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RESEARCH ARTICLE

Disentangling direct from indirect effects of habitat disturbance on multiple components of biodiversity

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Abstract

1. Human habitat disturbance affects both species diversity and intraspecific genetic diversity, leading to correlations between these two components of biodiversity (termed species–genetic diversity correlation, SGDC). However, whether SGDC predictions extend to host-associated communities, such as the intestinal parasite and gut microbial diversity, remains largely unexplored. Additionally, the role of dominant generalist species is often neglected despite their importance in shaping the environment experienced by other members of the ecological community, and their role as source, reservoir and vector of zoonotic diseases. New analytical approaches (e.g. structural equation modelling, SEM) can be used to assess SGDC relationships and distinguish among direct and indirect effects of habitat characteristics and disturbance on the various components of biodiversity.
2. With six concrete and biologically sound models in mind, we collected habitat characteristics of 22 study sites from four distinct landscapes located in central Panama. Each landscape differed in the degree of human disturbance and fragmentation measured by several quantitative variables, such as canopy cover, canopy height and understorey density. In terms of biodiversity, we estimated on the one hand, (a) small mammal species diversity, and, on the other hand, (b) genome-wide diversity, (c) intestinal parasite diversity and (d) gut microbial heterogeneity of the most dominant generalist species (Tome's spiny rat, *Proechimys semispinosus*). We used SEMs to assess the links between habitat characteristics and biological diversity measures.

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3. The best supported SEM suggested that habitat characteristics directly and positively affect the richness of small mammals, the genetic diversity of *P. semispinosus* and its gut microbial heterogeneity. Habitat characteristics did not, however, directly impact intestinal parasite diversity. We also detected indirect, positive effects of habitat characteristics on both host-associated assemblages via small mammal richness. For microbes, this is likely linked to cross species transmission, particularly in shared and/or anthropogenically altered habitats, whereas host diversity mitigates parasite infections. The SEM revealed an additional indirect but negative effect on intestinal parasite diversity via host genetic diversity.
4. Our study showcases that habitat alterations not only affect species diversity and host genetic diversity in parallel, but also species diversity of host-associated assemblages. The impacts from human disturbance are therefore expected to ripple through entire ecosystems with far reaching effects felt even by generalist species.

KEYWORDS
biotic interactions, host genetic diversity, human disturbance, intestinal parasite diversity, microbiome heterogeneity, species diversity

1 | INTRODUCTION

The abiotic environment embodies a principle selection agent for biological communities. As such the environment determines both the overall species diversity of the biological community and the genetic diversity within a species in parallel, resulting in species–genetic diversity correlations (SGDCs; Vellend & Geber, 2005; Figure S1). Following SGDC expectations, habitat characteristics such as size and connectivity influence species diversity and intraspecific genetic diversity (MacArthur & Wilson, 1963), as seen in tenebrionid beetles distributed across 15 islands of varying sizes in the Aegean Archipelago (Papadopoulou et al., 2011). Such collinearity between species diversity and genetic diversity of individual species in relation to habitat size is a common pattern (Vellend et al., 2014; e.g. freshwater snails: Lamy et al., 2013; freshwater fishes: Fourtune et al., 2016; palaeotropical bats: Struebig et al., 2011), and a variety of habitat characteristics, such as humidity or temperature, can cause similar co-variation (temperate grass species: Kembel & Cahill, 2011; but see Marchesini et al., 2018, for a negative relationship in an alpine frog).

Equally, ecological interactions exert selection on both species diversity and intraspecific genetic diversity (Vellend & Geber, 2005; Figure S1). The genetic diversity in an ecologically dominant (i.e. common or functionally important) species is predicted to shape the environment and ecological interactions (and hence selection) experienced by the rest of the biological community with ramifications for overall species diversity (and subsequent evolution; Hendry, 2016; Vellend & Geber, 2005). Three-spined stickleback *Gasterosteus aculeatus* with distinct phenotypes, for example, affect the community of prey and nonprey species, the primary production, the biochemical composition and even spectral properties of light transmission in their habitat (Harmon et al., 2009; Matthews et al., 2016). Vice versa, changes in the diversity and relative abundance of coexisting species can lead to changes in the genetic diversity of the dominant species (Vellend & Geber, 2005). To stick with the example, changes to the prey community following stickleback predation affected the fitness, survival and, crucially, genetic diversity of the next generation of predators (Best et al., 2017).

SGDC relationships have traditionally been explored between genetic diversity of dominant species and the community's species diversity without considering the impact on host-associated assemblages, such as parasites or commensal micro-organisms. This is surprising given that parasite diversity differs vastly between habitats (Eizaguirre et al., 2011; Froeschke et al., 2010), host species diversity changes transmission and proliferation of parasites (i.e. dilution effect; Civitello, et al., 2015a; but see also Johnson et al., 2016) and host immunogenetic diversity alters cross-species transmission (Lively, 2010) and within-species resistance (Ekroth et al., 2019; King & Lively, 2012; Meyer-Lucht & Sommer, 2009). At the same time, parasites maintain genetic diversity (Cabalzar et al., 2019) and even drive host speciation (Bordes & Morand, 2008; Eizaguirre et al., 2012). Similarly, the environment (Alpízar et al., 2021; Fackelmann et al., 2021; Ruiz-Calderon et al., 2016) and host genetics (Grieneisen et al., 2021; Morella et al., 2020; Suzuki et al., 2019), as well as pathogenic infections (Sabey et al., 2021; Wasimuddin et al., 2019) determine the composition of the commensal microbiome. The gut microbiome itself can modulate host immunity and, thus, parasite or pathogen resistance (Armenteros et al., 2015; Brestoff & Artis, 2013; Näpflin & Schmid-Hempel, 2018). Yet, some of the links between parasite and microbial diversity in

relation to the environment, species diversity and host genetics remain unclear.

Moreover, global phenomena, such as climate change (Gilman et al., 2010), and local or regional disturbances, such as habitat fragmentation, agricultural intensification and contact with humans or livestock (Almeida-Rocha et al., 2020; Rybicki et al., 2020), can alter the link between the environment and species diversity or/and genetic diversity of single species. In butterfly communities of the Indonesian island of Kalimantan, changes in species richness mirror the allelic richness across rainforest habitats after regular disturbances by El Niño Southern Oscillation (Cleary et al., 2006), and the allelic diversity of papillose woolly bats *Kerivoula papillosa*, a forest specialist, declines in accordance with species richness following habitat fragmentation in the Malaysian rainforest (Struebig et al., 2011). Whether man-made or natural, understanding how and to which degree habitat disturbances shift biological assemblages, particularly those associated with common hosts, is uncertain and a knowledge gap both for conservation (Jiménez et al., 2020) and OneHealth programs (Gruetzmacher et al., 2021).

