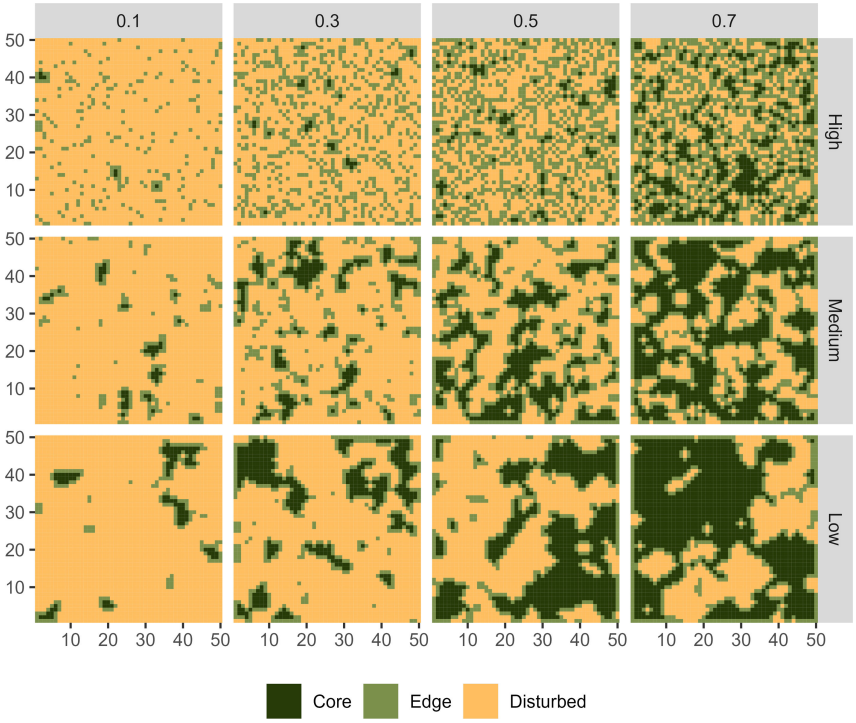

Figure 1. Landscapes used as input for the coevolutionary metacommunity model. Landscapes vary in the proportion of forest patches (0.1, 0.3, 0.5 and 0.7) and the level of fragmentation (high, medium and low).

(ii) Trait coevolution

Following colonization 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 [9,22] for coevolution within antagonistic communities. This model adapts the original phenotypic evolution equation [28] 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:

$$Z_i^{t+1} = Z_i^t + \varphi\left(S_i^t + E_i^t\right), \tag{2.6}$$

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:

$$S_i^t = m_i \sum_{j,\ j \neq i}^{N} q_{ij}^t I_{ij}^t, \tag{2.7}$$

where N is the number of species in the local network, m_i the level of coevolutionary selection and represents 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:

$$q_{ij}^t = \frac{a_{ij} e^{-\alpha\left(Z_j^t - Z_i^t\right)^2}}{\sum_{k,\, i \neq k}^{N} a_{ik} e^{-\alpha\left(Z_k^t - Z_i^t\right)^2}}, \tag{2.8}$$

where a_{ij} is an element of the local network adjacency matrix, a subset of the 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 $|Z_i - Z_j| \leq \varepsilon$ 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 $|Z_i - Z_j| > \varepsilon$, parasites do not affect host fitness, then $I_{ji}^t = 0$.

