Effects of habitat fragmentation on genetic diversity

By

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Dedication

To Mom and Dad. I am dedicating my thesis to both of you. You have always believed in me and given me all the support I have needed to succeed. I love you both and cannot thank you enough for everything you have done for me.

To my Rachel. I am dedicating my thesis to you, for your support, the motivation you give me every day, and reminding me that I look like I eat mango ice cream. I love you and thank you.

Abstract

Biodiversity continues to be lost at unprecedented rates; a loss that is in part underpinned by the erosion of intraspecific genetic diversity. Estimates of up to a tenth of intraspecific genetic diversity has been lost in the past two centuries. Habitat fragmentation is a proposed candidate driving this loss of genetic diversity. However, the predicted negative effects of fragmentation on genetic diversity may not generalize across species. Ecological differences between species and landscapes can alter the effects of fragmentation in species-specific ways. Studies have typically found that genetic diversity is negatively affected by fragmentation, yet these are often single-species studies or meta-analyses that may compound biases from single-species studies. To begin answering whether habitat fragmentation has a generalizable effect across species' genetic diversity, we use a macrogenetics approach to assemble a large dataset of genetic diversity while standardizing the measurement of habitat fragmentation. The combined framework provides a standardized methodology across a broad range of taxa and geographic regions that controls for methodological inconsistencies in the current literature, thereby enabling the synthesis of existing knowledge. In our analysis of North American mammals, birds, and amphibians, we found that genetic diversity in mammals and amphibians was generally negatively associated with fragmentation, whereas genetic diversity in birds was weakly negatively associated with fragmentation. These associations depended on multiple aspects of fragmentation and habitat area being controlled for; when these were not controlled for, associations disappeared. This result implies that fragmentation should be treated as an interdependent process. Given our coarse measure of habitat fragmentation, we consider these results robust and consistent with current theory and empirical work. For conservation and management, habitat fragmentation is generally associated with reduced mammal and amphibian genetic diversity and little to no association with bird genetic diversity.

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General Introduction

It is typically thought that the effects of habitat fragmentation on genetic diversity are generalizable across species and that species likely vary in their response to habitat fragmentation, given differences in dispersal ability, niche breadth, and habitat requirements (Didham et al., 2012; Keyghobadi, 2007; Laurance, 2008). I explore the conception, definition and contemporary understanding of habitat fragmentation and use a data syntheses approach to assess the generalizability of habitat fragmentation's effect on genetic diversity (Didham et al., 2012; Fischer & Lindenmayer, 2007; Riva et al., 2024; Riva & Fahrig, 2023).

Habitat fragmentation

The historical conception of habitat fragmentation

Although fragmentation is a common term in ecological papers, it is often imprecisely defined and conceived (see Haila, 2002 for a full review). The term fragmentation in the context of habitat was first used by Curtis (1956) in his work on the clearing of contiguous pre-European settlement forests into patches. Here, the term was used to describe the pattern of remaining forest after land removal for urbanization. But following the publication of 'Island Biogeography Theory' (IBT; MacArthur & Wilson, 1967), the usage of the term fragmentation began to change from an adjective to an ambiguous theory. MacArthur and Wilson (1967) briefly suggested, in a

single paragraph, that habitat patches might be analogous to islands surrounded by an inhospitable matrix, implying that some aspects of IBT may apply to habitat fragments on land (see Haila 2002). For example, IBT showed that smaller, more isolated islands had fewer species, and this was extended to terrestrial landscapes. Diamond (1975) suggested that this concept be applied to nature reserves, suggesting that "a predictive understanding of extinction might be obtained from island biogeography, since refuges of natural habitat in a sea of human-altered environment behave as islands for species dependent on natural habitat". This concept would guide fragmentation as a theory into the 1980s and beyond.

The historical conception of habitat fragmentation as a theory aids in understanding contemporary debates and interpretations. The consequences of habitat fragmentation for biodiversity are debated. The debates are epistemological, typically arising through discrepancies between IBT and terrestrial landscapes.

Habitat loss and habitat fragmentation

Separating habitat loss (i.e., amount of habitat) from fragmentation (i.e., configuration) is the most contentious theoretical mismatch in the IBT analogy (Haila, 2002; Laurance, 2008 Prugh et al. 2008). An analog to habitat loss is lacking in IBT (Laurance, 2008). Islands were formed over millions of years; hence, island formation predates faunal colonization and extinction dynamics, allowing an island to reach a quasi-equilibrium so that current patterns reflect ongoing immigration and extinction related to island size and isolation rather than the formation event (MacArthur & Wilson, 1967). In contrast, terrestrial habitat "islands" (i.e., habitat patches) generated by recent habitat loss do not guarantee that such an equilibrium is established (Gargiulo et al., 2025; Prugh et al., 2008). Instead, the recent formation event (i.e., habitat loss) continues to influence faunal patterns for a substantial time (Gargiulo et al., 2025;

Pinto et al., 2024). Thus, unless a landscape has reached a quasi-equilibrium following habitat loss, the amount of habitat in the landscape can confound the effects attributed to fragmentation (configuration) (Fahrig, 2003).

This mismatch between IBT and fragmented terrestrial landscapes has led to debate over how habitat amount should be examined in the context of fragmentation: should habitat amount be treated independently or in an interdependent manner with habitat fragmentation? One argument proposes that habitat loss (in terms of area), rather than fragmentation, drives most documented adverse effects of fragmentation. Under this reasoning, because habitat amount covaries with many fragmentation measures, fragmentation should be viewed as fragmentation per se, i.e., the breaking apart of habitat after accounting for amount (Fahrig, 2003). The counter-view is that habitat amount and fragmentation are inherently linked, and one cannot treat the two as statistically independent (Didham et al., 2012; Fletcher et al., 2018). Although differences between these perspectives may appear semantic, the choice of whether and how to include habitat amount in fragmentation analyses can change the direction or magnitude of inferred effects. To date, there is no consensus on best practices for handling variation in habitat amount in fragmentation studies.

The term fragmentation is a panchreston

The IBT analogy further diverges from terrestrial landscapes through various changes found in landscapes that do not occur on islands. In fact, when habitat is fragmentated there are several co-occurring landscape changes such as creation of patch edges, decreases in patch size, increases in inter-patch distances, and increases in the number of patches (Fischer & Lindenmayer, 2007; Haila, 2002; McGarigal et al., 2009). In this way, the term “fragmentation” is often used as an umbrella term encompassing multiple simultaneous processes and states.

Studies often focus on one or a different combination of these processes and this leads to difficult-to-compare empirical results, which hinders the synthesis of the effects of fragmentation on wildlife (Fischer & Lindenmayer, 2007).

The terrestrial matrix is not the sea

The matrix in a terrestrial landscape, unlike the sea, is not uniformly inhospitable (Laurance, 2008). IBT ignores landscape dynamics beyond the probabilistic arrival of colonists across a hostile matrix (Fischer & Lindenmayer, 2007; Haila, 2002; Laurance, 2008). In fact, the matrix in terrestrial landscapes strongly impacts connectivity, and is sometimes suggested to outweigh the effects of fragmentation on connectivity (Ramírez-Delgado et al., 2022; Watling et al., 2011). For example, a matrix composed of cattle pastures can have a greater effect on species extinction risk than one composed of regrowing (secondary) forests in a fragmented landscape (Laurance, 2008). The role of the matrix completely changes the fundamental predictors of extinction proneness, demonstrating that the IBT analogy can be weak and even misleading (Laurance, 2008).

Varied species response to fragmentation

IBT predicts a uniform response across species (Jacquet et al., 2017), but this is inappropriate for fragmentation in terrestrial landscapes. Habitat fragmentation affects different species in highly divergent ways, given that species vary in their ecological specialization, and this specialization dictates whether configuration effects will be negative (for specialists) or positive (for generalists)(Laurance, 2008; Riva et al., 2024). Similarly, the ability to tolerate modified habitats (matrix tolerance) and its correlates (e.g., low dietary specialization) are often identified as key predictors of species vulnerability (Fletcher et al., 2024; Laurance, 2008). Indeed, the species response is not uniform: some species decline sharply or disappear, others

remain roughly stable, and yet others increase, sometimes dramatically (Didham et al., 2012; Garrison, 2006; Laurance, 2008).

Scale of effect—Whose Fragmentation is it?

Less directly an artifact of the IBT analogy mismatch, but nonetheless important, the scale at which habitat fragmentation is analyzed can determine the direction of effect while limiting generalizations across studies (Fahrig, 2003; Fletcher et al., 2023; Garrison, 2006; McGarigal & Cushman, 2002). Scale in fragmentation often refers to measurement at the landscape or patch scale. Some argue that fragmentation should be measured at the landscape-scale because landscape processes outweigh local patch-scale processes (Fahrig, 2003; McGarigal & Cushman, 2002). Others contend that habitat fragmentation operates through local processes at the patch scale, and that patch-scale fragmentation should not be ignored (Chase et al., 2020; Fletcher et al., 2018). Importantly, measuring fragmentation at either patch- or landscape-scale is likely neither correct nor incorrect. Instead, the scale used to measure fragmentation must match the scale of the response variable (Fletcher et al., 2023). Recent work suggests a multi-scale approach that considers different scales (landscape-scale, patch-scale, within-patch-scale) as interdependent, while relying on the scale of the response variable (i.e., abundance, dispersal, occupancy, etc.)(Fletcher et al., 2023). Variations in the scale of measurement across studies have hindered progress toward a unified concept of habitat fragmentation.

The fragmentation debates

The intense debate over the consequences of habitat fragmentation for biodiversity, whether it's negative, positive, or neutral, is epistemological. On one side, viewing habitat amount interdependently of fragmentation and focused on local or patch-scale measurements, argues that fragmentation is inherently negative because the associated decrease in patch size,

increased isolation, and greater edge exposure drive local extinctions, population declines, and ecological decay (Chase et al., 2020; Didham et al., 2012; Fletcher et al., 2018; Haddad et al., 2015). This perspective typically aligns with conserving Single Large reserves in the Single Large or Several Small (SLOSS) debate (Diamond et al., 1976; Simberloff & Abele, 1982). Conversely, focus on landscape-scale analyses that control for habitat area, which contend that the effects of fragmentation per se are often weak, neutral, or even positive for biodiversity, especially at the landscape level (Fahrig, 2003; Fahrig et al., 2019; Riva & Fahrig, 2023). This positive view suggests that distributing the remaining habitat into Several Small patches can increase species richness (including those of conservation concern) by providing landscape-scale benefits, such as spreading the risk of catastrophe or enhancing connectivity between multiple resource types. These proponents argue that conservation efforts should prioritize maximizing habitat area regardless of habitat configuration (Fahrig, 2003; Riva & Fahrig, 2023).

Why synthesis matters in ecology & evolution—The big picture

Synthesis is essential to the scientific advancement of ecology and evolution because it provides the basis for developing and testing general theory (Arnqvist & Wooster, 1995). At the broadest level, the goal of synthesis is to address fundamental scientific uncertainties, such as the origin and arrangement of planetary biodiversity (Beaugrand, 2023), or to reveal unconscious study biases that hinder advancements in theory (Shade et al., 2018). By unifying concepts and integrating fields, syntheses enrich scientific understanding (Shade et al., 2018). This integrated approach is crucial for the application of knowledge to coherently summarize information for environmental policy and decision makers (Gerstner et al., 2017; Nakagawa et al., 2023).

Limits of single-system studies and narrative reviews

Single-system studies and traditional narrative reviews contain inherent limitations that can sometimes compromise generalizability. Narrative reviews, which traditionally summarize findings in ecology and evolution, can be "seriously flawed", often concluding that results across varied studies are merely 'inconsistent,' 'inconclusive,' or 'conflicting' (Arnqvist & Wooster, 1995). This potential weakness stems from narrative reviews' inability to provide quantitative measures of effect magnitude or to draw conclusions based on a standardized set of statistical procedures (Arnqvist & Wooster, 1995). Furthermore, researchers conducting single studies, often constrained to local or small scales, face the "burning problem of scaling," risking controversy when extrapolating localized patterns to broader ecological or geographical contexts (Beaugrand, 2023). Meta-analysis and aggregated raw datasets, conversely, pool multiple studies to increase sample size and reliability, thereby achieving robust, minimally biased scientific conclusions (Arnqvist & Wooster, 1995).

Macrogenetics—A novel synthesis method

To ask how generalizable the effect of habitat fragmentation is across species genetic diversity requires syntheses of habitat fragmentation data and genetic data. Synthesized habitat fragmentation data is readily available through spatial data (i.e., landcover maps), and tools. Instead, the bottleneck to generalizability persists with genetic data. Genetic diversity is challenging to synthesize, given its overall paucity, and difficulties in re-processing and aggregating raw datasets (Leigh et al., 2021; Paz-Vinas et al., 2021).

Macrogenetics is an approach that synthesizes genetic data to address questions about the generalities of patterns. This approach enables the generalization of evolutionary and ecological ideas, such as habitat fragmentation, by exploring broad taxonomic, and spatial scales, across dozens to thousands of species (Leigh et al., 2021). Macroecological concepts are rooted in

population genetic theory and use intraspecific genetic diversity, which encompasses within-population genetic diversity and among-population genetic differentiation (Leigh et al., 2021). By conducting large-scale investigations, macrogenetics can help examine the effects of habitat fragmentation on genetic diversity and differentiation, yielding generalizable results that transcend local context.

Why macrogenetics for habitat fragmentation

Macrogenetics is useful to answer whether habitat fragmentation has a generalizable effect on genetic diversity. Single-species studies are key to the advancement of knowledge in ecology, yet represent only one data point; this would not generalize across species due to a myriad of differences among studies and species such as dispersal ability or landscape context (Keyghobadi, 2007). A macrogenetic approach allows these contingencies to be evaluated across species and regions, revealing shared drivers of genetic diversity and differentiation (Leigh et al., 2021; Paz-Vinas et al., 2021). By synthesizing large, cross-taxon datasets, macrogenetic analyses can distinguish general patterns of habitat fragmentation from system-specific noise and produce management-relevant insights into how fragmentation shapes genetic variation (González et al., 2020).