Given the established connection between environmental disturbance, biodiversity loss and zoonosis (Gibb et al., 2020; Keesing et al., 2010), a better understanding of the complex interplay between habitat characteristics, species diversity and intraspecific genetic diversity as well as the patho- and microbiome is essential. Especially the role of generalist species, which often thrive in anthropogenically altered habitats and function as disease reservoirs or vectors (Fackelmann et al., 2021; Johnson et al., 2020; Keesing & Ostfeld, 2021), remains obscure. In order to understand the permeability of habitat disturbance across various layers of biological diversity and decipher their reciprocity, we applied structural equation modelling (SEM, Grace et al., 2010) to field data from a neotropical mammal community sampled across habitats with various degrees of human disturbance and fragmentation in central Panama. Aside from mammalian species richness, the model used genome-wide diversity (single-nucleotide polymorphism, SNP), intestinal helminth diversity and gut microbiome heterogeneity of the generalist Tome's spiny rat *Proechimys semispinosus*—an important pathogen reservoir and common throughout all sites (Heni et al., 2020; Paraskevopoulou et al., 2020; Schmid et al., 2018)—to test six discrete and mechanistically sound predictions that are based on and/or expand on the conceptual model of Vellend (see Figure 1 for detailed description of each prediction, Vellend & Geber, 2005).

2 | MATERIALS AND METHODS

2.1 | Study sites

The 22 study sites in the Panama Canal area (Figure S2) are located in four different landscapes that differ in their degree of human disturbance and fragmentation. Five sites represent largely undisturbed continuous lowland rainforest habitats that are embedded in a large matrix of similar habitat. Six sites are isolated forested islands that lie within the Gatún Lake and that originate from former hilltops of continuous primary lowland forests that were surrounded by water after the flooding of the Panamá Canal about 100 years ago (Rogers, 2014). Another 11 sites are embedded in an agricultural matrix, six of them are in smaller forest fragments and five are located in teak plantations. The sites in the lowland continuous forest and on the forested islands have been protected by the Barro Colorado Nature Monument (BCNM) for over 70 years. The islands represent fragmentation without further human disturbance (Fackelmann et al., 2021). In contrast, the study sites in the forest fragments and plantations are located in an area that is subjected to intense land-use changes and an increase in the human population during the last 60 years after the construction of the Transístmica highway in the 1950s (Rompré et al., 2008).

2.2 | Habitat characterization

The degree and frequency of human disturbance and fragmentation can result in divergent habitat characteristics across sites, and we therefore measured fragment size and vegetation structure at each site. This accounts for differences in the fine-scale habitat structure aside from their broad classification into four landscape categories. The total fragment size each sampling location (Figure 2a) was measured using Google Earth (https://earth.google.com/web/) and QGIS v.3.6.3 (QGIS Development Team, 2018). We measured three vegetation structure variables (canopy cover, canopy height and understorey density, Figure 2b–d) at 10–20 positions, as described in Hiller et al. (2020; see Supporting Information for details).

All continuous values were scaled using the 'BASE' package (Becker et al., 1988) in R version 3.6.1 (R Core Team, 2019). In order to incorporate both the categorical variable 'landscape type' and the continuous habitat features and, thus, account for natural variation between study sites, we performed a factor analysis of mixed data (FAMD, Pagés, 2004) using the R package 'FACTOMINER' (Lê et al., 2008). Here, we included the variables 'landscape type', 'fragment size', 'canopy cover', 'canopy height' and 'understorey density' and used the orthogonal coordinates of these habitat characteristics in the subsequent analysis.

2.3 | Small mammal trapping and sampling

The small mammal community was sampled between September and May during three field seasons in the 2013/14, 2014/15 and 2016/17. Animals were live-trapped for five consecutive nights at each study site. Within each site, we used 100 evenly spaced trapping stations (consisting of three traps each) occurring at 20-m intervals along parallel trapping lines (for more details, see Schmid et al., 2018). We identified mammal species based on morphological characteristics and took ear biopsies, which we stored in absolute ethanol for subsequent DNA extraction. We were able to collect two fresh faecal samples from 262 captured spiny rats—our focal generalist—from inside their trap; one was stored in 95% ethanol

for later parasite screening and the other was stored in RNAlater (Ambion) for microbiome sequencing.

2.4 | Small mammal species richness

We calculated the Chao1 index (Chao, 1984) in order to estimate small mammal species diversity for each study site by using EstimateS version 9.1.0 (Colwell & Elsensohn, 2014) on data pooled from all field seasons. The Chao1 index is particularly useful for datasets such as ours that are skewed towards low-abundance species (summarized by Kim et al., 2017; see Supporting Information for using Shannon exponent instead, Figure S3). After log transformation, the distribution of Chao1 did not deviate from a normal distribution.

2.5 | Genome-wide diversity (SNPs) of the dominant small mammal species

We used SNP genotyping to infer the genomic diversity of the most common small mammal species in our study system, the Tome's spiny rat *P. semispinosus*. We extracted DNA from the ear tissue samples by using the NucleoSpin® 96 Tissue Kit (Macherey-Nagel). Genotyping-by-sequencing (GBS) library preparation with the restriction enzyme MsII and library sequencing (paired-end 150 bp reads) with Illumina NextSeq 500 V2 technology was conducted by LGC Genomics GmbH. The sequencing coverage was *ca*. 3 M reads per individual. SNP calling was performed using the de novo pipeline of STACKS v2.2 (Catchen et al., 2011, 2013) following the developers' recommendations (Paris et al., 2017; Rochette & Catchen, 2017). We used a minimum minor allele frequency of 0.1 and a maximum observed heterozygosity of 0.95 and filtered for SNPs that were present in at least 85% of the individuals and at least in 10 of the 22 investigated study sites. We further restricted our analysis to the first SNP per locus to reduce the risk of working with highly linked SNPs. We used BayeScan (Foll & Gaggiotti, 2008) to identify loci potentially under positive selection and excluded them such that a final dataset of 6,917 presumably selectively neutral SNP loci from 262 individuals was available ($n_{\text{Continuous Forest}}$ = 108, $n_{\text{Forested island}}$ = 70, $n_{\text{Forest fragment}}$ = 54, $n_{\text{Plantation}}$ = 30). To describe the genomic diversity of an individual, we used VCFtools 0.1.15 (Danecek et al., 2011) and calculated the individual inbreeding coefficient *F* as a measure for individual heterozygosity. We inversed the values (1—inbreeding coefficient *F*) such that higher values represented a higher degree of individual genomic diversity.