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

$$E_i^t = (1 - m_i)\left(\theta_i - Z_i^t\right), \tag{2.9}$$

where θ_i is the environmental optimum of species i. θ_i 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):

$$\theta_i = f_i \theta_f + (1 - f_i)\theta_d. \tag{2.10}$$

Parasite θ_i was calculated as the average of all its host's θ_i. 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:

$$Z_i^{t+1} = Z_i^t + \varphi(\theta_i - Z_i^t) \tag{2.11}$$

(iii) 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. At each time step, simulations included local colonization and extinction events, followed by the coevolution among species within each patch (figure 2). Each model scenario was iterated for 1000 time steps, which was sufficient to reach a steady state in which both the global abundance and the global mean and standard deviation of traits for each species no longer changed between time steps (electronic supplementary material, figures S1 and S2) [20]. 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 ($m_i = 0.5$), while parasites responded strongly to co-evolutionary selection ($m_i = 0.7$). The intrinsic colonization and extinction probabilities of the parasite were set to 0.6 and 0.5, respectively. Here we show the results with intermediate parameter values, 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 colonization values, different landscape configurations and initial conditions, and scenarios without host evolution. Their results are qualitatively similar to those presented here and are described in the electronic supplementary material. Simulations were performed with Julia v.1.4.2 [29].

(c) 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 degree in the local and regional networks becomes more similar.
(2) The mean degree of trait matching between parasites and their co-occurring hosts across all patches (equation (2.1)).

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.

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 realized 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 [30], calculated with the 'nestednodf' function in the 'vegan' package [31]. Modularity quantifies the tendency of interactions to cluster within the network and was calculated using a greedy optimization algorithm available in the 'igraph' package [32]. The four network metrics were summarized using principal component analysis (PCA) in the 'vegan' package [31]. 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 (0.51), size (−0.50), modularity (−0.51) and nestedness (0.48) (electronic supplementary material, figure S3).

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 (resulting in 31 125 pairwise patch comparisons) per landscape. Patch sampling was conducted to reduce computation effort. We calculated the dissimilarity using the Whittaker measure [33]. While this measure is partitioned into turnover (β_{st}) and rewiring (β_{os}), we have no opportunity for the latter in our model, and thus, we considered the former only. We analysed interaction turnover (β_{st}) across habitat type (within and between), proportion of forest cover and fragmentation level using generalized additive models (GAMs) with landscape identity as a random factor in the package 'mgvc' [34].

To identify which factors contribute in a direct and indirect way to the outcomes 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), 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 each value by its standard deviation using the 'scale' function in the 'Base' package in R. We analysed the relationships among all potential predictors for the two eco-evolutionary descriptors (relative degree and mean trait-matching), the network structure and the parasite extinction rate. Model residuals were analysed using the 'DHARMa' package and the 'testResiduals' function [35]. Predictors with a high variance inflation factor (VIF) were identified and removed from each model. Outliers were removed to ensure the best fit based on regression deletion diagnostics using the 'cooks.distance' function. Finally, if the model for each eco-evolutionary descriptor included the network structure or the extinction rate as explanatory factors, we developed a