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Are there generalizable effects of habitat fragmentation on genetic diversity in vertebrates?

Abstract

Habitat fragmentation, the division of continuous habitat into smaller, more isolated patches, is increasing globally. Fragmentation's link to declines in genetic diversity could underpin biodiversity loss via extinction vortexes and reductions in mean population fitness. It is proposed that fragmentation diminishes population genetics by lowering effective population size, increasing genetic drift, and restricting gene flow. However, fragmentation may not necessarily decrease genetic diversity, as even low levels of gene flow can maintain diversity, and contemporary genetic diversity reflects the accumulation of past environmental conditions. We predicted that habitat fragmentation would reduce genetic diversity by increasing random allele loss (drift), limiting the introduction of new alleles, and increasing genetic differentiation among populations. In this study, we test the effects of habitat fragmentation on genetic diversity using microsatellite data from 2,233 mammal, bird, and amphibian populations sampled across 104 species in North America. Specifically, we assess effective population size, population genetic structure (Fst), and multiple measures of genetic diversity. To quantify fragmentation, we calculate habitat amount alongside three fragmentation metrics that capture patch isolation, aggregation, and shape and size. We found evidence that habitat fragmentation is generally negatively associated with mammal and amphibian genetic diversity, and weakly associated with bird genetic diversity. When we did not statistically control for multiple fragmentation metrics and habitat amount simultaneously (i.e., in our bivariate models), we found no associations between genetic diversity and either fragmentation or habitat amount. In addition, we expected that lower levels of habitat amount would increase the association between fragmentation metrics and genetic diversity, but we found no discernible pattern indicating that the amount of habitat in

the landscape moderated the magnitude of this association. Interestingly, we found individual species vary widely in their responses. These findings provide evidence that habitat fragmentation is generally negatively associated with genetic diversity.

Introduction

Biodiversity is being lost at rates that suggest we may be entering a sixth mass extinction (Cowie et al., 2022). A key component of this loss is the erosion of intraspecific genetic diversity, which underpins populations' capacity to adapt to environmental change and avoid extinction (Frankham et al., 2017; Shaw et al., 2025). Global assessments estimate an average decline of 6–10% in genetic diversity across populations (Exposito-Alonso et al., 2022; Leigh et al., 2019). Although the Kunming–Montreal Global Biodiversity Framework has formally recognized the genetic diversity crisis by setting targets for its conservation, many populations are experiencing ecological disturbance without receiving corresponding management or monitoring (Shaw et al., 2025).

Habitat fragmentation is among the most pervasive drivers of biodiversity loss, and it can erode genetic diversity by reducing population size and limiting gene flow among populations (Keyghobadi, 2007; Pfeifer et al., 2017; Schlaepfer et al., 2018). Empirical evidence generally supports this relationship, with studies on individual species often reporting reduced genetic diversity in fragmented landscapes (Belasen et al., 2022; Gracanin et al., 2023; Rowan et al., 2022). Similarly, meta-analyses across taxa suggest that genetic diversity tends to be lower in fragmented compared to contiguous landscapes (Lino et al., 2019; Rivera-Ortíz et al., 2015; Schlaepfer et al., 2018).

However, the lack of standardized approaches to measuring habitat fragmentation limits our ability to generalize its effects on genetic diversity (Keyghobadi, 2007). Habitat

fragmentation is multifaceted, encompassing edge effects, patch isolation, patch size, and patch shape. Fragmented landscapes can vary widely in structure, with no two landscapes identical in their fragmentation patterns. This heterogeneity likely contributes to inconsistent species responses across studies (McGarigal et al., 2009). Moreover, the effects of fragmentation can be more pronounced in areas with limited habitat availability, and some species may be more affected when fragmentation coincides with such conditions (Andrén, 1994a; Swift & Hannon, 2010; Villard & Metzger, 2014).

Generalizability of previous work is further hindered by potential confirmation bias, and the "File Drawer" problem (Rosenthal, 1979). Confirmation bias may arise when researchers preferentially study landscapes with pronounced fragmentation, or, in some instances, overstate the effects on genetic diversity (Fahrig, 2017). Additionally, the file-drawer problem, where null or weak results remain unpublished, can distort our overall understanding of fragmentation's impact on genetic diversity.

To address these limitations, we combined a macrogenetic approach with standardized measurements of habitat fragmentation to assess whether fragmentation consistently affects genetic diversity across species. Macrogenetic analyses use archived genetic datasets, thereby mitigating publication bias in meta-analyses that rely on potentially biased literature testing how habitat fragmentation affects genetic diversity, as the macrogenetic data were not originally collected to test for fragmentation effects. Importantly, this does not mitigate bias in the published genetic data; it only addresses publication bias potentially present in meta-analyses. By integrating these data with publicly available land-cover maps, we calculated multiple landscape metrics to quantify habitat amount and configuration consistently across species.

We used microsatellite markers because they are readily available and effectively capture genetic diversity, providing robust estimates of genetic drift and population structure (Selkoe & Toonen, 2006). To quantify genetic diversity, we analyzed metrics that represent within-population diversity, between-population differentiation, and the influence of random allele loss. Within-population diversity was measured using allelic richness, the count of alleles at a sample site corrected for sample size, and gene diversity, the average probability that two randomly selected alleles at a sample site differ; including both metrics provides complementary insights, as allelic richness is sensitive to the loss of rare alleles and thus reflects more recent changes in genetic variation. Between-population differentiation was quantified using the fixation index (Fst), which measures the degree of genetic divergence among populations. Finally, we estimated effective population size (Ne) to assess the strength of genetic drift, representing the random removal of alleles from populations over time.

We quantified habitat fragmentation using landscape metrics that measure the structural configuration of habitat patches (McGarigal & Cushman, 2002). Habitat fragmentation is often viewed as landscapes with smaller, more isolated patches, a process that directly reflects changes in structural connectivity. Landscape metrics provide a standardized and assumption-light method for quantifying this structure, in contrast to more complex approaches such as network analyses (Foltête & Vuidel, 2025). They allow simultaneous assessment of multiple spatial characteristics of fragmentation, including habitat amount and configuration.

We considered habitat as land-cover classes that categorize the Earth's surface according to features such as vegetation type. To ensure robustness, we considered three proxies of habitat: forest-based, species-specific, and forest fragmentation intensity (a measure of the rate of recent fragmentation). We selected four landscape metrics that align most closely with the conceptual

definition of fragmentation: mean patch size, mean nearest-neighbour distance, edge density, and the proportion of the landscape classified as habitat (i.e., habitat amount).

Our goal was to generalize the effects of habitat fragmentation on genetic diversity. We analyzed raw microsatellite data from 114 studies, encompassing 2,233 populations across 104 species of North American birds, mammals, and amphibians. In this thesis, we sought to include as many terrestrial vertebrate species as possible in North America; however, only data on bird, mammal, and amphibian species were sufficiently abundant to analyze, given our modelling approach. By integrating standardized landscape metrics with macrogenetic data, our approach enables a cross-taxon test of whether fragmentation consistently affects genetic diversity. This synthesis provides an empirical foundation for developing conservation frameworks that can efficiently monitor and prioritize genetic diversity across fragmented landscapes.

Methods

Genetic data assembly. We expanded a previously compiled and published North American mammal, bird, and amphibian microsatellite dataset containing 93 species (19 amphibian; 33 bird; and 41 mammal species) with 2,033 genetic sampling sites (Figure 1; 664 amphibian; 551 bird; and 818 mammal sites) by programmatically searching Dryad (https://datadryad.org) and DataONE https://www.dataone.org). Studies were retained if they included georeferenced sampling sites in North America. We excluded datasets that may bias genetic diversity estimates, such as island sites, genetic rescue, translocation, or captive populations, from the analysis (see Figure S1 for the PRISMA-style flow). Reptiles were excluded from analysis because available microsatellite data were too sparse for meaningful inference. Site coordinates were standardized to WGS 84 and extracted from datasets,

manuscripts, or georeferenced maps as needed. See Supplementary S1-S2 for search queries, exclusion criteria and full georeferencing procedure.

Genetic response variables. We estimated within population genetic diversity for each site by calculating gene diversity (i.e., expected heterozygosity) and allelic richness. Gene diversity measures the evenness and diversity of alleles, while being minimally sensitive to sample size (Nei, 1973). Allelic richness measures the number of alleles, where uneven sample sizes are controlled through rarefaction (Foulley & Ollivier, 2006). We calculate population-specific Fst to estimate population genetic structure, which can be interpreted as divergence from an ancestral population and is calculated as the genetic differentiation among populations (Kitada et al., 2021). We calculate Effective population size (Ne) to estimate the rate at which genetic diversity is lost due to genetic drift over time. See Supplementary S3 for genetic metric calculations, procedural details and software.

Habitat fragmentation predictor variables. We used annual 300-metre resolution land-cover maps (1992 to 2015) from the European Space Agency dataset (ESA; Defourny et al. 2023; see table S11 for landcover class description). For each genetic sampling site, we quantified habitat configuration within a 10-km radius using four landscape predictors: habitat amount, mean patch area, mean nearest-neighbor distance among habitat patches, and edge density. We ran three parallel fragmentation analyses: (i) forest-defined habitat (1992 land-cover map; Table S12), (ii) species-specific habitat defined from literature-linked land-cover classes (1992 land-cover map), and (iii) forest-fragmentation-intensity estimated as the temporal rate of change in landscape metrics across 1992–2015. See Supplementary S4 for cropping/reprojection details, class descriptions, metric and habitat definitions, intensity estimation, full procedural details, and software.

Statistical analysis. We tested for relationships between genetic diversity and habitat fragmentation using Bayesian mixed-effects multiple linear models fit separately for amphibians, mammals, and birds. Models used all four fragmentation metrics (habitat amount, patch distance, mean patch size, and edge density) as fixed effects species-specific random intercepts and slopes. All variables were centered and scaled and regularizing normal priors were used for slope terms, N(0, 1) We assessed and controlled for spatial structure in our genetic response variables using detrending and eigenvector-based spatial covariates. We tested pairwise correlations using Pearson's correlation coefficient across the four-fragmentation metrics: habitat amount, patch distance, edge density, and mean patch size. Additional analyses (bivariate models, PCA-based fragmentation index models, and habitat-amount interaction models) are described in the Supplementary (S8–S10). See Supplementary S6-S7 for full model specification, collinearity thresholds, full procedure and software.

Results

Genetic dataset

We found twelve new studies that corresponded to twelve species (3 amphibian; 6 bird; 3 mammal) and 218 genetic sampling sites (35 amphibian; 175 bird; 9 mammal) and added these to the existing database. Our final dataset used 122 studies (104 species; 2,233 genetic sampling sites) when combined with the originally compiled dataset (110 studies; 93 species; 2,015 genetic sampling sites). There were 21 species of amphibians, with 695 populations; 39 species of birds with 721 populations; and 44 species of mammals that had 817 populations.

Habitat fragmentation-Genetic diversity (multiple linear regressions)

Fragmentation metric collinearity. The correlations among fragmentation metrics across forest fragmentation, species-specific fragmentation, and forest fragmentation intensity were typically significant (Figures S11-S13). Edge density and habitat amount were the most highly correlated for forest and species fragmentation metrics (|r| = 0.68 and |r| = 0.69, respectively). For intensity of forest fragmentation, habitat amount and edge density were the most correlated (|r|=0.34).

General effect of habitat fragmentation. Our multiple linear regressions indicated that increased fragmentation was associated with less genetic diversity in mammals (Figure 2; Table 1) and amphibians (Figure 3; Table 1) and there was a weak unclear association with birds (Figure 4; Table 1). Species-specific random effects revealed that increased fragmentation was associated with both increases and decreases in genetic diversity across species (Figure 2-4; see also Supplementary section's S8-S10 for additional model results).

Mammals-Habitat amount. In mammals, populations occupying landscapes with greater available habitat tended to be better connected and more genetically diverse. Forest habitat amount had a negative relationship with Fst (Estimate = −0.17; 95% CI = −0.37 to 0.02; pd = 0.97; Figure 2B; Table 1) and a positive relationship with both allelic richness (Estimate = 0.12; 95% CI = −0.03 to 0.28; pd = 0.96; Figure 2B; Table 1) and gene diversity (Estimate = 0.13; 95% CI = 0.00 to 0.26; pd = 0.99; Figure 2B; Table 1). This was reinforced by evidence that species-specific habitat amount in mammals held a negative relationship with Fst (Estimate = −0.17; 95% CI = −0.33 to −0.01; pd = 0.98; Figure 2F; Table 2) and a positive relationship with gene diversity (Estimate = 0.10; 95% CI = −0.01 to 0.20; pd = 0.97; Figure 2F; Table 2).

Mammals-Edge density. Populations in landscapes with higher edge density experienced greater genetic differentiation and lower genetic diversity. Forest-edge density in mammals had a positive relationship with Fst (Estimate = 0.12; 95% CI = 0.00 to 0.25; pd = 0.96; Figure 2B; Table 1) and a negative relationship with gene diversity (Estimate = −0.08; 95% CI = −0.16 to 0.00; pd = 0.97; Figure 2B; Table 1).

Mammals-Patch size. Mammal populations in landscapes with larger patches tended to be less genetically diverse and more genetically structured. Forest patch size held a negative relationship with mammal gene diversity (Estimate = −0.10; 95% CI = −0.19 to 0.00; pd = 0.97; Figure 2F; Table 1). More weakly, forest patch size also showed a negative relationship with allelic richness (Estimate = −0.09; 95% CI = −0.19 to 0.02; pd = 0.93; Figure 2F; Table 1) and a positive relationship with Fst (Estimate = 0.12; 95% CI = −0.04 to 0.26; pd = 0.94; Figure 2F; Table 1).