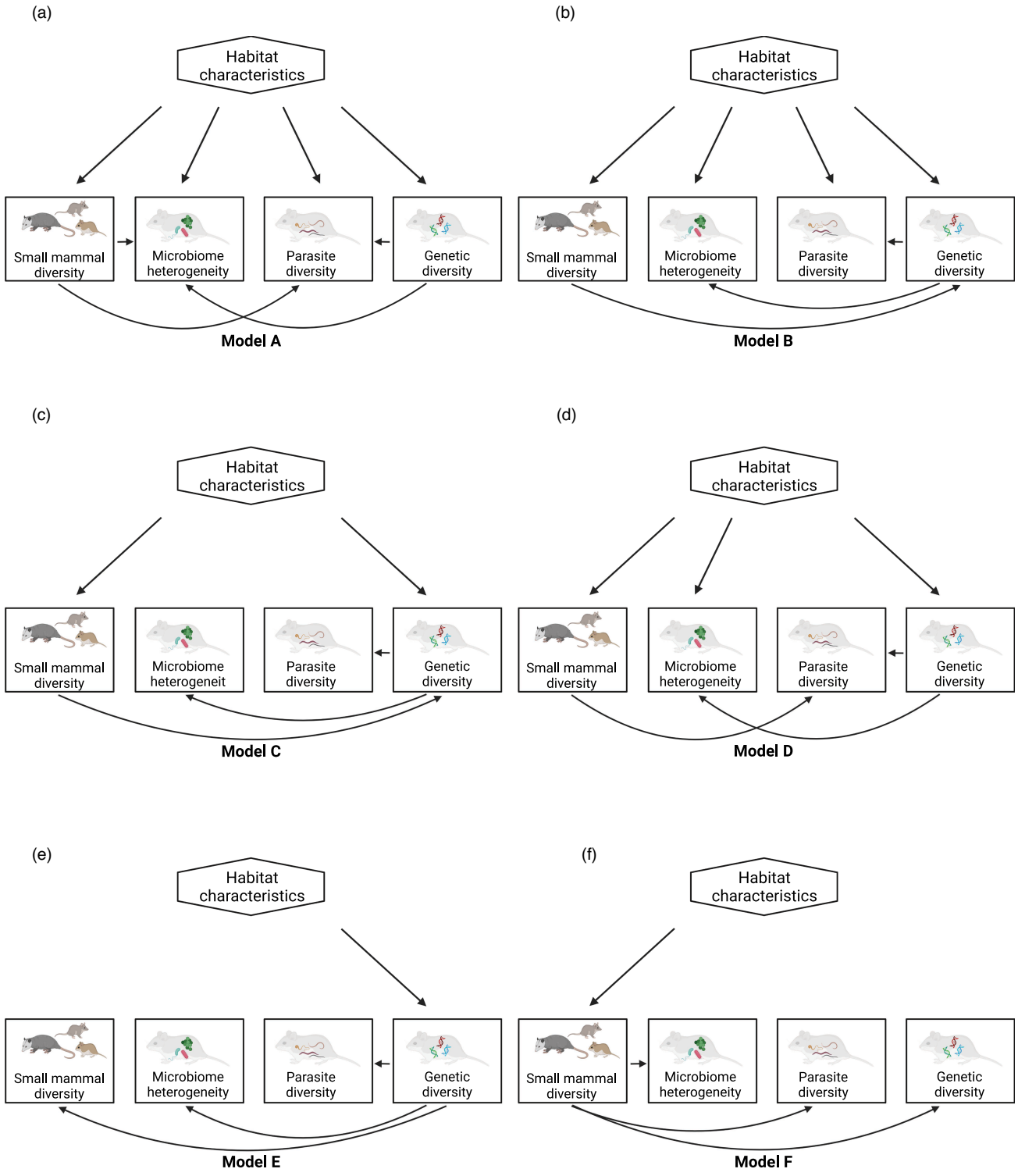
2.6 | Intestinal parasite screening of the dominant small mammal species

For the intestinal parasite screening of the spiny rats, we used the McMaster flotation technique and a potassium iodide solution with a specific weight of 1.5 g/ml mixed with faecal matter (Froeschke et al., 2010; Meyer-Lucht & Sommer, 2005). This method identified 14 different egg morphotypes (i.e. at least 14 different intestinal helminth species) in faeces of *P. semispinosus* (details in Heni et al., 2020). We calculated the exponential of Shannon parasite entropy (Hill numbers with $q = 1$) for each *P. semispinosus* individual by using the package 'DIVERSE' v.0.1.5 (Guevara et al., 2016). We chose this index because it considers species richness and the proportional abundance of species to describe helminth parasite diversity.

2.7 | Microbiome diversity of the dominant small mammal species

The 16S rRNA gene sequencing data of the V4 region used to describe the gut microbial community of the spiny rat were extracted from an earlier study (Fackelmann et al., 2021; see Supporting Information for a short description of the analysis). After filtering, we arrived at an average read count of 15,838 (±4,772 *SD*) per individual. We first calculated within each site the inter-individual differences in microbial community using the Jaccard distance, which emphasis taxa identity over taxa abundance, as commonly done in microbiome research (Comin et al., 2021; Lozupone et al., 2007). This index equally weights the presence of rare and common species and we assumed that habitat differences manifested themselves