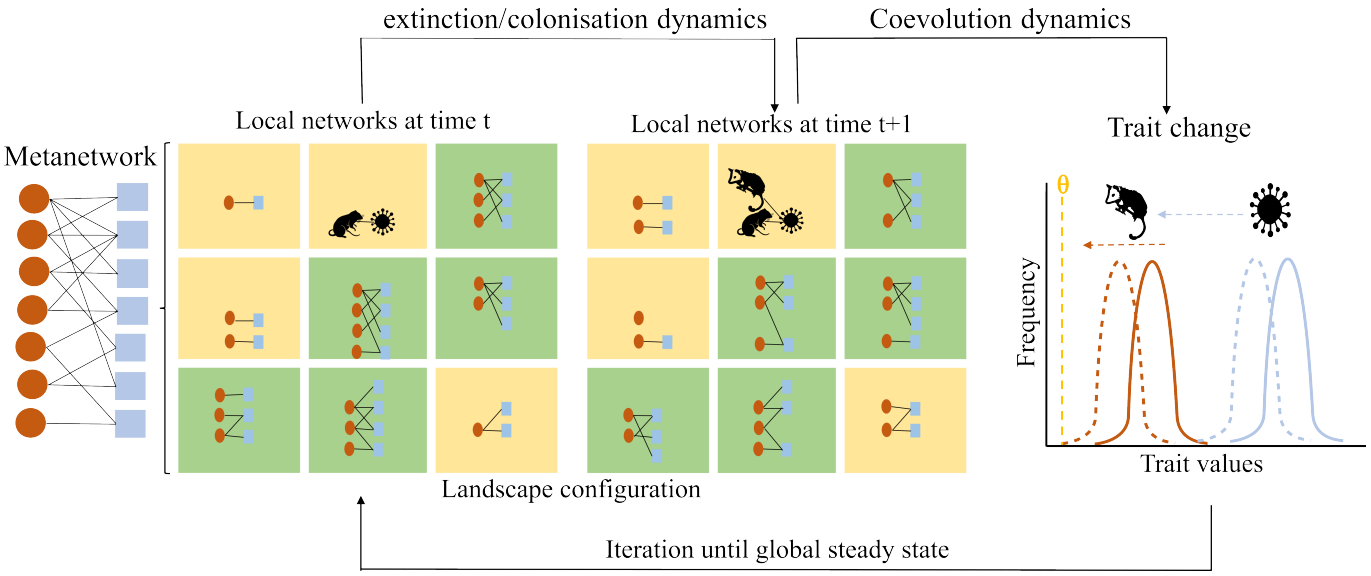

Figure 2. Schematic figure of the spatially explicit coevolutionary model. The metanetwork based on the BMPO database [21] was first established in each patch, followed by a first step of species extinction, creating local networks that are subsets of the metanetwork. At each step, we simulated extinction and/or colonization dynamics, followed by species coevolution within each patch, repeating this sequence until we reached a global steady state. The extinction and/or colonization events reshuffle local networks, while coevolution results from trait-matching or mismatching associated with species' local interactions.

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 [36]. All data analysis was conducted using R v.4.2.3 [26].

3. Results

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

The structure of host–parasite interaction networks is strongly influenced by local landscape factors, particularly the type of patch habitat ($R^2 = 0.93$; $F = -4.93$) (figure 3). Forest core patches tend to support large, poorly connected and modular networks, whereas forest edge patches are associated with more nested structures (electronic supplementary material, figure S1 and table S4). By contrast, disturbed patches are characterized by small yet more connected and nested networks (figure 3A; electronic supplementary material, 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 3B; electronic supplementary material, 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 ($R^2 = 0.28$; $F = 26.29$; figure 4A), whereas dissimilarity between habitats is affected by forest cover and fragmentation ($R^2 = 0.45$; $F = 159.16$; figure 4B). 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. By contrast, heterogeneity between forest edge networks decreases with increasing forest cover (figure 4A; electronic supplementary material, 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 4B; electronic supplementary material, table S7).

(b) 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 realization of the parasite's potential interactions, so when the parasite's relative degree is low, it indicates that the parasite is interacting with only a subset of its potential host species. 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 5A,C).

At the landscape scale, the relative degree declines as parasite extinction rates increase ($\beta = -0.04$) (figure 5A,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 with non-zoonotic ones ($\beta = -0.36$), with the greatest reduction observed in disturbed patches ($\beta = -0.13$) (figure 5A,C). By contrast, parasites in core forest patches exhibit higher relative local degrees than those in disturbed or