Mammals-Patch distance. Landscapes with greater distances between patches may contain mammal populations that are less genetically differentiated and experience reduced genetic drift. Forest patch distance held a weak but evident negative relationship with Fst (Estimate = −0.06; 95% CI = −0.17 to 0.04; pd = 0.93; Figure 2B; Table 1) and a weak but evident positive relationship with effective population size (Estimate = 0.27; 95% CI = −0.16 to 0.71; pd = 0.90; Figure 2B; Table 1).

Habitat fragmentation in birds. Reduced habitat amount and increased patch isolation were associated with lower genetic diversity in birds, while greater species-specific habitat availability was weakly associated with increased genetic differentiation. Forest habitat amount held a negative relationship with allelic richness (Estimate = −0.12; 95% CI = −0.34 to 0.12; pd = 0.89; Figure 4B; Table 1). Species-specific habitat amount held a positive relationship with Fst

(Estimate = 0.09; 95% CI = −0.05 to 0.28; pd = 0.89; Figure 4F; Table 2). In addition, distance between forest patches held a weak negative relationship with gene diversity (Estimate = −0.02; 95% CI = −0.11 to 0.11; pd = 0.89; Figure 4B; Table 1).

Amphibians-Habitat amount. Our analysis indicated reduced genetic diversity and structure in landscapes with greater habitat amount. Forest habitat amount held a strong positive relationship with allelic richness (Estimate = 0.17; 95% CI = 0.01 to 0.33; pd = 1.00; Figure 3B; Table 2). In contrast, species-specific habitat amount showed a strong negative relationship with Fst (Estimate = −0.46; 95% CI = −1.01 to 0.08; pd = 0.96; Figure 3E; Table 2). Forest habitat amount in amphibians held a negative relationship with Fst (Estimate = −0.36; 95% CI = −0.79 to 0.08; pd = 0.94; Figure 3B; Table 2) and a positive relationship with gene diversity (Estimate = 0.24; 95% CI = −0.06 to 0.53; pd = 0.90; Figure 3B; Table 2). Forest edge density also showed weak relationships with effective population size (Estimate = −0.10; 95% CI = −0.25 to 0.06; pd = 0.92; Figure 3A; Table 2) and gene diversity (Estimate = 0.12; 95% CI = −0.06 to 0.29; pd = 0.92; Figure 3A; Table 2). Finally, species-specific habitat amount showed a weak positive relationship with allelic richness (Estimate = 0.13; 95% CI = −0.05 to 0.33; pd = 0.92; Figure 3E; Table 2), and species-specific edge density showed a weak positive relationship with Fst (Estimate = 0.18; 95% CI = −0.08 to 0.47; pd = 0.91; Figure 3E; Table 2).

Amphibians-Edge density. Greater edge density was associated with reduced genetic diversity and increased genetic structure Forest edge density in amphibians showed a negative relationship with allelic richness (Estimate = −0.11; 95% CI = −0.21 to 0.00; pd = 0.97; Figure 3A; Table 2) and a positive relationship with Fst (Estimate = 0.13; 95% CI = −0.06 to 0.32; pd = 0.96; Figure 3A; Table 2). A similar negative relationship between edge density and allelic

richness was observed when edge density was calculated using species-specific habitat (Estimate = −0.11; 95% CI = −0.23 to 0.01; pd = 0.96; Figure 3E; Table 2).

Amphibians-Patch size. Larger patch size was associated with lower genetic diversity and higher genetic structure in amphibian populations. Larger forest patches were associated with lower allelic richness (Estimate = −0.20; 95% CI = −0.40 to −0.03; pd = 0.97; Figure 3D; Table 2) and lower gene diversity (Estimate = −0.25; 95% CI = −0.49 to −0.03; pd = 0.99; Figure 3D; Table 2), as well as greater genetic structure (Estimate = 0.36; 95% CI = 0.07 to 0.70; pd = 0.99; Figure 3D; Table 2).

Forest fragmentation intensity on genetic diversity. Forest fragmentation intensity's relationship with genetic diversity and structure were generally weak and taxon-specific (Table 3). In amphibians, intensity of forest habitat amount change showed a weak positive relationship with Fst (Estimate = 0.22; 95% CI = −0.10 to 0.59; pd = 0.92; Figure 5B), while intensity of forest edge density change held a weak negative relationship with gene diversity (Estimate = −0.06; 95% CI = −0.14 to 0.03; pd = 0.92; Figure 5A). In mammals, intensity of forest habitat amount change showed a weak negative relationship with Fst (Estimate = −0.05; 95% CI = −0.14 to 0.03; pd = 0.89; Figure 5J) and a strong positive relationship with gene diversity (Estimate = 0.06; 95% CI = 0.01 to 0.11; pd = 0.98; Figure 5J). Intensity of forest patch size change in mammals also showed a weak positive relationship with Fst (Estimate = 0.08; 95% CI = −0.02 to 0.22; pd = 0.94; Figure 5L). No notable relationship between forest fragmentation intensity was observed in bird genetic diversity metrics (probability of direction < 0.89 across metrics).

Variation explained by models. Our models showed that habitat fragmentation explains substantial variation in genetic diversity. Across all models, R^2c and R^2m estimates suggest that species-level differences in genetic responses to fragmentation accounted for most of the

explained variance (Tables 1–3). For the forest fragmentation models, R^2c ranged from 7% to 92%, while R^2m ranged up to 30% (Table 1). Although lower, the marginal R^2 values are biologically meaningful: explaining one-third of the variance in genetic diversity with fragmentation metrics alone is notable, given that interspecific genetic differences have accumulated over millions of years. Models using species-specific habitat definitions showed comparable explanatory power (R^2c: 6–88%; R^2m: 0.4–17%; Table 2), as did models based on forest-intensity fragmentation (R^2c: 3–90%; R^2m: 0.7–32%; Table 3).

Discussion

We found evidence that habitat fragmentation was negatively associated with genetic diversity in North American mammals and amphibians, and weakly associated with genetic diversity in birds. Notably, the magnitude of parameter estimates were highest when the effects of different fragmentation metrics and habitat amount were statistically controlled for in the analysis. The relationship between genetic diversity and habitat fragmentation varied substantially across species: some species exhibited higher genetic diversity in fragmented landscapes, whereas others showed lower genetic diversity.

Mammal genetic diversity

We found compelling evidence that habitat fragmentation is negatively associated with mammal genetic diversity. Consistent with landscape genetics theory, lower habitat amount and higher edge density are associated with both population genetic diversity and differentiation in mammals (Holderegger & Wagner, 2008). We observed a strong relationship among habitat amount, species-specific habitat fragmentation, and forest fragmentation intensity. No other landscape and genetic metrics held notable effects across forest fragmentation, species-specific habitat fragmentation, and forest fragmentation intensity. Landscape genetics theory predicts that reductions in habitat area decrease functional connectivity, thereby lowering gene flow and

increasing among-population genetic differentiation (Holderegger & Wagner, 2008). Theory also predicts that in landscapes with less habitat, populations are smaller and thus lose alleles more rapidly due to genetic drift, becoming more differentiated over shorter time scales (Holderegger & Wagner, 2008; Keyghobadi, 2007). Empirical work in mammals has shown that less habitat in a landscape can increase population genetic differentiation (Day et al., 2024; Kierepka et al., 2020; Taylor & Hoffman, 2014).

Previous work has suggested that habitat amount moderates the effects of fragmentation, but our study does not provide support for this in mammals (Andrén, 1994b; Swift & Hannon, 2010). Instead, habitat amount and fragmentation likely act simultaneously on mammal genetic diversity. Strikingly, habitat amount did not have a detectable association with genetic diversity when habitat fragmentation was not accounted for, as indicated by our bivariate models. This provides support for the idea that habitat amount and configuration affect organisms interdependently (Andrén, 1994b; Swift & Hannon, 2010). However, habitat amount did not appear to have an interactive association (i.e., a lack of multiplicative association in a regression) with habitat fragmentation, as noted by our models that used habitat amount interactively(Table S8-S10; Figure S8-S10). Taken together, these results imply that habitat amount has a notable association with genetic diversity when the fragmentation is statistically controlled, but habitat amount does not moderate (i.e., increase or decrease further) the magnitude of association between fragmentation and genetic diversity.

Our finding that habitat fragmentation is associated with reduced mammal genetic diversity is likely robust, given that this relationship is detected using coarse landcover-based metrics. Our method for measuring habitat fragmentation uses landcover maps, which classify areas of the landscape according to vegetation and other physical attributes which can suggest

proxies for potential habitat, but do not necessarily measure true habitat. It also assumes that habitat factors and other environmental factors do not determine habitat. In addition, for smaller organisms, a resolution of 300 m may have missed important microhabitats and a total spatial extent of 10 kilometers could have included measurements of habitat fragmentation that would be irrelevant to an organism that has a smaller dispersal distance.

Our findings are consistent with previous work indicating that fragmentation reduces genetic diversity in mammals. Studies have measured habitat fragmentation differently. As Keyghobadi (2007) notes, studies either qualitatively classify landscapes as fragmented or quantify fragmentation for a single landscape before assessing populations' genetic structure (Ćosić et al., 2013; Dixon et al., 2007; Gaines et al., 1997; Gracanin et al., 2023; Haag et al., 2010; Murphy et al., 2017; Napolitano et al., 2015; Wang et al., 2017; Wultsch et al., 2016). Other studies define fragmentation based on specific barriers such as rivers, roads, or large gaps in contiguous habitat (Ćosić et al., 2013; Napolitano et al., 2015; Wang et al., 2017). Even with discrepancies in how fragmentation is defined and measured, there is evidence of a negative relationship with genetic diversity.

Bird genetic diversity

Habitat fragmentation appeared to be weakly associated with bird genetic diversity. Importantly, the 39 individual bird species varied in their response to fragmentation, from negative to null to positive, as shown by the slope coefficients (see Figure 4; Figure S2-S4). These findings are consistent with previous empirical studies, which have generally reported either a null effect or species-specific variation in response to habitat fragmentation (Canales-Delgadillo et al., 2012; Croteau et al., 2007; Harrisson et al., 2012; Lindsay et al., 2008; Zuckerberg et al., 2014). The variation in effects on birds may reflect their high mobility, which

enables them to traverse landscapes effectively, thereby maintaining gene flow (Canales-Delgadillo et al., 2012; Croteau et al., 2007; Harrisson et al., 2012; Lindsay et al., 2008). One study found that genetic diversity in some bird species was negatively affected by fragmentation, whereas genetic diversity in another species was positively affected (Zuckerberg et al., 2014). Our findings, along with those of previous studies, suggest that habitat fragmentation does not have a uniform effect on genetic diversity in birds; rather, it should be examined at the species level.

Amphibian genetic diversity

Most amphibian fragmentation metrics behaved as predicted by landscape genetics, with increased fragmentation associated with reduced genetic diversity and increased genetic structure. Greater forest and species-specific habitat amount was generally associated with higher allelic richness and gene diversity and lower genetic differentiation, while increased edge density was associated with reduced genetic diversity and elevated Fst (Figure 3A). These patterns are consistent with classical landscape-genetic expectations for amphibians, in which reduced habitat availability and increased fragmentation limit dispersal, reduce effective population sizes, and increase the influence of genetic drift (Cushman, 2006). Despite variation in the magnitude of parameter estimates across metrics, the overall direction of these relationships suggests that habitat fragmentation can negatively influence amphibian population genetic structure and diversity.

In contrast to these expected patterns, forest patch size showed a strong and directionally unexpected relationship with amphibian genetic diversity. Larger forest patches were associated with increased genetic differentiation and reduced allelic richness and gene diversity. This result contrasts with theoretical predictions and empirical studies suggesting that larger habitat patches should support larger, more stable populations with higher genetic diversity and reduced genetic

structure (Cushman, 2006; Dixo et al., 2009). Notably, this effect was observed only when habitat was defined by forest cover, indicating that the observed relationship may be specific to the forest-based habitat characterization rather than a general response to patch size across habitat definitions.

This unexpected patch-size effect likely reflects limitations in using forest cover as a proxy for amphibian habitat. Amphibian persistence and dispersal are often governed by fine-scale environmental features such as microclimate, moisture availability, and the spatial distribution of aquatic breeding sites, which are not necessarily captured by forest extent alone (Dixo et al., 2009; Popescu & Hunter Jr., 2011). Consequently, larger forest patches may encompass environmentally heterogeneous areas that do not facilitate functional connectivity among breeding populations. Under this interpretation, larger forest patches may not correspond to greater effective population sizes or increased gene flow, resulting instead in higher genetic structure and reduced diversity.

Multivariable analysis to reveal effects of fragmentation

Our results indicated that analyzing multiple habitat fragmentation metrics reveals otherwise hidden relationships with genetic diversity. Bivariate models showed no detectable relationships, whereas multiple linear regression revealed several significant relationships. This aligns with guidance to model habitat amount alongside configuration metrics and to treat fragmentation as a multifaceted phenomenon rather than a single index (Frazier & Kedron, 2017; Manel & Holderegger, 2013; Uuemaa et al., 2009). Ecologically, fragmentation alters multiple landscape properties simultaneously (amount, edge, patch size/number, isolation), producing diverse combinations with unique impacts on population size, movement/connectivity, and thus genetic diversity, reinforcing that a multivariate analysis is required (Cushman et al., 2006; Fahrig, 2003; Jackson & Fahrig, 2014).