FIGURE 1 The six *a priori* models for possible interactions between habitat characteristics and various components of biodiversity (extension to the conceptual model of Vellend & Geber, 2005; Figure S1). Model A and B test whether habitat characteristics affect all components of biodiversity, namely small mammal diversity, the spiny rat's genetic diversity, helminth diversity and microbiome heterogeneity, in parallel. The two models only differ in the predicted relationships between the diversity measures. (a) Model A assumes that small mammal diversity and the spiny rat's genetic diversity affect its microbiome heterogeneity and helminth diversity, whereas in (b) Model B, we predict that the small mammal diversity influences the genetic diversity of the spiny rat and that the spiny rats' genetic diversity influences its helminth diversity and microbiome heterogeneity. (c) Model C tests for a role of species diversity on the genetic diversity of the spiny rat with consequences for microbiome heterogeneity and helminth diversity. In this model habitat characteristics only influence small mammal diversity and the spiny rat's genetic diversity. (d) Model D assesses direct and parallel effects of the habitat characteristics on the small mammal diversity and the spiny rat's genetic diversity and microbial heterogeneity but not on the spiny rat's helminth diversity. Instead, helminth diversity is only influenced by the small mammal diversity and the spiny rat's genetic diversity, which, in turn, influences the microbiome heterogeneity. (e) Model E assumes that the genetic diversity of the dominant generalist species, *Proechimys semispinosus*, influences all other measures of diversity. Vice versa, (f) Model F poses that small mammal diversity impacts all other measures of species diversity. Plotted with BioRender.com



particularly through the presence of less common bacteria. We then used the 'divergence' function of the R package 'MICROBIOME' (Lathi & Shetty, 2019) to estimate the heterogeneity of the microbiome. This method calculates, for each individual, the dissimilarity between its microbial community in reference to the metapopulation mean. While the microbiome heterogeneity correlated with alpha diversity (e.g. Shannon; see Figure S4), we used beta diversity because it is the more appropriate measure to represent dissimilarities between microbial communities varying in some group variable (such as health, sex, location; Zaneveld et al., 2017).

2.8 | Structural equation models

Structural equation models (SEMs) can test hypotheses and causal networks of a priori models that include direct and indirect effects

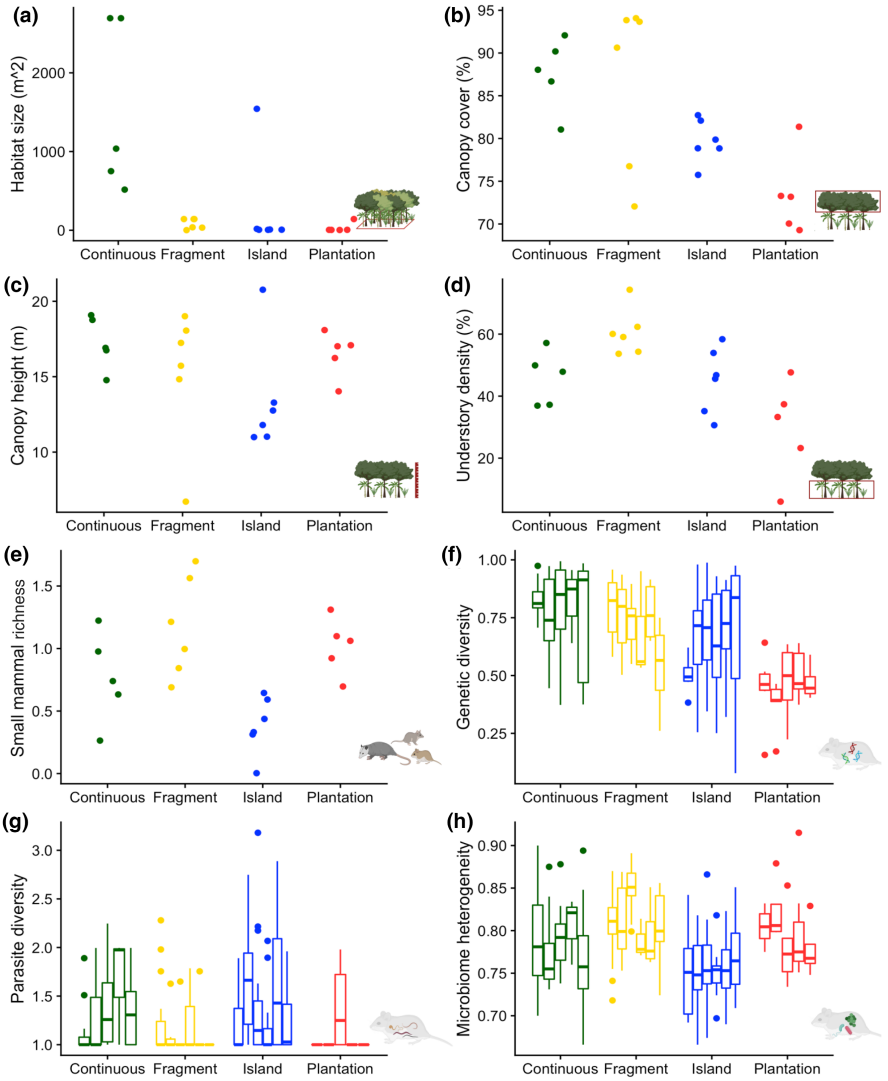


FIGURE 2 Site-specific habitat characteristics (a–d) and small mammal species richness (Chao1) (e) across 22 study sites in the Panama Canal region. Box plots of host-specific information on (f) genetic and (g) intestinal parasite diversity (exponential of Shannon entropy) as well as (h) microbiome heterogeneity (Jaccard divergence) measured in 262 Tome's spiny rats *Proechimys semispinosus*. Green: continuous lowland rainforest; yellow: forest fragments embedded in agricultural landscape; blue: forested islands in the Panama Canal, red: teak plantations. Icons plotted with BioRender.com

and composite variables, which are variables that are specified by causal indicators (Grace et al., 2010; Kline, 2015). We first specified a set of six different a priori models as biologically sound relationships among habitat characteristics and the various measures of biodiversity. These models incorporated small mammal species richness, gastrointestinal parasite diversity, microbiome heterogeneity and genomic diversity of the dominant generalist rodent species (*P. semispinosus*), while simultaneously including indirect effects and interactions between the variables (Figure 1).