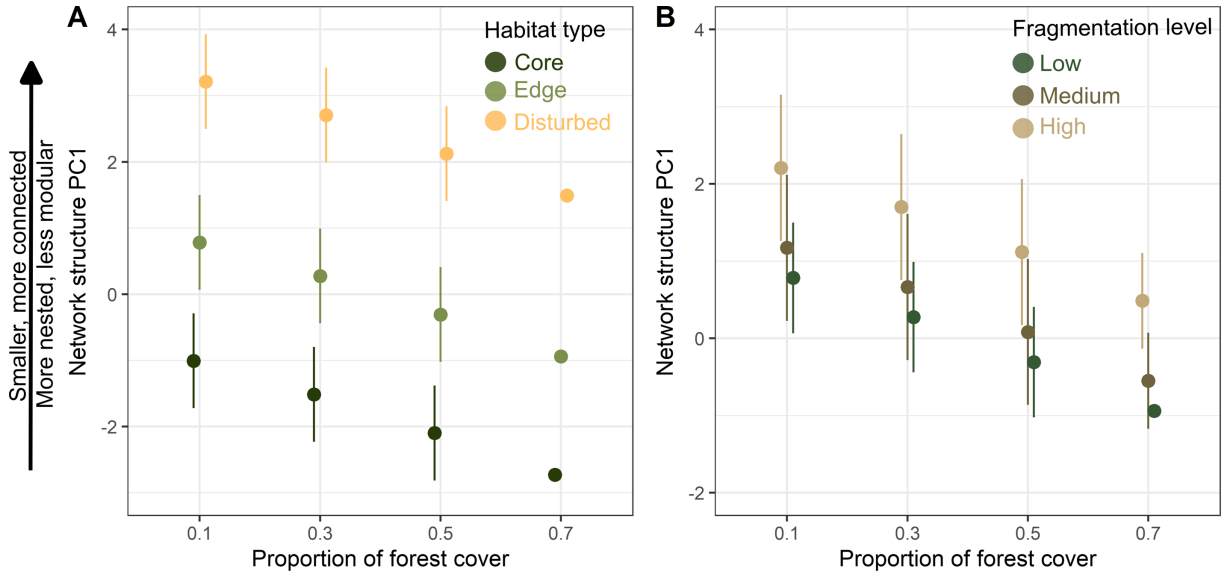

Figure 3. Relationship between network structure (first axis of the PCA–PC1) and the different landscape aspects. (A) Local network structure by habitat type (dark green: forest core, light green: forest edge, yellow: disturbed patch) and landscapes with different proportions of forest cover (*x*-axis). (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).

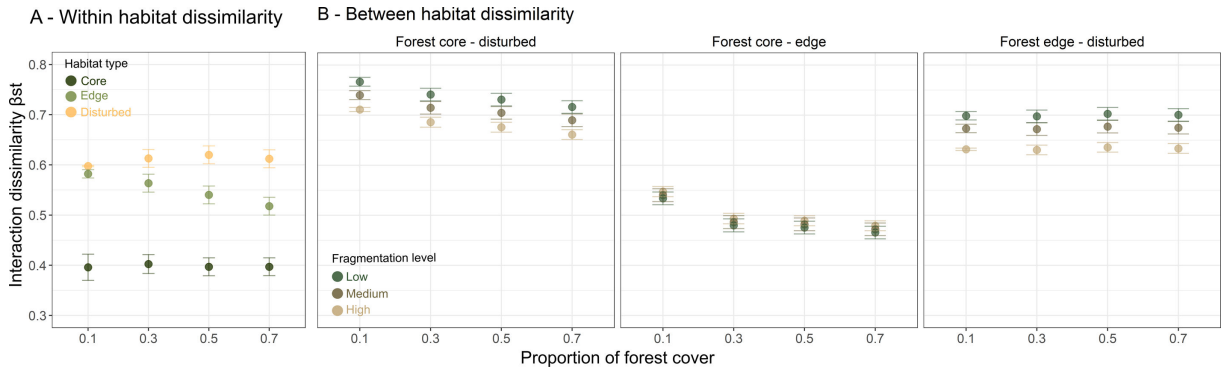

Figure 4. Beta diversity due to interaction turnover (βst) calculated between local networks within and between habitat types. (A) Pairwise comparisons between local networks in the same habitat types and their relationship with the proportion of forest cover. Colours indicate patches' habitat type (dark 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).