We acknowledged the inherent challenge of collinearity among the fragmentation metrics used in our study. As detailed in the Methods section, we implemented several rigorous analytical techniques to manage this potential statistical issue. While we detected correlations between some habitat fragmentation metrics and habitat amount, these correlations were generally modest ($|r| < 0.5$), with only two of eighteen reaching values between 0.68 and 0.69 (Dormann et al., 2013). These values, while warranting caution, do not necessarily preclude reliable parameter estimates in multivariable models (Dormann et al., 2013). Our chosen methods—specifically the use of centered and scaled predictors and Bayesian mixed-effects models with weakly regularizing priors—provided sufficient mitigation against collinearity-induced variance inflation, ensuring that our inferences remained robust and were not materially affected by the observed correlations.

Comparable synthesis work

Despite the myriad methodological approaches used in empirical studies, several meta-analyses have examined general patterns linking habitat fragmentation to genetic diversity. These syntheses report effects that are consistent with our findings (Lino et al., 2019; Rivera-Ortíz et al., 2015; Schlaepfer et al., 2018). Although inconsistent definitions of fragmentation across studies can limit direct comparisons, reliance on study-specific definitions can also be a strength, as it allows fragmentation to be quantified at biologically meaningful scales tailored to focal species. This allows authors to determine the scale, and what 'habitat' is for their focal species, which are limitations of our approach. Taken together, the convergence of results across approaches provides robust support for a negative effect of habitat fragmentation on genetic diversity in vertebrates, particularly in mammals and amphibians.

Our results agree with previous work on how urbanization impacts genetic diversity (Schmidt et al., 2020; Schmidt & Garroway, 2021). Recent studies show that mammal populations in urbanized areas are more genetically differentiated and exhibit less genetic diversity, consistent with our finding that habitat area affects mammals. This comparison is important because habitat fragmentation and amount were quantified at a relatively coarse, semi-arbitrary scale, yet still captured patterns in genetic diversity like those observed in studies of urbanization. These results suggest that habitat fragmentation and amount derived from landcover maps may have potential as a coarse screening tool for monitoring mammal genetic diversity, although targeted, species-specific validation is still required. Similarly, the weak association of fragmentation with bird genetic diversity mirrors patterns reported in urbanization studies, reinforcing the conclusion that birds are generally less sensitive to broad-scale landscape modification.

Should fragmentation have a weak effect on genetic diversity?

Our findings align with theory and empirical evidence, though it is equally plausible that fragmentation has little to no effect on genetic diversity. Theory assumes that gene flow–the primary mechanism affected by habitat fragmentation–will be limited across species. However, empirical work implies fragmentation will have a weak effect on gene flow change across species and landscapes (e.g., Amos et al., 2014; Harrisson et al., 2012; Kobayashi et al., 2018). It has been suggested that variation in how fragmentation affects gene flow results from interactions between species' dispersal capacity and the type of matrix between patches (Didham et al., 2012; Keyghobadi, 2007; Villard & Metzger, 2014). For example, one study found that when controlling for matrix type in a fragmented landscape, only the least mobile species lost genetic connectivity (Harrisson et al., 2012). Similarly, another study found that, after

controlling for dispersal capacity, some matrices were more restrictive of gene flow than others (Van Buskirk, 2012).

Time lags in genetic responses may conceal grander effects of habitat fragmentation that are developing without notice (Epps & Keyghobadi, 2015; Gargiulo et al., 2024; Pinto et al., 2024). Although we used the oldest spatial data available that was suitable for our analysis and microsatellites to reduce time lag, these methods do not prevent the potential of delayed genetic responses (Epps & Keyghobadi, 2015). Furthermore, the duration of time lag following fragmentation depends on multiple species- and population-level variables. At the species level, generation length, mutation rate, and dispersal distance affect the rate of genetic diversity change. Short-lived species with higher mutation rates and longer dispersal capacity manifest genetic responses faster (Epps & Keyghobadi, 2015). At the population level, smaller effective population sizes experience stronger genetic drift, leading to more rapid changes in allelic frequencies. In addition to population and species variables, fragmentation can extend time lags by decreasing connectivity, which delays the time it takes for alleles to reach an equilibrium (Landguth et al., 2010). Together, various population, species, and landscape factors create variable time lags that obscure the effects of fragmentation on genetic diversity.

With relation to biodiversity

Genetic and species diversity are expected to exhibit similar spatial patterns and to decline in fragmented landscapes (Keyghobadi, 2007; Schmidt et al., 2022). Although recent work reports fewer species in fragmented compared to continuous landscapes (Gonçalves-Souza et al., 2025), this pattern has long been debated in the literature with evidence supporting both positive and negative effects (Didham et al., 2012; Fahrig, 2003; Fletcher et al., 2018; Riva & Fahrig, 2023). Studies revealing negative effects of fragmentation on species diversity are well-controlled, large-scale experiments that directly account for matrix type, habitat amount,

configuration type, and time since fragmentation (Haddad et al., 2015; Laurance et al., 2002, 2011). In contrast, studies that repurpose data rarely account for variation among studies, leading to conflicting results on whether fragmentation increases or decreases species diversity (e.g., Fahrig, 2017; Gonçalves-Souza et al., 2025). Our results on genetic diversity reflect a less mixed pattern: mammal and amphibian genetic diversity were negatively associated with fragmentation, whereas bird genetic diversity was only weakly associated with fragmentation.

Conclusion

Our study provides strong evidence that habitat fragmentation is a driver of declines in genetic diversity. This thesis shows that habitat fragmentation is harmful to mammal and amphibian genetic diversity. While no clear pattern emerged in how habitat fragmentation affects birds' genetic diversity, the precautionary principle indicates that habitat fragmentation should be treated as detrimental to birds' genetic diversity. We propose that fragmentation likely has a strong effect on genetic responses because our methods were coarse, potentially masking fragmentation's effects on genetic diversity. Further exploration of aspects of habitat fragmentation not covered in this thesis, such as matrix composition, can improve understanding of where habitat fragmentation will affect genetic diversity to support conservation planning and advance our understanding of microevolutionary processes.

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Tables

Table 1. Parameter estimates from multiple linear regressions of forest fragmentation metrics on genetic diversity metrics with species as a random effect. Each response variable (allelic richness, fixation index [Fst], gene diversity, and effect population size [Ne]) corresponds to its own model across all three taxa classes, which results in 12 models.

	Parameter Estimate [95% Credible Interval Range]; probability of direction					
	Patch distance	**Habitat amount**	**Edge Density**	**Patch size**	**N of Species; Sites**	**R^2 Conditional; Marginal**
Amphibian						
Allelic richness	-0.01 [-0.14 to 0.15]; 0.62	0.17 [0.01 to 0.33]; 1	-0.11 [-0.21 to 0]; 0.97	-0.2 [-0.4 to -0.03]; 0.97	21; 551	0.76; 0.103
Fst	-0.03 [-0.37 to 0.4]; 0.54	-0.36 [-0.79 to 0.08]; 0.94	0.13 [-0.06 to 0.32]; 0.96	0.36 [0.07 to 0.7]; 0.99	20; 547	0.63; 0.305
Gene diversity	0.06 [-0.11 to 0.24]; 0.77	0.24 [-0.06 to 0.53]; 0.9	-0.1 [-0.25 to 0.06]; 0.92	-0.25 [-0.49 to -0.03]; 0.99	21; 551	0.85; 0.162
Ne	0.06 [-0.11 to 0.22]; 0.77	-0.02 [-0.21 to 0.18]; 0.59	0.12 [-0.06 to 0.29]; 0.92	0.08 [-0.13 to 0.29]; 0.79	21; 445	0.07; 0.022

Bird						
Allelic richness	-0.03 [-0.19 to 0.12]; 0.66	-0.12 [-0.34 to 0.12]; 0.89	0.06 [-0.1 to 0.21]; 0.78	0.11 [-0.09 to 0.33]; 0.81	37; 506	0.41; 0.08
Fst	0.07 [-0.18 to 0.31]; 0.88	0.12 [-0.14 to 0.38]; 0.72	0.06 [-0.13 to 0.29]; 0.71	0.01 [-0.16 to 0.17]; 0.59	36; 501	0.51; 0.118
Gene diversity	-0.02 [-0.11 to 0.11]; 0.89	-0.06 [-0.21 to 0.08]; 0.78	-0.01 [-0.09 to 0.06]; 0.53	0.02 [-0.06 to 0.1]; 0.52	37; 506	0.92; 0.052
Ne	-0.06 [-0.31 to 0.18]; 0.74	-0.05 [-0.33 to 0.23;]; 0.63	-0.01 [-0.2 to 0.17]; 0.55	-0.07 [-0.3 to 0.16]; 0.72	31; 349	0.1; 0.028
Mammal						
Allelic richness	0.02 [-0.06 to 0.09]; 0.61	0.12 [-0.03 to 0.28]; 0.96	-0.02 [-0.11 to 0.06]; 0.81	-0.09 [-0.19 to 0.02] 0.93	40; 661	0.64; 0.073
Fst	-0.06 [-0.17 to 0.04]; 0.93	-0.17 [-0.37 to 0.02]; 0.97	0.12 [0 to 0.25]; 0.96	0.12 [-0.04 to 0.26] 0.94	35; 645	0.45; 0.174
Gene diversity	0.03 [-0.03 to 0.09;] 0.72	0.13 [0 to 0.26]; 0.99	-0.08 [-0.16 to 0]; 0.97	-0.1 [-0.19 to 0]; 0.97	40; 661	0.77; 0.088
Ne	0.27 [-0.16 to 0.71]; 0.9	0.06 [-0.12 to 0.26]; 0.75	0.02 [-0.1 to 0.14]; 0.64	0.02 [-0.16 to 0.21] 0.61	38; 542	0.22; 0.062

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Table 2. Parameter estimates from multiple linear regression of species-specific habitat fragmentation metrics on genetic diversity metrics with species as a random effect. Each response variable (allelic richness, fixation index [Fst], gene diversity, and effect population size [Ne]) corresponds to its own model across all three taxa classes which results in 12 models.

	Parameter Estimate [95% Credible Interval Range]; probability of direction					
	Patch distance	**Habitat amount**	**Edge Density**	**Patch size**	**N of Species; Sites**	**R^2 Conditional; Marginal**
Amphibian						
Allelic richness	-0.06 [-0.21 to 0.06]; 0.86	0.13 [-0.05 to 0.33]; 0.92	-0.11 [-0.23 to 0.01]; 0.96	-0.03 [-0.18 to 0.14]; 0.69	20; 597	0.69; 0.028
Fst	-0.01 [-0.25 to 0.21]; 0.53	-0.46 [-1.01 to 0.08]; 0.96	0.18 [-0.08 to 0.47]; 0.91	0.06 [-0.46 to 0.55]; 0.62	19; 593	0.42; 0.174
Gene diversity	-0.01 [-0.18 to 0.16]; 0.53	0.15 [-0.14 to 0.44]; 0.86	-0.06 [-0.22 to 0.08]; 0.82	-0.01 [-0.34 to 0.31]; 0.52	20; 597	0.81; 0.043
Ne	0.24 [-0.18 to 0.74]; 0.86	0.12 [-0.1 to 0.34]; 0.85	0.07 [-0.14 to 0.27]; 0.76	-0.03 [-0.25 to 0.17]; 0.62	20; 420	0.08; 0.05
Bird						
Allelic richness	-0.01 [-0.13 to 0.09]; 0.6	0.07 [-0.08 to 0.21]; 0.82	0.02 [-0.11 to 0.14]; 0.6	0 [-0.14 to 0.14]; 0.53	38; 549	0.36; 0.014
Fst	0.09 [-0.05 to 0.28]; 0.89	0.17 [-0.4 to 0.75]; 0.72	0.04 [-0.07 to 0.16]; 0.78	-0.16 [-0.69 to 0.35]; 0.74	36; 543	0.45; 0.049

Gene diversity	-0.01 [-0.07 to 0.04]; 0.68	-0.02 [-0.14 to 0.11]; 0.61	-0.01 [-0.06 to 0.04]; 0.72	0.04 [-0.04 to 0.11]; 0.84	38; 549	0.88; 0.004
Ne	-0.04 [-0.19 to 0.1]; 0.72	0.08 [-0.15 to 0.32]; 0.76	-0.05 [-0.2 to 0.11]; 0.73	0.02 [-0.22 to 0.31]; 0.55	33; 378	0.06; 0.027
Mammal						
Allelic richness	-0.02 [-0.14 to 0.08]; 0.66	0.06 [-0.1 to 0.21]; 0.77	0.03 [-0.06 to 0.11]; 0.76	-0.03 [-0.13 to 0.07]; 0.74	37; 641	0.61; 0.01
Fst	0.03 [-0.2 to 0.26]; 0.63	-0.17 [-0.33 to -0.01]; 0.98	0.02 [-0.1 to 0.15]; 0.64	0.05 [-0.08 to 0.19]; 0.78	32; 628	0.27; 0.032
Gene diversity	-0.02 [-0.13 to 0.08]; 0.62	0.1 [-0.01 to 0.2]; 0.97	0.01 [-0.07 to 0.08]; 0.56	-0.03 [-0.11 to 0.05]; 0.77	37; 641	0.73; 0.011
Ne	0.35 [-0.27 to 0.96]; 0.87	0.08 [-0.06 to 0.23]; 0.88	0.07 [-0.08 to 0.21]; 0.82	0.02 [-0.12 to 0.16]; 0.59	35; 493	0.7; 0.084

15 **Table 3.** Parameter estimates from multiple linear regression of forest fragmentation intensity metrics on genetic diversity metrics

16 with species as a random effect. Each response variable (allelic richness, fixation index [Fst], gene diversity, and effect population size

17 [Ne]) corresponds to its own model across all three taxa classes which results in 12 models.