The data used in our SEM included information on site-specific habitat characteristics (Figure 2a–d) in form of the first two dimensions of the FAMD, the small mammal species richness calculated as Chao1 (Figure 2e) in each of our 22 sites, and genetic (genome-wide SNP sequencing data) diversity in form of the inverse inbreeding coefficient, gastrointestinal parasite diversity estimated as Shannon diversity and gut microbial diversity measured as microbiome heterogeneity of 262 spiny rats (Figure 2f–h). Prior to modelling, we tested for multivariate outliers by using the Mahalanobis distance of the R package 'STATS' (R Core Team, 2019) and inspected the distributions of all variables by using the R package 'FITDISTRPLUS' (Delignette-Muller & Dutang, 2015). If required, we log-transformed variables to improve the fit to the normal distribution. We verified the absence of extreme multicollinearity (Kline, 2015) and followed the generally proposed procedure for SEM specification (Grace et al., 2010; Kline, 2015). In structural equation modelling, a model fits the observed data to the extent that the model-implied covariance matrix is equivalent to the empirical co-variance matrix, that is, the model fit determines the degree to which the structural equation model fits the sample data (Schermelleh-Engel et al., 2003). For each model, we verified the requirement of identifiability (Kline, 2015) and assessed the model fit with the Chi-square test ($p > 0.05$ = acceptable, Barrett, 2007), the Akaike information criterion (AIC), the Bayesian information criterion (BIC), Bentler's comparative fit index (CFI > 0.95 = good fit), the Tucker–Lewis index (TLI, >0.9 = adequate fit), the root mean square error of approximation (RMSEA, <0.1 = adequate fit) and the standardized root mean square (SRMR, <0.10 = adequate fit) (summarized by Kline, 2015). For reference, the summary of all model parameters used to test for identifiability for the SEM reported in the results section (Table 1) was also compared to SEMs run on data where (a) the small mammal species diversity was calculated as Shannon index instead of Chao1, (b) parasite diversity was calculated as Simpson index instead of Shannon

TABLE 1 Comparison of the model fit of the six a priori models. Indices show model A to have an excellent fit, whereas all other models have a poor fit. AIC, Akaike information criterion; BCI, Bayesian information criterion; CFI, Bentler's comparative fit index; Chisq, Chi-square value; DF, number of degrees of freedom; RMSEA, root mean square error of approximation; SRMR, standardized root mean square; TLI, Tucker–Lewis index

Model	Chisq	df	p-value >0.05 = acceptable	CFI>0.95 = good fit	TLI>0.9 = adequate fit	AIC smaller is better	BIC smaller is better	RMSEA <0.1 = adequate fit	SRMR <0.10 = adequate fit
Model A	4.060	4	0.398	1.000	0.998	−483.911	−433.954	0.008	0.028
Model B	37.448	5	0.000	0.776	0.374	−455.503	−409.114	0.151	0.073
Model C	74.194	7	0.000	0.545	0.091	−426.856	−387.604	0.182	0.124
Model D	23.374	6	0.001	0.882	0.725	−470.844	−428.024	0.100	0.062
Model E	50.772	6	0.000	0.690	0.278	−445.052	−402.232	0.162	0.102
Model F	52.774	6	0.000	0.696	0.291	−446.128	−403.308	0.161	0.08

diversity and (c) all biodiversity components except genetic diversity of the host were calculated as Shannon indexes (Table S2). We decided not to derive a Shannon index for the host's genetic diversity, because in the absence of a reference genome, this would be hard to interpret (Ma et al., 2020). We analysed the SEM framework with the R packages 'LAVAAN' (Rosseel, 2012), 'SEMPLOT' (Epskamp, 2019) and 'SEMTOOLS' (Jorgensen et al., 2019) and used the maximum likelihood estimator (MLM) to obtain robust standard errors and scaled test statistics. By using a distance-based redundancy analysis (dbRDA), we confirmed that geographic dependence is unlikely to have contributed strongly to our results (see Supporting Information for details and results of the dbRDA).

2.9 | Ethics approval and permits

All work was carried out with full ethical approval (Smithsonian IACUC protocol 2013-0401-2016-A1-A7 and 2016-0627-2019-A1-A2) and the samples were exported to Germany with the permission of the Panamanian Government (SE/A-21-14–SE/A-12-18, SEX/A-22-15, SEX/A-24-17, SEX/A-120-16 and SEX/A-52-17). More details on animal handling are described in Schmid et al. (2018).

3 | RESULTS

3.1 | Habitat characteristics

The study sites and landscape types differed vastly in important habitat characteristics (Figure 2a–d): the percentage canopy cover, for example, was highest in continuous forest sites, followed by fragments, islands and, finally, plantations. In addition, all habitat characteristics, whether continuous or categorical, were represented in the first two dimensions of the computed FAMD, which explained 64.41% of the variation (for more details, see Figure S5). The study sites of the four landscapes (which mainly reflect the type of matrix in which they are located and their degree of isolation) were separated in these dimensions. The study-site-specific habitat information in our SEMs was then used in form of principal coordinates of the first two dimensions and constitutes the composite variable 'habitat characteristics'. Given habitat varying in disturbance and fragmentation differed consistently in certain characteristics, this composite variable also functions as proxy for the degree of human disturbance.

3.2 | Structural equation models

Model comparison indicated that habitat characteristics directly affected multiple levels of biodiversity, with model A providing the best fit to the data containing Chao1 to represent small mammal species richness, the inverse inbreeding coefficient for genetic diversity of spiny rats, Shannon index for helminth diversity, microbiome heterogeneity for inter-individual microbial diversity (Table 1). Models B-F fit poorly (Table 1) and

a comparison with models containing (i) Shannon index instead of Chao1 for the small mammal species diversity, and (ii) Simpson index instead of Shannon diversity for helminth diversity were consistent with our main model, although of an inferior fit (Supplementary Table S2). The reasons for the difference might relate to the fact that Chao1 gives more weight to low-abundance small mammal species, whereas Shannon diversity also considers relative abundance of parasite species. Using (c) only Shannon diversity indices for all biodiversity metrics except genetic diversity did not satisfy model fit criteria (Table S2). Below, we only present the results of the best-fitting model A (Figure 3). In general, the results indicated a parallel effect of habitat characteristics on the different components of biodiversity, and indirect interactions between species and host genetic diversity and host-associated assemblages.

Specifically, we found evidence for positive effects of habitat characteristics on small mammal species richness (std.est = 0.31, 95% CI [0.20, 0.42], $p < 0.001$, Figure 3a,b, Table S3) and on microbiome beta heterogeneity (std.est = 0.25, 95% CI [0.14, 0.36], $p \leq 0.001$, Figure 3a,c, Table S3). Equally, habitat characteristics were positively correlated with the spiny rat's genetic diversity (std.est = 0.31, 95% CI [0.20, 0.41], $p < 0.001$, Figure 3a,e, Table S3). The effect sizes of habitat characteristics on these three variables were similar and the diversity at all levels was usually higher in study sites belonging to the landscape categories 'continuous forest' or 'forest fragment' than for small islands (Figure 3b,c,e).