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 5A). As expected, parasite relative degree increases with host abundance (β = 0.15) (figure 5A,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 6A,C). Smaller, more connected and nested networks achieve higher trait matching than larger, sparsely connected and modular networks (β = 0.36) (figure 6A,B). This aligns with findings at the landscape level: trait matching slightly decreases in landscapes with higher forest cover (β = −0.08) (figure 6A). 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.

4. Discussion

Species coevolution shapes complex interactions, such as parasitism, and is influenced by ecological processes at the population and community level [37]. Changes in colonization and extinction processes mediated by deforestation alter species spatial distributions across the landscape, which can drive distinct trajectories of local rapid coevolution [38–41]. Here, we demonstrate that habitat type drives the coevolution and metacommunity dynamics of hosts and parasites. Moreover, the habitat amount and its configuration within a landscape scale up these patterns, influencing parasite persistence and distribution dynamics.

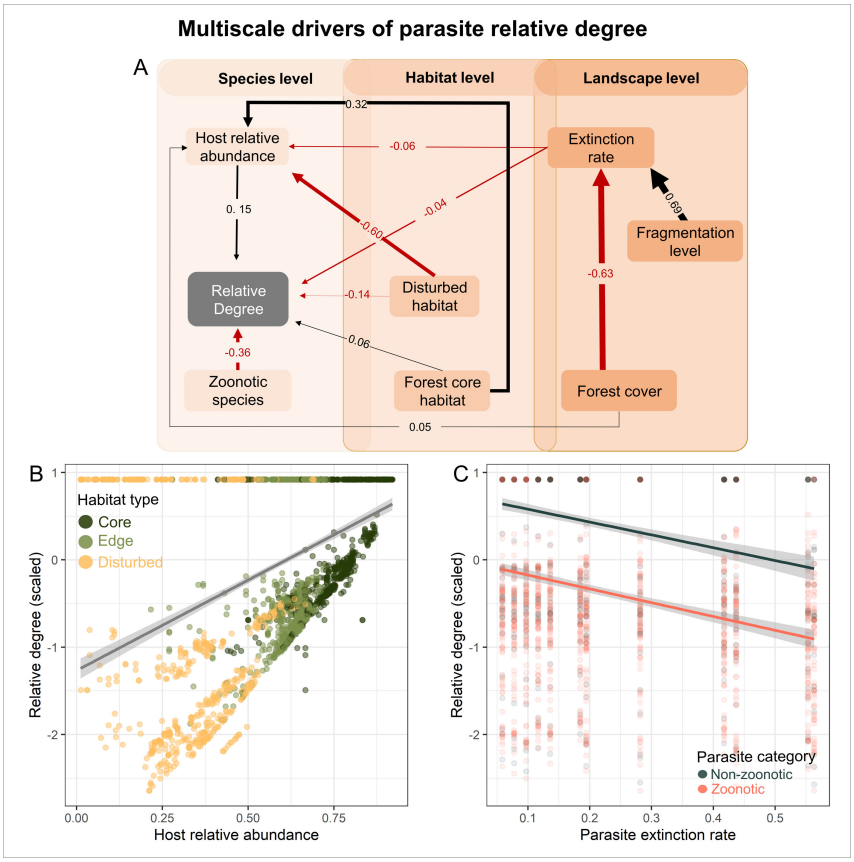

Figure 5. (A) Piecewise structural equation model (PSEM) diagram describing the effects of landscape level (proportion of forest cover, fragmentation and parasite extinction rate), habitat level (forest core and disturbed patches) and species level (zoonotic species and host abundance) variables on the 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 standardized 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).