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	Parameter Estimate [95% Credible Interval Range]; probability of direction					
	Patch distance	**Habitat amount**	**Edge Density**	**Patch size**	**N of Species; Sites**	**R^2 Conditional; Marginal**
Amphibian						
Allelic richness	-0.01 [-0.08 to 0.06] 0.66	-0.04 [-0.18 to 0.05] 0.77	0.01 [-0.07 to 0.08] 0.58	0.05 [-0.06 to 0.17] 0.84	21; 561	0.72; 0.074
Fst	-0.04 [-0.13 to 0.05] 0.8	0.22 [-0.1 to 0.59] 0.92	0.03 [-0.1 to 0.15] 0.68	-0.05 [-0.15 to 0.05] 0.86	20; 557	0.6; 0.323
Gene diversity	0.02 [-0.03 to 0.08] 0.82	-0.14 [-0.41 to 0.11] 0.86	-0.06 [-0.14 to 0.03] 0.92	-0.02 [-0.07 to 0.04] 0.73	21; 561	0.86; 0.179
Ne	-0.01 [-0.13 to 0.11] 0.57	0.01 [-0.13 to 0.14] 0.54	0.02 [-0.12 to 0.15] 0.59	0.06 [-0.1 to 0.23] 0.76	21; 384	0.04; 0.016
Bird						
Allelic richness	0 [-0.14 to 0.13] 0.52	0.02 [-0.09 to 0.13] 0.63	0.02 [-0.08 to 0.12] 0.67	-0.01 [-0.13 to 0.11] 0.56	37; 480	0.3; 0.01
Fst	0.01 [-0.11 to 0.16] 0.57	0.06 [-0.06 to 0.17] 0.83	0.02 [-0.11 to 0.15] 0.59	-0.01 [-0.13 to 0.09] 0.6	36; 475	0.47; 0.181

Gene diversity	0.02 [-0.03 to 0.11] 0.75	-0.01 [-0.06 to 0.04] 0.73	-0.02 [-0.08 to 0.03] 0.81	0.01 [-0.04 to 0.06] 0.65	37; 480	0.9; 0.045
Ne	-0.41 [-1.57 to 0.77] 0.76	0.07 [-0.09 to 0.26] 0.8	-0.15 [-0.58 to 0.26] 0.77	-0.05 [-0.22 to 0.12] 0.73	31; 319	0.37; 0.188
Mammal						
Allelic richness	-0.04 [-0.14 to 0.07] 0.79	0.03 [-0.06 to 0.12] 0.74	-0.01 [-0.08 to 0.06] 0.62	-0.02 [-0.09 to 0.05] 0.72	40; 649	0.57; 0.007
Fst	-0.03 [-0.15 to 0.12] 0.71	-0.05 [-0.14 to 0.03] 0.89	0.04 [-0.04 to 0.13] 0.86	0.08 [-0.02 to 0.22] 0.94	35; 633	0.37; 0.144
Gene diversity	0 [-0.09 to 0.08] 0.52	0.06 [0.01 to 0.11] 0.98	0.01 [-0.05 to 0.06] 0.6	-0.03 [-0.09 to 0.03] 0.86	40; 649	0.74; 0.083
Ne	-0.01 [-0.19 to 0.18] 0.53	-0.03 [-0.13 to 0.08] 0.69	0.04 [-0.06 to 0.15] 0.8	0.02 [-0.08 to 0.13] 0.67	38; 506	0.03; 0.012

Figures

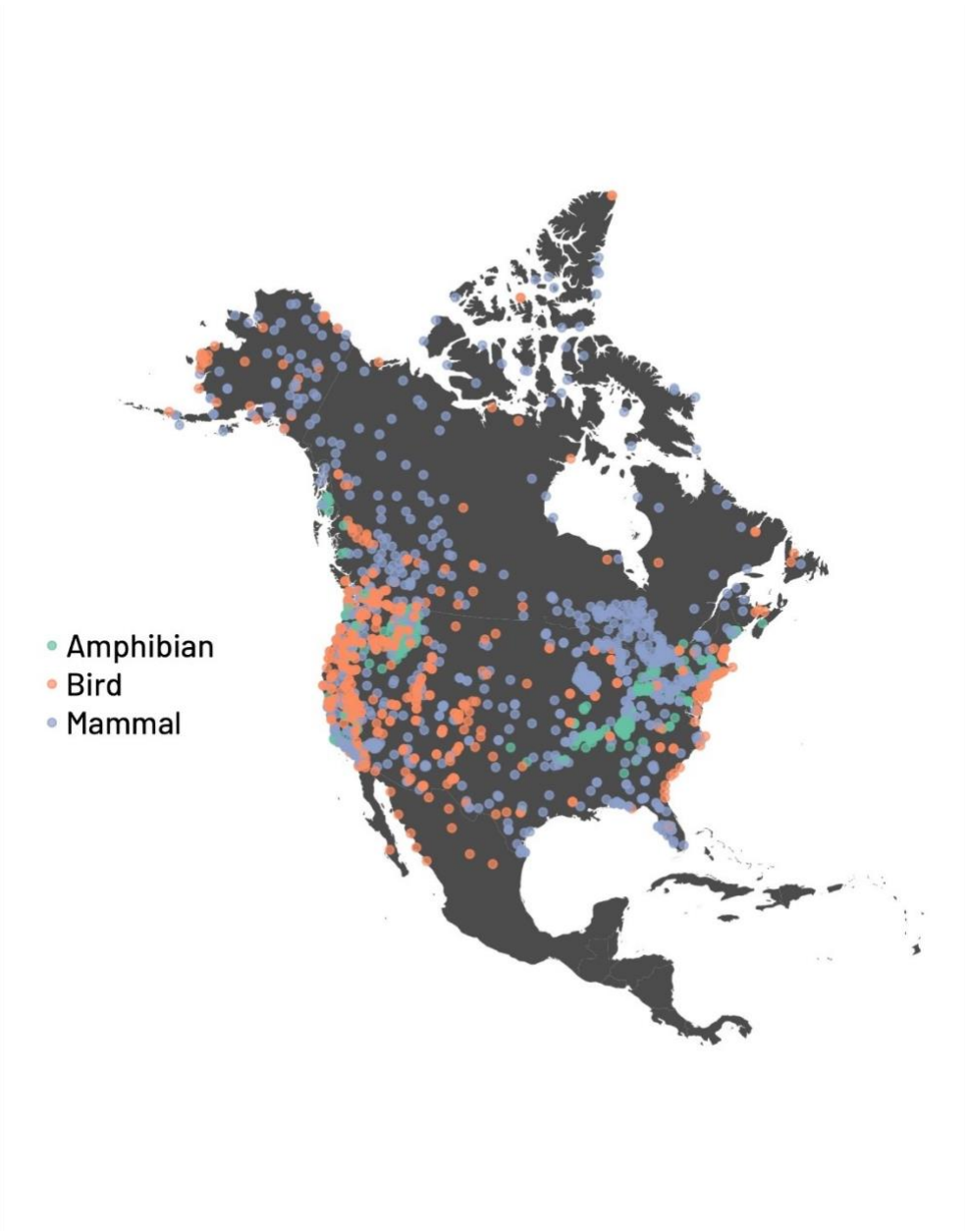

Figure 1. Map of 2,233 sample sites across North America for the 104 mammal, bird and amphibian species examined. 817 sites were mammal (blue points), 721 sites were bird (orange point) and 695 sites were amphibian (green points).

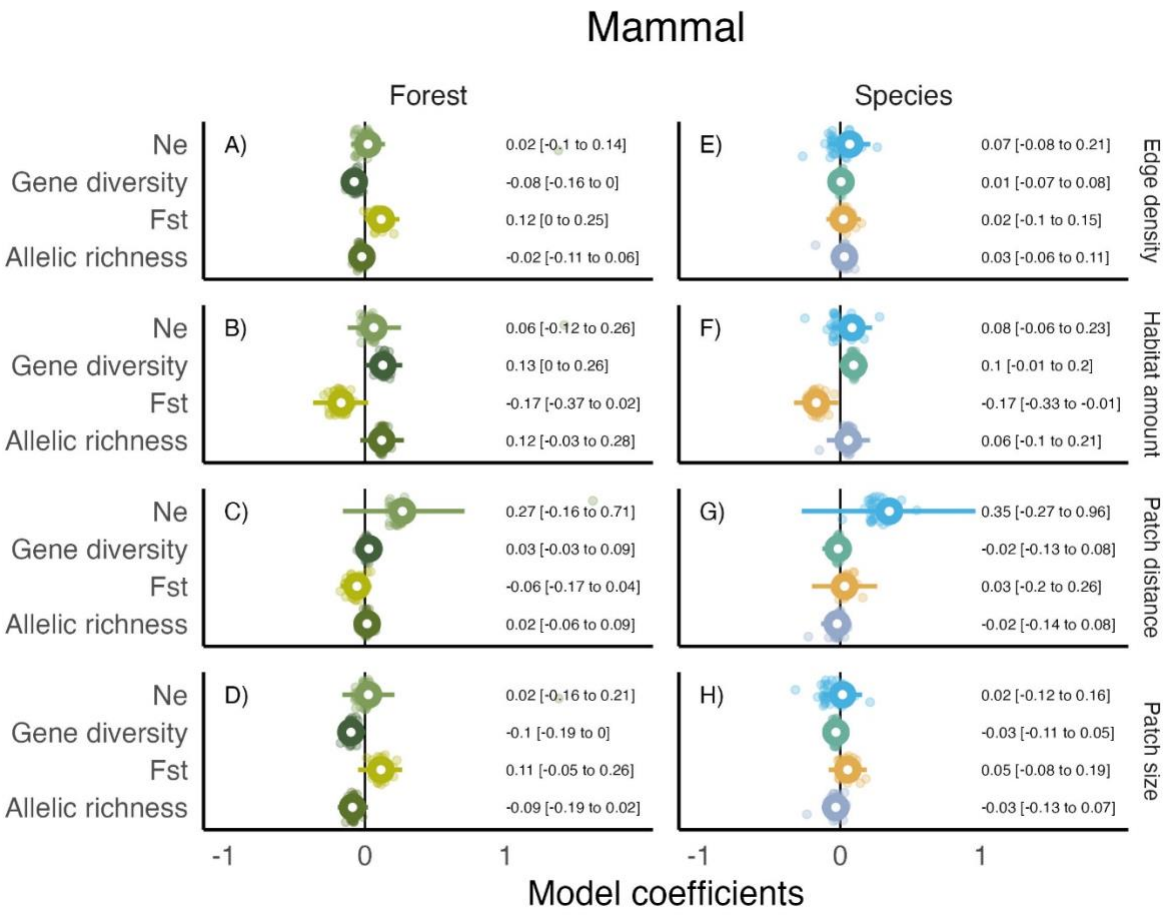

Figure 2. Bayesian multiple linear regressions for mammals with species as a random effect. There are eight total models with four attributed to forest fragmentation and four to species-specific habitat fragmentation. Models used anywhere from 35 to 40 species and 445 to 661 sites. The X axis represents the parameter estimates (i.e., 'Model coefficients'). All data was standardized to a mean of 0. Response variables are on the left Y axis (effective population size [Ne], gene diversity, fixation index [Fst] and allelic richness) and are modeled separately across forest fragmentation (A-D) and species-specific habitat fragmentation (E-H). Predictor variables of the multiple linear regression include edge density (A & E), habitat amount (B & F), patch distance (C & G), and mean patch size (D & H).

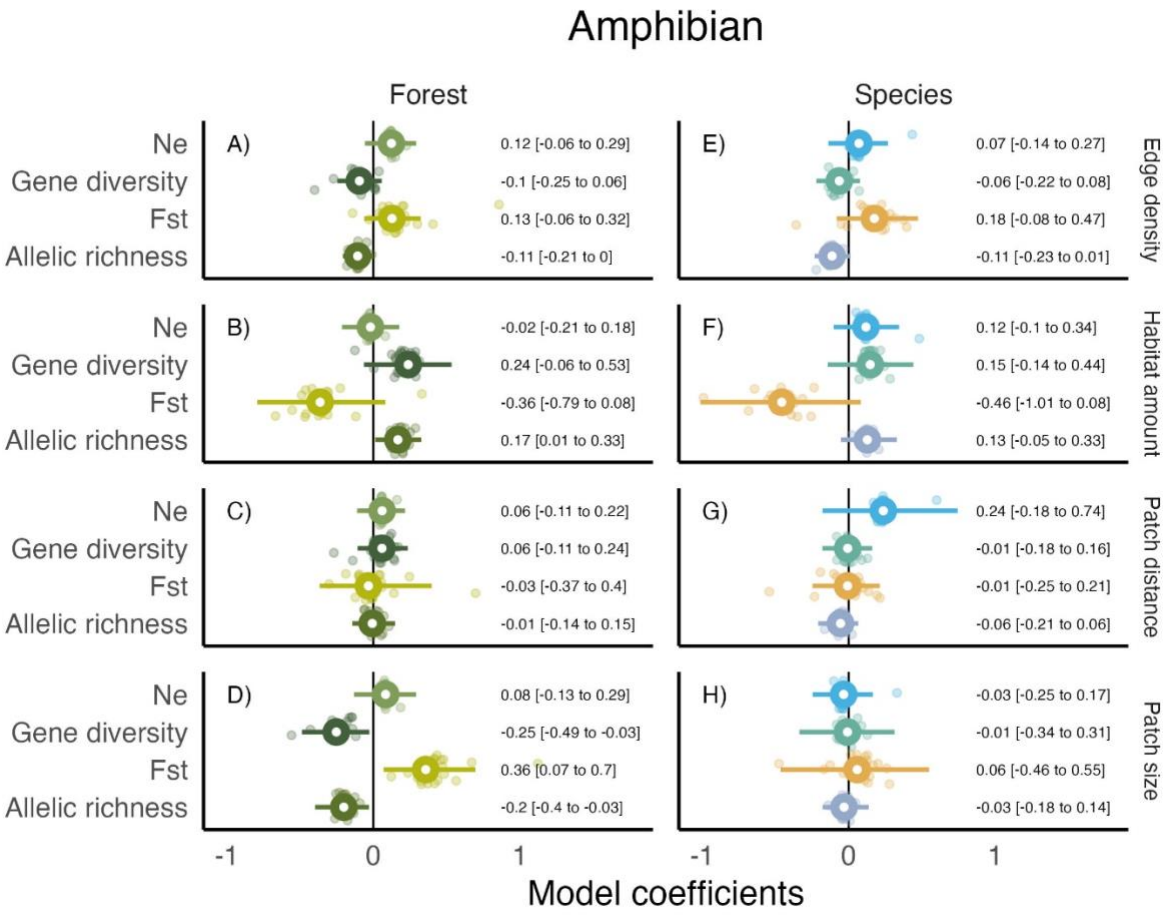

Figure 3. Bayesian multiple linear regressions for amphibians with species as a random effect. There are eight total models with four attributed to forest fragmentation and four to species-specific habitat fragmentation. Models used anywhere from 19 to 21 species and 420 to 597 sites. The X axis represents the parameter estimates (i.e., 'Model coefficients'). All data was standardized to a mean of 0. Response variables are on the left Y axis (effective population size [Ne], gene diversity, fixation index [Fst] and allelic richness) and are modeled separately across forest fragmentation (A-D) and species-specific habitat fragmentation (E-H). Predictor variables of the multiple linear regression include edge density (A & E), habitat amount (B & F), patch distance (C & G), and mean patch size (D & H).