We did not find strong evidence for a direct effect of the habitat characteristics on the parasite diversity (std.est = −0.09, 95% CI [−0.19, 0.01], $p = 0.08$, Figure 3a,d, Table S3). Instead, we found evidence for indirect effects of the habitat characteristics on parasite diversity (see Table S3 for estimates), as we uncover a negative correlation of parasite diversity and small mammal species richness (std.est = −0.29, 95% CI [−0.40, −0.19], $p < 0.001$, Figure 3a, Table S3). The spiny rat's parasite diversity was positively correlated with its genomic SNP diversity (std.est = −0.26, 95% CI [0.15, 0.36], $p < 0.001$, Figure 3a, Table S3).

We found no evidence for a relationship between genetic diversity measured as genomic SNP diversity and the host's microbiome heterogeneity (std.est = −0.09, 95% CI [−0.21, 0.20], $p = 0.12$, Table S3). Instead, we observed that small mammal species richness was positively associated with the spiny rat's microbiome heterogeneity (std.est = 0.24, 95% CI [0.14, 0.34], $p < 0.001$, Figure 3a, Table S3). The microbiome heterogeneity was correlated with both the habitat characteristics and the small mammal species richness, both variables having similar effect sizes. The effect sizes of the paths between the diversity measures were generally slightly smaller than the effect sizes of the habitat characteristics on each diversity measure.

4 | DISCUSSION

Species diversity and genetic diversity within a species are often strongly correlated owing either to shared selection by the environment or/and the interplay between organisms themselves (Vellend & Geber, 2005). As human disturbances continue to alter pristine ecosystems, it is important to understand how pervasive changes to the biological community are. Our SEM approach indicated that habitat characteristics of tropical landscapes with negligible to acute human influence impacted three components of diversity, namely small mammal species diversity, intraspecific genetic diversity and host microbiome heterogeneity directly and in parallel. In contrast, the intestinal parasite diversity of the dominant rodent, the Tome's spiny rat *P. semispinosus*, was better explained by direct interactions with the small mammal community and is, thus, only indirectly affected by the habitat characteristics. We further identified a direct positive relationship between small mammal species richness and the microbiome of the dominant rodent. Intestinal parasite diversity was also negatively associated with small mammal species richness and host genetic diversity.

4.1 | Parallel effects of habitat characteristics

The highest small mammal species richness was observed in the forest fragments surrounded by agricultural matrix, whereas forested islands had the lowest species richness. While counterintuitive, habitat disturbance and fragmentation per se may not decrease species diversity. Instead, when the total available habitat is large, as is the case for fragments or plantations embedded in agricultural matrix, fragmentation is predicted to increase species diversity (Rybicki et al., 2020), particularly for highly mobile generalist species (Devictor et al., 2008). Vice versa, if the total amount of habitat is limited, such as on islands, fragmentation decreases species diversity (Papadopoulou et al., 2011; Rybicki et al., 2020). These findings align with results found for bat species richness compared between islands within and the mainland surrounding Gatún Lake (Meyer & Kalko, 2008). At the same time, the absence of specialized predators in fragmented or managed landscapes may enable generalist mesopredators, like rodents or marsupials, to prosper (Schmid et al., 2018). As a consequence, other taxa, such as birds, might suffer from the predator release of several generalist mesopredators (Crooks & Soulé, 1999). While not assessed here, it is therefore likely that fragmented habitats suffer from a community reshuffling, which is masked by the relative success of generalists (Brändel et al., 2020; Matthews et al., 2014; Meyer & Kalko, 2008).

In line with expectations from SGDC findings, habitat characteristics also directly affected the genetic diversity of the dominant rodent generalist: genetic diversity was highest for habitat characteristics found in continuous forests and forest fragments, whereas the lowest genetic diversity was correlated with habitat characteristics found in teak plantations; and the genetic diversity of individuals on islands showed the largest variance between study sites. This supports the previous argument that highly mobile generalist species can maintain their genetic diversity across fragmented landscapes surrounded by agricultural matrix, but only partly on isolated forested islands and not in strongly modified environments, such as the intensively managed teak plantations (Rybicki et al., 2020). The variance on islands can be explained, on one hand, by bottleneck effects occurring as a result of the flooding of the Panama Canal that probably isolated individuals on