Our results set the theoretical basis for understanding the dilution and coevolution effect hypothesis [18]. The dilution effect hypothesis relates host biodiversity to the prevalence of parasites on host populations [16]. 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 perturbation [42], such as the spread and spillover of parasites [43]. 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 [44,45]. By contrast, more nested and connected structures, which we found in highly disturbed habitats, facilitate the transmission of parasites [46]. Our findings suggest that highly degraded landscapes compromise the property of core habitats to regulate parasite spread by changing the structure and distribution of interactions [47,48]. 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 an increase in the abundance of host species with greater parasite diversity. In return, overall parasite diversity diminished with increased fragmentation and deforestation, potentially leading to increased prevalence and intensity of infection among the remaining highly abundant hosts [49]. Our model showed regional extinction of parasite species, while host richness persisted, suggesting parasite biodiversity loss may precede the loss of free-living species. There is evidence for a causal relationship between the reduction of host diversity and natural habitat degradation impacts, whereas here we show that this effect may occur faster for parasites [50–52]. Healthy ecosystems, characterized by species persistence and resilience to disturbances, are associated with greater diversity of parasite assemblages, as they are known to shape the organization of trophic interactions and prevent dominance by a few species, both hosts and parasites [53].

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 [54]. In degraded landscapes, reduced connectivity

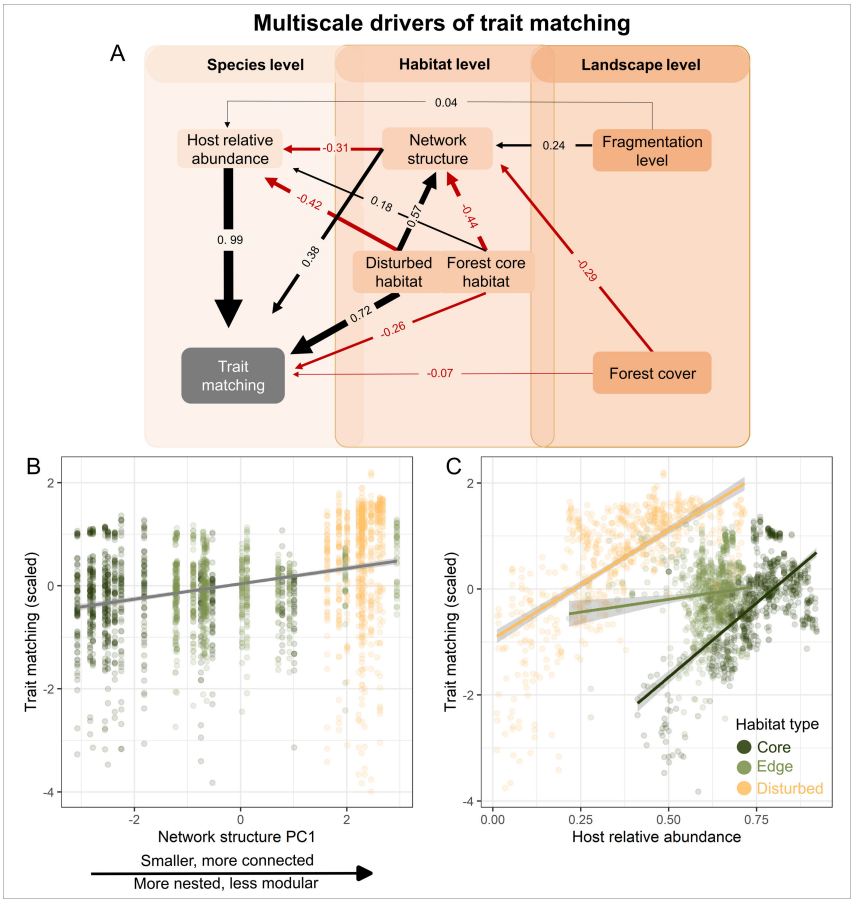

Figure 6. (A) Piecewise structural equation model (PSEM) diagram describing the effects of landscape level (proportion of forest cover, and fragmentation), habitat level (network structure, forest core and disturbed patches) and species level (host relative abundance) variables on the trait matching 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 standardized 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).

can constrain host and parasite movement, increasing parasite extinction rates, limiting gene flow and interaction opportunities. This promotes localized coevolutionary dynamics and increases the probability that new parasite variants emerge [54,55]. 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 specialized 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 [18]. 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 [18]. Isolated populations tend to be more susceptible to new infections due to a decrease in the diversity of resistant phenotypes in host populations [47]. 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 [56,57]. 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 [58]. The loss of suitable but low-competence hosts is a key factor driving increased parasite prevalence among the remaining hosts [49]. 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 [59].