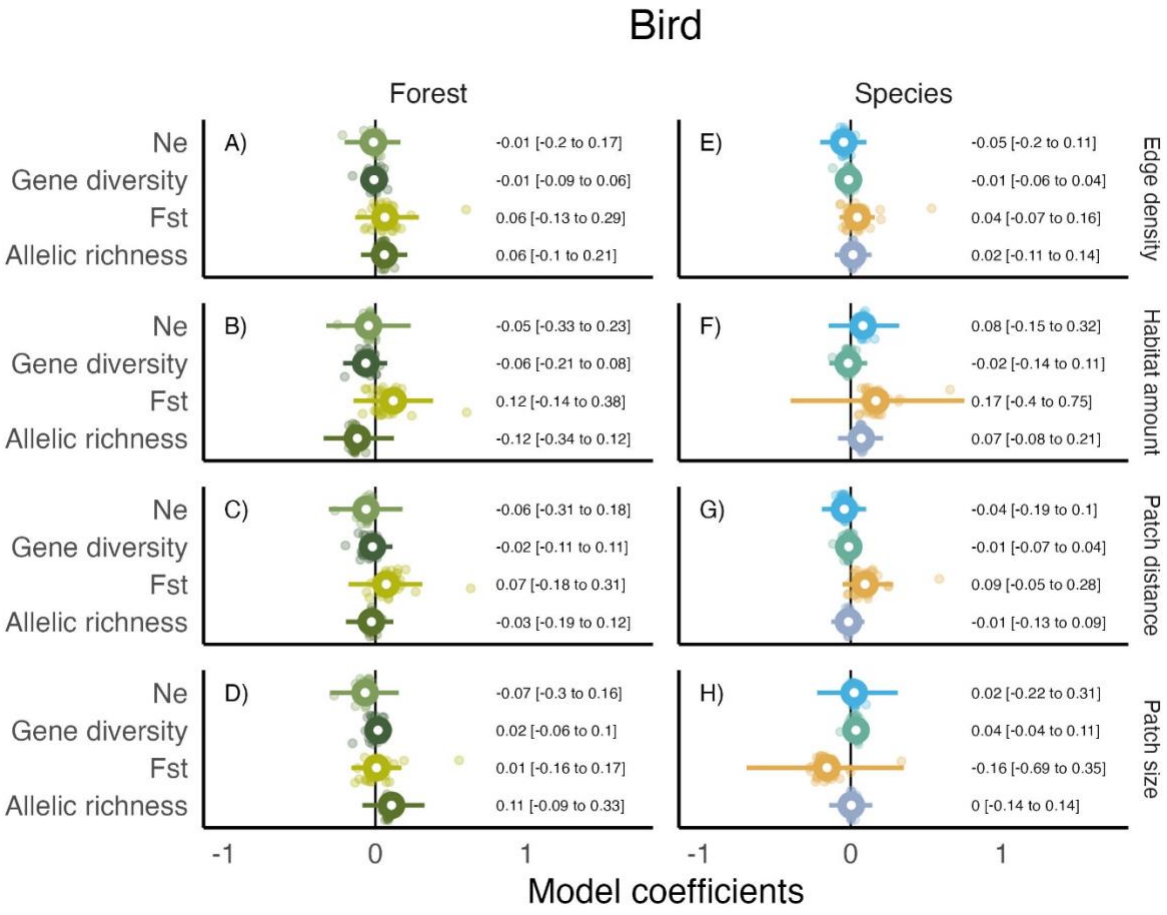

Figure 4. Bayesian multiple linear regressions for birds with species as a random effect. There are eight total models with four attributed to forest fragmentation and four to species-specific habitat fragmentation. Models used anywhere from 31 to 38 species and 378 to 549 sites. The X axis represents the parameter estimates (i.e., 'Model coefficients'). All data was standardized to a mean of 0. Response variables are on the left Y axis (effective population size [Ne], gene diversity, fixation index [Fst] and allelic richness) and are modeled separately across forest fragmentation (A-D) and species-specific habitat fragmentation (E-H). Predictor variables of the multiple linear regression include edge density (A & E), habitat amount (B & F), patch distance (C & G), and mean patch size (D & H).

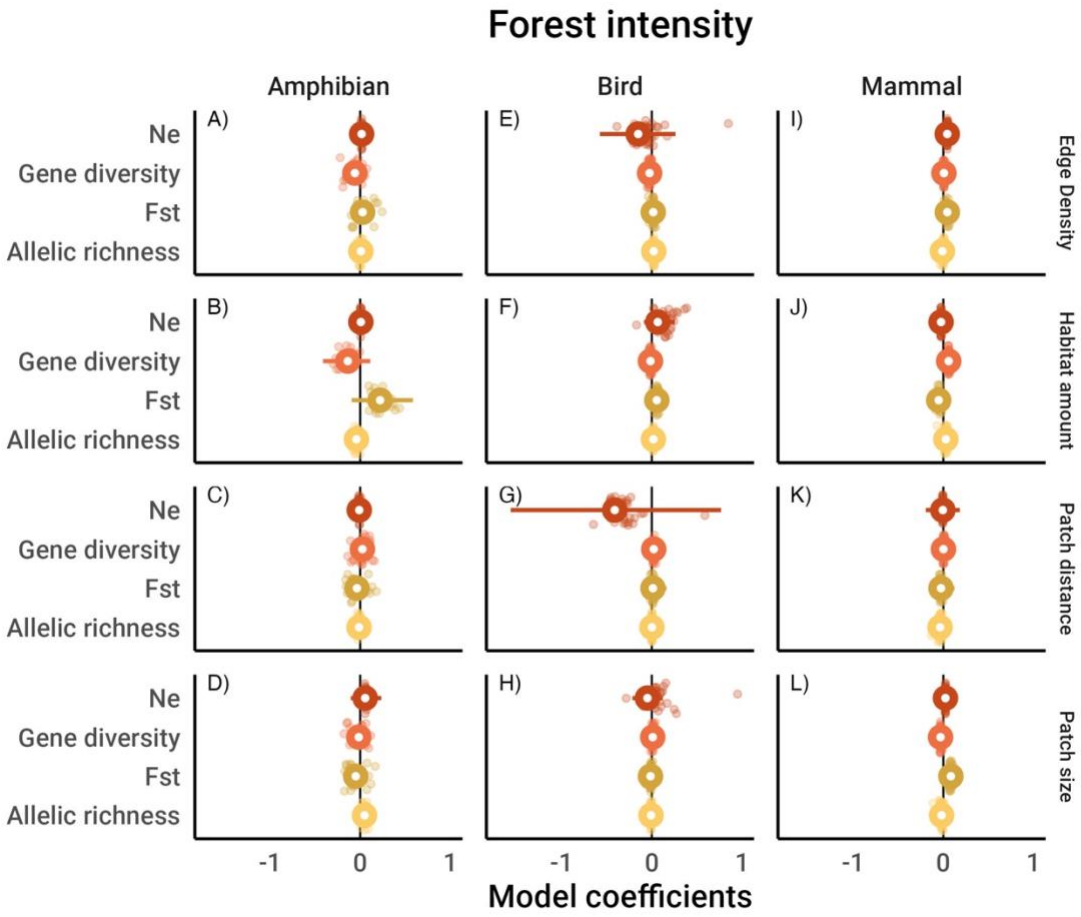

Figure 3. Bayesian multiple linear regressions of forest fragmentation intensity for amphibians, birds, and mammals with species as a random effect. There are twelve models in total, with four assigned to each: amphibians, birds, and mammals. Models used anywhere from 20 to 40 species and 384 to 649 sites. The X axis represents the parameter estimates (i.e., 'Model coefficients'). All data was standardized to a mean of 0. Response variables are on the left Y axis (effective population size [Ne], gene diversity, fixation index [Fst] and allelic richness) and are modeled separately across forest fragmentation (A-D) and species-specific habitat fragmentation (E-H). Predictor variables of the multiple linear regression include edge density (A & E), habitat amount (B & F), patch distance (C & G), and mean patch size (D & H).

General Discussion

Overview

My thesis asked whether habitat fragmentation is generalizable across species using collated genetic data from North American birds, mammals, and amphibians. I used landscape metrics derived from global landcover maps, and raw microsatellite data aggregated from public data repositories. The landscape metrics consisted of landscape scale measurements that captured the 'patches get smaller and farther apart' notion of fragmentation along with habitat amount and edge effects. Genetic diversity metrics reflected allelic variation, genetic drift, and between population genetic differentiation. Each is useful in assessing its impact because they are predicted to be affected by fragmentation.

Limitations

Fragmentation could have been measured at a finer extent. Due to computational limitations, we used landcover maps with a 300-meter grain size rather than the available 30-meter grain-size maps. It is often suggested to measure fragmentation at the finest scale reasonable to avoid creating fake patterns, losing real mechanisms, and misestimating how strong fragmentation effects actually are (Fletcher et al., 2023). This is often referred to as the 'Modifiable Areal Unit Problem', where the amount of fragmentation you measure changes because the grain size changed, not due to landscape changes (Buzzelli, 2020). For example, a 30% habitat landscape with one large patch versus many small patches can appear similar when using a coarser grain size. Thus, our estimates of fragmentation were less accurate than they could have been.

A further limitation of this study is that the exact timing of genetic sampling was unknown, potentially introducing temporal misalignment between the genetic data and the timing of habitat fragmentation. Because genetic diversity often responds to habitat loss and

fragmentation with substantial time lags, allele frequencies can continue to reflect pre-fragmentation or earlier landscape configurations for many generations after disturbance (Landguth et al., 2010; Mona et al., 2014; Piotti, 2009). More broadly, temporal mismatches between genetic and landscape datasets are a well-known criticism of landscape genetic approaches (Carvalho et al., 2019; Landguth et al., 2010). Consequently, the relationships we observed between habitat fragmentation and genetic diversity could reflect this temporal misalignment, rather than true fragmentation effects.

Our inferences are also constrained by our focus on a relatively narrow taxonomic slice, which may not be representative of broader taxonomic-level genetic responses to habitat fragmentation. The literature indicates that the genetic consequences of fragmentation vary among major organismal groups and depend strongly on traits such as dispersal ability, ecological specialization, and life-history strategy (Keyghobadi, 2007; Kierepka et al., 2016; Schlaepfer et al., 2018). Because our focal taxa occupy a small part of this broader trait and taxonomic space, the relationships we detected between habitat fragmentation and genetic diversity may not translate directly to taxa with contrasting life histories (e.g. low-dispersal invertebrates or long-lived plants), and our study should therefore be interpreted as providing evidence for these particular taxonomic groups.

Significance

My thesis presents the most extensive study to date on the effects of habitat fragmentation on genetic diversity. While several meta-analyses have addressed this question, ecological meta-analyses exhibit substantial heterogeneity among the included studies, in part due to measurement differences (Stewart, 2010). Furthermore, meta-analyses can overestimate effect size due to publication bias, where the prevalent paradigm is favoured (Koricheva, 2003; Kotiaho & Tomkins, 2002). Meta-analyses are no doubt useful, but do not resolve publication

bias. My thesis improves synthesizing studies with methodological differences and publication bias by consistently and independently measuring fragmentation and genetic diversity across sites through raw publicly available spatial data.

My thesis suggests that the effects of habitat fragmentation on genetic diversity are typically negative for mammals and amphibians, and have little effect on birds. Mammals and amphibians yielded the greatest number of effects from fragmentation, whereas birds yielded very few. This was expected, given that birds have high vagility. In amphibians and mammals, habitat area, edge density, and patch size appeared to be important predictors of genetic diversity. My thesis provides evidence that habitat fragmentation has generalizable effects on species.

Future Research

This thesis provides strong evidence that habitat fragmentation can be a useful indicator for degraded population genetic diversity. Given that measuring genetic diversity is expensive and not always accessible, using habitat fragmentation as an early indicator can be useful for land managers and researchers, particularly when prioritizing conservation resources. Unfortunately, measuring habitat fragmentation also requires specialized skills (i.e., spatial analysis and advanced data analysis) that may be inaccessible. Moreover, although the concept of fragmentation is understood, its practical measurement is difficult. This often requires defining habitats and their spatial extents and identifying them using spatial data. Thus, developing a cheap, intuitive, and accessible method for assessing habitat fragmentation could prove useful. Providing a tool that addresses species-specific habitat requirements while making the measurement of habitat fragmentation accessible would be powerful for future research and conservation efforts.