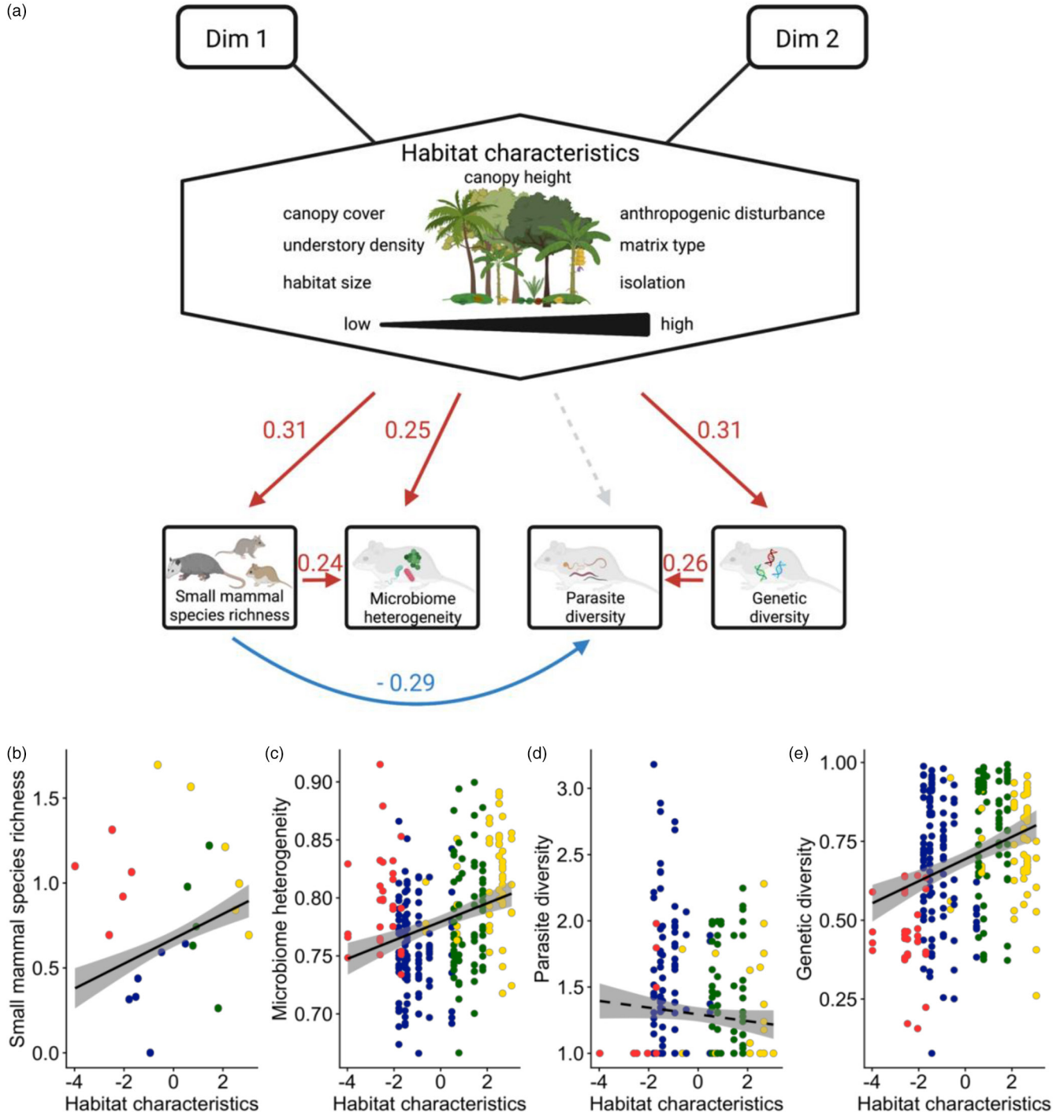


FIGURE 3 Results of the best-fitting structural equation model. (a) Plot of the paths of model A. The edge labels indicate the standardized estimates, which also represent effect sizes and show by how many standard deviations (*SD*s) the outcome changes when the predictor goes up by 1 *SD*. Red indicates a positive relationship ($p < 0.001$), blue indicates a negative relationship ($p < 0.001$) and the grey dotted arrow indicate a tendency ($p = 0.08$). Panels (b–e) show the predicted values ('factor scores') of the structural equation modeling (SEM) for the composite variable 'habitat characteristics' plotted against the variables (b) small mammal species richness, (c) microbiome heterogeneity, (d) parasite diversity and (e) genetic diversity of the spiny rat *Proechimys semispinosus*. The regression line is shown in black when significant and is dashed when marginal in the SEM. The 95% confidence interval is shaded in grey. Dimension 1 (Dim 1) and 2 (Dim 2) are the scores (i.e. principle coordinates) of the first two dimensions of the factor analysis of mixed data (FAMD). Green points: continuous lowland rainforest; yellow points: forest fragments embedded in agricultural landscape; blue points: forested islands in the Panama Canal; red points: teak plantations. SEM paths plotted with BioRender.com

former mountain tops. The Panama Canal was found to be an effective barrier for dispersal and hence gene flow between populations of Geoffroy's tamarin (*Saguinus geoffroyi*; Díaz-Muñoz, 2012) and frugivorous bats, such as *Carollia perspicillata* (Meyer et al., 2009). On the other hand, some islands are able to maintain extremely high population densities and high genetic diversity owing in part to missing predators and possibly rare immigration events from the mainland during droughts (Schmid et al., 2018); Mantled howler monkeys *Alouatta palliata*, for example, exhibit high levels of genetic diversity on the largest island, Barro Colorado Island, also used as one of our study sites (Milton et al., 2009).

Similar to the islands, the teak plantations are somewhat isolated because they are surrounded by unfavourable habitat such as cattle pasture and other teak plantations that might all limit gene flow or the immigration of genetically diverse individuals. Equally, forest fragments are surrounded by agricultural pastures, although we did not find decreased levels of genetic diversity here, possibly because the forest fragment itself represents suitable habitat (for generalists). We suggest that the tight management that often involves clearance of the understorey, a generally lower tree species diversity and reduced canopy density are linked to the observed trend in plantations. The implication is that isolation is a strong predictor for the loss of genetic diversity, even in generalist species that typically become dominant in anthropogenically modified habitats.

Adding to the conceptual understanding of the SGDC framework, we also found evidence for parallel effects of habitat characteristics on the microbiome heterogeneity of the dominant rodent generalist. Individuals from forest fragments had higher microbiome heterogeneity than individuals from continuous forests and forested islands. This finding corroborates previous results on the differences between the landscape types with regard to both the alpha and beta microbiome diversity (Fackelmann et al., 2021). The study states that the abundance of some microbial taxa, although present across all landscapes, differed between the two protected landscapes and the anthropogenically disturbed landscape. Moreover, the microbiomes of individuals from forest fragments surrounded by agricultural matrix contained more taxa associated with domesticated animals and their potential pathogens (Fackelmann et al., 2021). Collectively, this argues for far-reaching and concurrent changes to several components of diversity following human encroachment (e.g. Bordes et al., 2015; Jiménez et al., 2020; Struebig et al., 2011), which might, in turn, enable the emergence and persistence of novel zoonotic diseases (Keesing et al., 2010; Keesing & Ostfeld, 2021; Schmid et al., in review).

4.2 | Species diversity but not host genetic diversity affects the microbiome

Additionally, we found an indirect positive correlation between small mammal species richness and the heterogeneity of the spiny rat's gut microbiome. The gut microbiome is acquired from the environment and is therefore modulated by interspecies interactions (Adair & Douglas, 2016). Microbial species can be dispersed across multiple species (Brown et al., 2020). Indeed, increased human–wildlife and livestock–wildlife contact changes the microbiome diversity of spiny rats (Fackelmann et al., 2021). Our results therefore underscore that the host-associated microbial community depends on both direct habitat differences and indirect modulation by the species community, such as, for example, even seen in the phyllosphere microbiome of Maple trees (Lajoie & Kembel, 2021) or the gut microbiome of Caribbean Cleaning Gobies (Xavier et al., 2019).