While previous models focus on either spatial structure or coevolution in isolation [15,60,61], 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 emphasized the influence of landscape and environmental change on different ecological interactions [10,20]. 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 [5]. 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 [62,63]. 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 [18,59]. Third, the model does not include pathogen-specific traits such as transmission mode or latency, or individual-level infection dynamics, which could influence eco-evolutionary feedbacks. Fourth, we do not model interspecific interactions between hosts, such as predation or competition. These interactions are likely to affect host distribution and the probability of transmission, especially in highly fragmented landscapes [64,65]. Future studies should aim to integrate more detailed trait-based models and explore dynamic spillover processes in multi-host systems. Moreover, given evidence that climate change can elevate spillover risk [66,67], future studies should explicitly investigate the interactive effects of land-use and climate change on host–parasite eco-evolutionary dynamics. For example, existing models that assess climate-driven changes in the probability of parasite sharing often overlook the potential dilution effect maintained by connectivity among natural habitats, as well as the consequences of biodiversity loss (across both host and parasite species) for spillover probability and coevolutionary adaptation. Consequently, variation in community composition, ecosystem context and spatial scale (from local to regional) is likely to generate divergent outcomes in transmission dynamics.

Enhancing landscape configurations that preserve the integrity of core areas 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 network [61]. Hence, conservation and restoration actions should not only focus on diminishing fragmentation *per se*, but on preserving the integrity of forest core habitats [61,68,69]. For example, decision makers should aim to maintain or restore ecological corridors and manage edge zones [70]. Corridors can enhance functional connectivity, facilitating movement of host populations and promoting more stable interaction networks [71]. 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 preserve the integrity of their natural core habitats, by diminishing edge effects and allowing dispersal between patches, 'dilute' the distribution of parasites within the host community. Hence, maintaining the connectivity between forest fragments also leads to more homogeneous coevolutionary trajectories. Furthermore, host abundance drives interaction and coevolutionary patterns that regulate parasite infection and influence the persistence of parasite diversity across 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.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Data and code for model and analysis reproducibility are available in Figshare [72]. This manuscript is deposited at EcoEvoRxiv (https://doi.org/10.32942/X2V65B).

Supplementary material is available online [73].

Declaration of AI use. We used AI-assisted technologies to improve the readability and language of the work. AI was also used to improve and optimize the analysis code written in R.

Authors' contributions. A.P.L.C.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, visualization, writing—original draft, writing—review and editing; K.A.G.: conceptualization, formal analysis, methodology, resources, software, validation, visualization, writing—original draft, writing—review and editing; G.R.W.: conceptualization, data curation, project administration, validation, writing—review and editing; P.S.D.: supervision; C.S.A.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This work was funded by the Serrapilheira Institute (1912-32354). A.P.L.C. was supported by VPPCB-FIOCRUZ Postdoctoral Program, K.A.G. by the University of Zurich Postdoc Grant (grant FK-22-114) and Marie Sklodowska-Curie Actions Postdoctoral Fellowship (grant EP/Z000831/1), and C.S.A. by Comunidad de Madrid, 2022-T1/AMB-24091.

Acknowledgements. We thank the researchers present at the Workshop 'Adaptive networks for parasite spillover' for their valuable discussions and insights that led to this work, and SALVE-ICMBio (Processo de Avaliação do Risco de Extinção da Fauna Brasileira—Instituto Chico Mendes de Conservação da Biodiversidade) for providing the database used as input for our model.

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