To further the understanding of the effects of habitat fragmentation on genetic diversity, a unified definition is required in the literature. The definition of fragmentation is vague and 'fragmented', as evidenced by discrepancies in how it is measured. These measurement discrepancies and epistemological disagreements lead to a stagnation of knowledge, with more effort devoted to debating the validity of empirical data. Future work should attempt to create a unified definition and measurement technique. Importantly, the field of landscape genetics has shifted its focus from fragmentation to analyses that measure functional connectivity in the landscape through graph theory and circuit theory (McRae et al., 2008; Murphy et al., 2015) . It is important that researchers be explicit about how they measure fragmentation, so that these nuances can be carefully examined and fragmentation research unified.

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Supplemental Material

S1. Genetic data compilation

Database searches and screening

We built on previously compiled and published North American mammal, bird, and amphibian microsatellite data using the same search and collection methodology (Schmidt et al., 2020, 2022; Schmidt & Garroway, 2021). We did not test reptile genetic diversity because the available genetic data had a sample size too small for meaningful results. To update the previously compiled dataset, we conducted two data searches on October 16th, 2024: one in Dryad (a repository of open access research data, (https://datadryad.org) and another in DataONE, which consolidates datasets across many data sites, (https://www.dataone.org).

We first acquired a list of North American species names from the IUCN database, including all species regardless of Red List status (IUCN, 2025). Using the search terms "microsat," "short tandem," and "single tandem," we queried both databases using 'R' (R Core Team, 2024). For Dryad, we used the jsonlite package (Ooms, 2014), and for DataONE, we used the dataone package (Jones et al., 2022).

To filter the identified studies, we first removed those published before the data searches conducted by Schmidt et al. (2020, 2022) and Schmidt & Garroway (2021), assuming they had already been screened. We then screened abstracts to ensure they measured microsatellites. The remaining datasets were screened for location (North America) and required georeferenced sampling. Studies with factors that may influence genetic diversity estimates, such as island sites, genetic rescue, translocation, or captive populations, were excluded from the analysis.

Search results

Our database searches identified 644 results from Dryad and 469 from DataONE. After filtering for publication dates and removing studies already screened by previous work, we identified 53 new Dryad studies and 0 new DataONE studies. Six papers were subsequently removed after abstract screening because they did not measure microsatellites. After screening the remaining 47 studies for location, georeferenced sampling, and exclusionary factors (e.g., island sites, translocations), twelve studies were retained from the Dryad search. These were added to the 110 studies from Schmidt et al., 2020, 2022 and Schmidt & Garroway, 2021 for a grand total of 122 studies, encompassing 104 species and 2,233 populations for our final analysis (see Figure S1). There were 21 amphibian species, 695 populations; 39 bird species, 721 populations; and 44 mammal species, 817 populations.

S2. Site georeferencing

We recorded the geographic coordinates of sites from Dryad datasets when available. Otherwise, we reviewed the published article for text coordinates or geo-referenceable maps. We extracted coordinates from geo-referenceable maps using QGIS (QGIS Development Team, 2024) if locations were in a figure but coordinates were not provided. All coordinates used the WGS84 (World Geodetic System 1984) coordinate system and where necessary, we reprojected from other systems. We followed the same protocol for collecting geographic site coordinates as the original dataset that we are adding to (See Schmidt et al., 2020 S1).

S3. Genetic response variables

Genetic diversity estimates

We estimated within population genetic diversity at each site by calculating gene diversity (i.e., expected heterozygosity) and allelic richness. Importantly, compiled microsatellite data can vary in sample size and may contain rare alleles, leading to biased estimates of genetic

diversity. We account for bias in estimates and sample size by using gene diversity and allelic richness.

Gene diversity measures the evenness and diversity of alleles. We selected gene diversity because it is minimally affected by sample size, as it is calculated as the ratio of the number of copies of an allele to the total number of alleles sampled. Also, allele frequency is squared, so the contribution of rare alleles is low, minimizing bias from rare alleles (Nei, 1973). Similarly, bias of varying sample sizes in allelic richness calculations is reduced by use of rarefaction sampling to standardize allele richness estimates to the smallest sample size among populations being compared (Foulley & Ollivier, 2006). We used the adegenet package (Jombart et al., 2025) to calculate gene diversity, and heirfstat (Goudet et al., 2022) to calculate allelic richness in R (R Core Team, 2024).

Population genetic structure

We estimate population genetic structure with population-specific Fst, which can be interpreted as divergence from an ancestral population by calculating the genetic differentiation among populations (Kitada et al., 2021). Fst is calculated in R (R Core Team, 2024) using 'hierfstat' (Goudet et al., 2022) and because the calculation requires at least two populations, studies that only sampled one site were excluded from these analyses.

Effective population size

Effective population size (Ne) indicates the rate at which genetic diversity is lost due to genetic drift over time. To calculate Ne, we used NeEstimator 2.1 (Do et al., 2014) with the linkage disequilibrium method. Rare alleles can inflate the Ne estimate, so rare alleles below a threshold frequency of 0.1 ($P_{crit} = 0.1$) were excluded to minimize Ne estimate bias (Waples & Do, 2010). The linkage disequilibrium method has lower accuracy in large populations due to

low linkage disequilibrium, resulting in estimates of infinity. We removed sites that yielded infinity estimates from further analysis.

S4. Land cover data and fragmentation predictors

Land Cover Data

We used the 300-metre-resolution global landscape-cover maps from 1992 to 2015 generated by the European Space Agency (ESA; Defourny et al., 2023), which comprise 37 landscape-cover classes. We cropped each map to cover only North America (170°W to 20°W; 7°N to 85°N) using geopandas (Jordahl et al. 2020) in Python then reprojected to the North American Albers Equal Area Conic (ESRI:102008) using the package pyproj in Python.

Philosophy of measuring fragmentation

To measure habitat fragmentation, we first treat it as a construct. A construct is a theory or idea that contains multiple concepts and is considered subjective. Next, we use a series of criteria to guide the selection of metrics to measure the construct of habitat fragmentation. Importantly, the measurement should reflect the construct of habitat fragmentation. In addition, for our findings to be useful to researchers, managers and policy makers, we follow suggestions from Kupfer (2012). Our analysis should use widely available, readily calculable, and interpretable data for scientists and a range of non-scientists.

Habitat fragmentation is the reduction in natural habitat that leads to fewer, smaller patches, often farther apart within a landscape. Hence, habitat fragmentation is the loss of structural connectivity within a landscape. Importantly, we will attempt to measure habitat fragmentation as the structural connectivity of a landscape.

There are several potential ways to measure habitat fragmentation, but we focus on landscape metrics and network analyses. Network analyses investigate how animals move

between habitat patches by defining the connections between those patches (Foltête & Vuidel, 2025). Landscape metrics are indices of habitat spatial configuration and focus on the structural connectivity of that landscape. (Frazier & Kedron, 2017). Whereas network analyses aim to bridge the gap between structural and functional connectivity in a landscape. While both landscape metrics and network analyses can accurately measure fragmentation, Occam's razor suggests that landscape metrics are preferable because of their simplicity.

In fact, landscape metrics boast greater data availability, simplicity, and interpretability over network analyses. Network analyses use graph theory to determine which habitat patches are connected for a given species, using dispersal data or resistance surfaces. This represents a substantial increase in the data required (Calabrese & Fagan, 2004; Kupfer, 2012). On the other hand, landscape metrics use landcover data that is widely and freely available. In addition, interpreting network analyses can be challenging and requires knowledge of graph theory to understand how topological metrics such as eigenvector centrality relate to ecological measures. While some landscape metrics similarly lack interpretability, many are more interpretable than network analysis metrics, such as average patch size, or average distance between patches.

A criticism of landscape metrics is that they do not explain ecological processes (Kupfer, 2012). A premise of this argument is that structural connectivity does not adequately correlate with functional connectivity. This is not a concern for us. We are instead concerned with whether the measurement can represent the construct of habitat fragmentation (Lambert & Newman, 2023). It does not matter if the measurement reveals an effect of the construct on the dependent variable. Instead, the measurement's relevance to the construct is the primary criterion for its selection. Choosing measurements for constructs according to whether they reveal effects in a hypothesized relationship leads to confirmation bias. Thus, whether landscape metrics reveal an

effect of habitat fragmentation on ecological processes does not dictate whether they accurately measure habitat fragmentation.

We opted to use landscape metrics due to data availability, interpretability, and their ability to accurately reflect habitat fragmentation (see the supplementary materials for further explanation of the rationale for selecting the fragmentation metrics). We measured landscape metrics at the patch level but used summary statistics to assess spatial configuration across the landscape (e.g., mean patch area). Given the many landscape metrics, we selected those that accurately represent habitat fragmentation while remaining simple and interpretable.

Fragmentation metric selection

We chose the mean habitat patch area and the mean Euclidean nearest neighbour distance between patches (McGarigal et al., 2009). These metrics directly estimate the average patch size and distance between patches, indicating whether patches are getting smaller and farther apart. Additionally, we chose edge density because, as patches are divided, the number of patch edges increases. This represents a distinct phenomenon from patches becoming smaller and farther apart, capturing an additional dimension of fragmentation. Finally, we include the proportion of landscape area for each site where genetic diversity is measured, that is, habitat (i.e., habitat amount) throughout our analysis.

Spatial scale selection

As the scale used to calculate landscape metrics can affect results, we select spatial scales appropriate for genetic diversity (Cushman & Landguth, 2010). The spatial scale's scope or upper limit is set by the spatial extent (i.e., the total geographic range being considered) and its

lower limit by the grain size. We select a broad spatial extent of 10 kilometres, which will likely capture regional fragmentation levels well. We use this extent consistently across 104 species to ensure comparability (Tobler's First Law of Geography; Tobler 1970). For grain size, we use a 300-meter resolution.

Defining habitat to measure habitat fragmentation

We define habitat using landcover classes from the European Space Agency (Defourny et al., 2023). Land cover classes categorize the Earth's surface based on physical attributes such as vegetation types, anthropogenic features, and water bodies (see Table S11 for description of classes). We use three approaches to measure habitat fragmentation in parallel analyses. Specifically, we use forest fragmentation, species-specific fragmentation, and intensity of forest fragmentation.

We selected forest cover as a habitat indicator (see Table S12 for breakdown of forest classes used) because multiple studies in forest ecosystems show that % forest cover reliably reflects habitat availability across species, particularly when assessing fragmentation and habitat amount (Pardo et al., 2024; Pfeifer et al., 2017; Repullés & Galán-Acedo, 2025). Forest cover is a useful measurement from a conservation and management perspective as it is easy to define. However, forest cover may not accurately capture 'habitat' for all species. To measure species-specific habitat, we linked land cover classes to species habitat using peer-reviewed literature for each of our 104 species.

Intensity of (forest) habitat fragmentation

The rate of fragmentation may also influence genetic diversity, so we estimated the intensity of forest fragmentation over time (Gargiulo et al., 2024). To do this, we calculated each landscape metric for every site where genetic sampling occurred in each year and estimated the

rate of change using linear regression. For each site and landscape metric, we fit a regression with year as the independent variable and the landscape metric as the dependent variable and extracted the slope coefficient. This slope represents the rate of change in the landscape metric over a 23-year period, with values farther from zero indicating quicker changes in fragmentation. We expected higher rates of landscape change to be associated with larger changes in genetic diversity.

Raster processing and metric calculation

To calculate landscape metrics, we created new landcover maps by reclassifying the original landcover maps. We designated which classes were considered habitat for each fragmentation analysis and then reclassified the maps as either habitat or non-habitat. For forest fragmentation, this involved consolidating the eleven original land-cover classes classified as forest. With species-specific habitat fragmentation, a new reclassified map was generated for each species.

For both forest and species-specific habitat fragmentation, we reclassified the 1992 landscape cover map; we used the oldest landscape cover map that met our criteria to allow time for changes in allelic frequency to manifest, because contemporary genetic diversity can be shaped by historical landscapes (DiLeo & Wagner, 2016; Gargiulo et al., 2024; Keyghobadi, 2007). To assess the intensity of habitat fragmentation, we reclassified all maps from 1992 to 2015 as forest cover, in the same way that we did forest fragmentation. We used Python to reclassify maps for all analyses.

Landscape Metric Calculations

We calculated landscape fragmentation metrics within the 10-km extent of each genetic sampling site. This included: the proportion of landscape that is designated as habitat; the mean

Euclidean nearest neighbor distance; edge density; and the mean patch size. Fragmentation metrics are calculated using landscapemetrics (Hesselbarth et al. 2019) in R (R Core Team 2024).

Mean patch area is the arithmetic mean of patch areas, where patches are contiguous regions of the same cover class (habitat) and areas are computed on a Euclidean plane. To find the mean Euclidean Nearest-Neighbour distance between patches (hereafter referred to as mean patch distance) we calculated the arithmetic mean of the shortest straight-line (Euclidean) distances from each habitat patch to the nearest patch of the same landscape cover class, measured edge-to-edge. We calculate edge density as the total length of all 'true' edges (i.e., the shared boundaries where adjacent patches belong to different cover classes) divided by the total landscape area defined by our spatial extent (i.e., 10 kilometers). Habitat amount is measured as the proportion of the landscape extent that is of a landscape cover class designated as habitat. It is used in models as a decimal: 0 indicates no habitat, and 1 indicates the entire spatial extent is habitat.

S5. Philosophy behind statistically modelling fragmentation

Given the complex nature of fragmentation, we adopted multiple modelling approaches (see Supplementary methods for additional analyses). While fragmentation is often defined in terms of multiple metrics (e.g., patches get smaller and farther apart) it is unclear whether any single metric alone has a notable effect on genetic diversity. In addition, the amount of habitat can suppress or exacerbate fragmentation's effects on genetic diversity. Both points lead to several distinct questions about how fragmentation affects genetic diversity.

Our primary analysis focused on how multiple metrics of fragmentation simultaneously affect genetic diversity, as species naturally experience these effects simultaneously. We use

other modelling approaches to examine whether individual metrics play disproportionate roles and how habitat amount affects fragmentation (see Supplementary methods).