Yet, we found no evidence that host genetic diversity measured as genome-wide SNP heterozygosity influenced the microbiome heterogeneity of spiny rats. A genetic heritable component in shaping the gut microbiome is known, for example, from human twin studies (Goodrich et al., 2016) or from experimental studies in mice (Org et al., 2015), although the mechanistic associations between genome-wide heterozygosity and the microbiome composition in wild hosts is not well understood. The absence of a correlation between genetic diversity and microbiome heterogeneity suggests that functional genetic markers, such as adaptive immune genes (i.e. Major Histocompatibility Complex, MHC; rodents: Pilosof et al., 2014; bats: Fleischer et al., 2022; lemurs: Montero et al., 2021) may be better predictors for microbiome heterogeneity than restriction-site associated SNP markers.

4.3 | Small mammal species richness and host genetic diversity impacts its parasite diversity

The model did not reveal a strong link between habitat characteristics and the diversity of the host's intestinal helminth parasites. This indicates that factors other than the level of human disturbance in the environment have a stronger impact on the intestinal parasite diversity of the dominant rodent species. Habitat fragmentation can impact parasite prevalence of haemosporidian blood parasites in the Lesser Antillean bullfinch *Loxigilla noctis* (Pérez-Rodríguez et al., 2018) or *Trypanosoma cruzi* prevalence sampled from a community of small mammals (Vaz et al., 2007). Life-history traits likely influence a parasite's response to habitat fragmentation (Froeschke et al., 2013), as is strongly suggested by the differential abundance of some helminth species sampled from *Sigmodontinae* rodents along a fragmentation gradient (Cardoso et al., 2016), but we are unable to capture such parasite species-specific pattern with our simple diversity index.

However, habitat characteristics indirectly affect parasite diversity via small mammal species richness and the genetic diversity of the generalist rodent host. Various hypotheses about the relationship between host species diversity and parasite diversity exist. One of them, coined the 'dilution effect' hypothesis, posits that communities with higher host species diversity experience a decreased disease risk (Ostfeld & Keesing, 2000). A 'dilution effect' is expected when host species differ in their quality for parasites, for example, when high-quality hosts occur in low abundance in species-rich communities (Ostfeld & Keesing, 2012). Ample support has been provided for this hypothesis (Civitello, et al., 2015a; Civitello, et al., 2015b; Johnson et al., 2013). In agreement with the 'dilution effect' hypothesis, we have found a lower parasite diversity in the generalist rodent host in study sites with higher small mammal species richness, and higher

parasite diversity at study sites with low species diversity, particularly on forested islands. We speculate that the high spiny rat density on the forested islands (Schmid et al., 2018) together with a loss of species diversity may be a driver of parasite species richness in those populations.

We observed an even stronger positive correlation between host genetic diversity and its parasite diversity than between small mammal species richness and the host parasite diversity. At first glance, this may be counterintuitive because genetically homogeneous populations have long been known to suffer from more severe pathogen outbreaks than diverse host populations (Altizer et al., 2003; King & Lively, 2012). However, parasites have been found to select for higher genetic diversity, reduce inbreeding (Cabalzar et al., 2019) or drive speciation (Bordes & Morand, 2008), often intimately linked to intrinsic habitat differences (Brunner et al., 2017; Eizaguirre et al., 2012). Experimental co-evolution has shown that diverse parasite communities impose stronger selection on host populations than single parasites, causing faster selective sweeps of resistance mutations and higher levels of host resistance (Betts et al., 2018). If a diverse parasite community selects against high degrees of homozygosity, a negative correlation between parasite diversity and inbreeding coefficients might be observed. Yet, such a relationship can only be explained on an evolutionary time-scale. As an alternative, one can investigate the diversity of functionally important genomic regions, such as the highly polymorphic genes of the MHC (Sommer, 2005), where we might expect to see a more obvious link to habitat effects driven by parasite-mediated selection (Feulner et al., 2015). The MHC class II diversity of five of six endemic Atlantic forest frog sampled across fragmented and continuous forests showed, for instance, marked declines in individuals from fragments, and especially when compared to neutral markers (Belasen et al., 2022). A loss in MHC class II heterozygosity was also associated with a higher probability of infection with the chytrid fungus *Batrachochytrium dendrobatidis* (Belasen et al., 2022). Likewise, toll-like receptors play an essential role in the host's innate immunity and were found to differ between spiny rats from continuous forest, fragments and islands, with repercussions for infections with some helminths and viruses (Heni et al., 2020). In the future, linking parasite diversity to diversity of functionally important sites of the genome might become more important to unravel selection dynamics in complex biological networks (e.g. Pilosof et al., 2014) than its link to simplistic measures of genetic diversity.

5 | CONCLUSIONS

Changes in habitat characteristics following human disturbances are one of the most important factors influencing ecological communities and species abundance patterns. Yet, comparably little attention has been paid to the interconnectedness of biological communities at various levels of biodiversity, and whether their response differs. This study documents the nature and strength of both direct and indirect, and, at times, parallel effects of habitat disturbance on biodiversity following SGDC predictions: habitat characteristics associated with a gradient of human disturbance were the strongest direct predictors for small mammal species richness, and the genetic diversity and microbial heterogeneity of a dominant generalist. However, we also found clear evidence for indirect effects of human disturbance on host-associated species assemblages via small mammal species richness and host genetic diversity. Changes to host genetic diversity and the host species assemblage in connection with a reshuffling of the host-associated micro and macro-organisms may also explain why anthropogenically altered habitats become sources of diseases. Taken together, our study illustrates how human disturbance impacts multiple components of biodiversity in parallel, and causes cascading effects among them.

AUTHOR CONTRIBUTIONS

Nina Isabell Schwensow conceived the manuscript, curated the data, performed initial bioinformatic and statistical analyses and wrote the first draft of the manuscript. Alexander Christoph Heni collected samples, measured habitat variables, estimated the habitat sizes, curated the data, performed statistical analyses and revised the manuscript. Julian Schmid collected samples, estimated small mammal species richness, measured habitat variables and performed intestinal parasite analyses. B. Karina Montero provided statistical support and contributed to the first draft of the manuscript. Stefan Dominik Brändel measured habitat variables and administrated permits. Tanja Katharina Halczok measured habitat variables. Gerd Mayer performed parasite egg counts. Gloria Fackelmann provided support for the microbiome analysis. Kerstin Wilhelm carried out laboratory work. Dominik Werner Schmid led the revision of the manuscript and edited the text, designed the graphical abstract and performed statistical analyses. Simone Sommer conceived, initiated and designed the project, supervised the study, edited and revised the manuscript. All authors approved the final version of the text.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.zs7h44jcx (Schwensow et al., 2022).

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