To focus on the combined effect of multiple metrics of habitat fragmentation, we used Bayesian multiple linear regressions that include mean patch distance, mean patch size, edge density, and habitat amount (see S6). In addition, we used Bayesian bivariate regression models to test the strength of the relationship between single fragmentation metrics and each genetic diversity metric (see S7). Finally, we created a 'fragmentation index' that incorporated patch distance, size, edge density, and habitat amount. To create the 'fragmentation index', we used the first principal component from a principal component analysis (see S8). We subsequently used the fragmentation index as the predictor variable in bivariate linear regressions across all genetic diversity metrics (i.e., principal component regression; see Supplementary methods). Lastly, to incorporate how habitat amount may alter the effect of fragmentation on genetic diversity, we included an interaction term for habitat amount in our principal component regression (see S9). We focus on multiple linear regression because it accounts for the simultaneous multifaceted effects of habitat fragmentation on genetic diversity, while allowing interpretation of individual landscape metrics associated with different aspects of habitat fragmentation while statistically controlling for the other components of fragmentation included in the model.

We modelled mammals, birds, and amphibians separately because we expected that each taxon would respond differently to habitat fragmentation. Before modelling, we assessed collinearity among fragmentation metrics to inform our modelling approach.

Bayesian statistics reduces Type I errors

Importantly, as the number of models and parameter estimates assessed is increased, as in our analysis, the chance of Type I errors increases. However, Bayesian statistics are well-suited

to address these concerns. By using regularizing priors, we can conservatively constrain parameter estimates. For instance, standardizing the variables in a linear regression and using a normal prior with mean zero and standard deviation one will shrink noisy parameter estimates to 0. Thus, for an effect to be present, the evidence needs to be substantial so that effects estimated when using regularizing priors are unlikely to be false positives (Gelman et al., 2017; Lemoine, 2019). Regularizing priors reduce false discovery rates in a manner similar to multiple testing adjustments but does so within the model rather than through external corrections. For this reason, we adopt the regularizing normal prior with mean zero and standard deviation one when estimating parameters associated with predictor variables (i.e., the slopes).

S6. Controlling spatial structure and fragmentation metric collinearity

Handling General Linear Spatial Trends

We first removed, where present, any general linear spatial trends from our genetic diversity metrics to satisfy the assumption of stationarity and improve spatial autocorrelation modelling (Borcard et al., 2018). To do so, we tested for general linear spatial trends by regressing latitude and longitude on genetic diversity metrics (Borcard et al., 2018). We performed this regression within subsets of the data corresponding to each unique combination of model variables, to avoid null values and produce detrended datasets. Where latitude and longitude showed strong evidence of affecting the genetic diversity metric (i.e., model P-Value < 0.05), we extracted the residuals for further analysis, we used the model residuals as the new response variable data for further analysis (Borcard et al., 2018).

Handling autocorrelation

We estimated Moran's I using model residuals to test for spatial autocorrelation unaccounted for by fragmentation or detrending using the package spdep (Bivand, 2002) in R (R Core Team 2024). To statistically control for spatial autocorrelation, we used distance-based

Moran's eigenvector maps (MEMs). MEMs allow us to capture the full spectrum of underlying spatial patterns in the data to separate spatial autocorrelation from the relationship between predictor and response variables. Technically speaking, MEMs are eigenvectors derived from a truncated spatial distance matrix constructed using the spatial coordinates of sampling sites (Borcard & Legendre, 2002). These eigenvectors represent orthogonal spatial patterns across multiple scales, capturing both broad and fine-scale spatial structure. MEMs can be included as spatial predictors in regression analyses to account for spatial autocorrelation. For autocorrelated models, we created distance-based Moran's eigenvector maps using Euclidean distances among sites as the basis for the spatial weighting matrix. We used a Gabriel Graph connection network to define neighbours, applying inverse distance weighting. We then selected the MEMs that best explained variation via forward selection in an autoregressive model using the adespatial package (Dray et al., 2025) in R (R Core Team, 2024). We reran autocorrelated models with the selected dbMEMs as covariates.

Fragmentation metric collinearity

Collinearity in predictive models is defined as substantial when $| r | > 0.7$ between predictors (Dormann et al., 2013). We tested pairwise correlations using Pearson's correlation coefficient across the four-fragmentation metrics: habitat amount, patch distance, edge density, and mean patch size. We followed the previous literature's advice that pairwise correlations do not distort model predictions when the correlation coefficient is below 0.7.

S7. Multiple linear regression models

We tested for relationships between genetic diversity and habitat fragmentation using Bayesian mixed-effects multiple linear regression models. For each taxon (amphibians, birds, mammals) and each genetic response variable, we included all four fragmentation metrics—

habitat amount, patch distance, mean patch size, and edge density—as fixed effects, resulting in 36 models (12 per habitat-fragmentation dataset). Species was included as a grouping factor with random intercepts and random slopes, and slope terms were assigned a regularizing normal prior, N(0,1). Models were fit in R (R Core Team 2024) using brms (Bürkner 2021).

Because fragmentation predictors are often correlated, multivariate models can exhibit inflated variance and unstable parameter estimates under collinearity. We addressed this using two complementary strategies. First, we centered and scaled all predictors, which improves numerical conditioning and reduces spurious parameter correlations (Gelman, 2008). Second, we used Bayesian mixed-effects models with weakly regularizing priors, which further mitigates collinearity-induced variance inflation through shrinkage and partial pooling of group-level effects (Gelman, 2008).

S8. Bivariate regression models

Methods

We used Bayesian bivariate mixed-effect models to test the effect of a singular fragmentation metric on a genetic diversity metric in isolation. We regressed each of the four fragmentation-intensity metrics against each of the four genetic-diversity metrics and split the models across the three taxa, resulting in 48 bivariate models. For each model, we used species as a random intercept and slope. We used a regularizing normal prior with mean 0 and standard deviation 1 for the slope parameters. We created these models using the package brms (Bürkner, 2021) in R (R Core Team 2024).

Results

Under forest habitat fragmentation, parameter estimates ranged from -0.14 to 0.19 across taxa with all 95% credible intervals crossing 0 (Figure S2; Table S4), suggesting individual metrics of forest fragmentation do not reveal an effect of fragmentation on genetic diversity.

Parameter estimates under species-specific habitat fragmentation ranged from -0.23 to 0.33 with most 95% credible intervals crossing 0 (Figure S3; Table S5). Fst in mammals held a negative relationship with habitat amount (Estimate = -0.2; CI 95% = -0.31 to –0.08; Figure S3-F) and patch size (Estimate = -0.11; CI 95% = -0.21 to –0.01; Figure S3-L). Mammal gene diversity held a positive relationship with habitat amount (Estimate = 0.13; CI 95% = 0.04 to 0.22; Figure S3-F) and patch size (Estimate = 0.07; CI 95% = 0.01 to 0.13; Figure S3-L).

Intensity of forest fragmentation parameter estimates ranged from –0.33 to 0.34 with all 95% credible intervals crossing 0. Intensity of forest fragmentation change does not appear to affect genetic diversity given these parameter estimates.

S9. Principal component regression (composite fragmentation index)

Methods

We tested whether fragmentation metrics could be used to predict genetic diversity of populations using principal component regression. The principal component regression was created by using the first component in a principal component analysis (referred to hereafter as the composite fragmentation index) in a Bayesian linear regression model with random slopes and intercepts for species in R (R Core Team 2024) using the package ‘brms’ (Bürkner, 2021) .

Results

We used the first principal component of the PCA as the 'composite fragmentation index'. For both forest and species fragmentation, habitat amount had the greatest influence on the index, and patch size had the second most (Figure S5-S6).

For forest fragmentation, the principal component regression explained between 2% and 87% when accounting for species differences (i.e., R^2 Conditional; Table S3); whereas the fixed effect, the Fragmentation Index, explained substantially less variance (R^2 Marginal: 0.1% to 1.7%; Table S3). The parameter estimates ranged from -0.18 to 0.17 with every model's 95% credible intervals crossing 0 (Figure S7). Principal component regression explained similar levels of variance in species fragmentation (R^2 Conditional: 2% to 88%; R^2 Marginal: 0.1% to 1.4%; Table S3) and forest fragmentation intensity (R^2 Conditional: 2% to 87%; R^2 Marginal: 0.1% to 1.2%; Table S3). For parameter estimates of species fragmentation (-0.18 to 0.17) and forest fragmentation intensity (-0.07 to 0.11) nearly all 95% credible intervals crossed 0 apart from species fragmentation of Fst in mammals (Estimate = -0.11; CI 95% = -0.22 to -0.01; Figure S7-C).

S10. Interactive effect of habitat amount models

Methods

To test whether the effect of habitat fragmentation intensity on genetic diversity depends on habitat amount, we create a categorical variable that classifies fragmentation as 'low', 'moderate', or 'high' habitat amount. We categorized habitats as low if they fell under 30% habitat amount; we adopted this number based on previous suggestions that fragmentation effects will not manifest until low habitat amount (>30%; Swift and Hannon 2010). To define landscapes as high, we used a threshold of 60% habitat amount, based on percolation theory,

which suggests habitat will remain well connected above 60% (With 2002). All landscapes between 30% and 60% were defined as having a 'moderate' habitat amount.

We incorporated habitat amount by including it as an interactive term into our principal component regression models. Using habitat amount as interaction, we ask whether the strength of the fragmentation-genetic diversity relationship changes according to the amount of habitat with the same fragmentation composite index used across all levels of a model.

Results

We expected a greater effect under low and moderate habitat amounts; however, although this was true in some instances, the effect was also greater under high habitat amounts. Overall, there was no discernible pattern across models and habitat-fragmentation types in the effect of habitat amount on the effect of habitat fragmentation on genetic diversity.

When examining forest fragmentation there was a greater effect of fragmentation under low habitat amount on amphibian's Ne (Estimate = -0.27; CI 95% = -0.5 to -0.04; Figure S7-D; Table S8), and mammal's Fst (Estimate = -0.12; CI 95% = -0.25 to 0.00; Figure S7-J; Table S8), and a greater effect under moderate habitat on bird's Ne (Estimate = -0.64; CI 95% = -1.23 to -0.04; Figure S7-H; Table S8).

In some instances, habitat fragmentation had a greater effect under higher habitat amount, such as in birds' gene diversity (Estimate = 0.3; CI 95% = 0.07 to 0.53; Figure S7-G); Table S8 and mammals' Ne (Estimate = 0.4; CI 95% = 0.03 to 0.76; Figure S7-L; Table S8). All other models' parameter estimates' 95% credible intervals crossed 0.

Species-specific habitat fragmentation had a greater effect under high habitat amount on amphibians' allelic richness (Estimate = -0.2; CI 95% = -0.38 to -0.03; Figure S8-A; Table S9)

and under low habitat amount, mammals' allelic richness (Estimate = 0.14; CI 95% = 0.03 to 0.26; Figure S8-I; Table S9).

The intensity of forest fragmentation had a greater effect under moderate habitat amount on bird's Fst (Estimate = 0.4; CI 95% = 0.06 to 0.74; Figure S9-F; Table S10) and Gene Diversity (Estimate = -0.22; CI 95% = -0.38 to -0.06; Figure S9-G; Table S10); it also had a great effect under high habitat amount on amphibian gene diversity (Estimate = -0.13; CI 95% = -0.24 to -0.03; Figure S9-C; Table S10). All other models' parameter estimates' 95% credible intervals crossed 0.

Species-specific habitat fragmentation had a greater effect under high habitat amount on amphibians' allelic richness (Estimate = -0.2; CI 95% = -0.38 to -0.03; Figure S8-A; Table S9) and under low habitat amount, mammals' allelic richness (Estimate = 0.14; CI 95% = 0.03 to 0.26; Figure S8-I; Table S9).

The intensity of forest fragmentation had a greater effect under moderate habitat amount on bird's Fst (Estimate = 0.4; CI 95% = 0.06 to 0.74; Figure S9-F; Table S10) and Gene Diversity (Estimate = -0.22; CI 95% = -0.38 to -0.06; Figure S9-G; Table S10); it also had a great effect under high habitat amount on amphibian gene diversity (Estimate = -0.13; CI 95% = -0.24 to -0.03; Figure S9-C; Table S10). All other models' parameter estimates' 95% credible intervals crossed 0.

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Tables

Table S1. Parameter estimates from multiple linear regression of the intensity of forest fragmentation metrics on genetic diversity metrics

	Parameter Estimate [95% Credible Interval Range]			
Response	**Patch distance**	**Habitat amount**	**Edge Density**	**Patch size**
Amphibian				
Ne	-0.01 [-0.13 to 0.11]	0.01 [-0.13 to 0.14]	0.02 [-0.12 to 0.15]	0.06 [-0.1 to 0.23]
Allelic richness	-0.01 [-0.08 to 0.06]	-0.04 [-0.18 to 0.05]	0.01 [-0.07 to 0.08]	0.05 [-0.06 to 0.17]
Gene diversity	0.02 [-0.03 to 0.08]	-0.14 [-0.41 to 0.11]	-0.06 [-0.14 to 0.03]	-0.02 [-0.07 to 0.04]
Fst	-0.04 [-0.13 to 0.05]	0.22 [-0.1 to 0.59]	0.03 [-0.1 to 0.15]	-0.05 [-0.15 to 0.05]
Bird				
Allelic richness	0 [-0.14 to 0.13]	0.02 [-0.09 to 0.13]	0.02 [-0.08 to 0.12]	-0.01 [-0.13 to 0.11]
Ne	-0.41 [-1.57 to 0.77]	0.07 [-0.09 to 0.26]	-0.15 [-0.58 to 0.26]	-0.05 [-0.22 to 0.12]
Gene diversity	0.02 [-0.03 to 0.11]	-0.01 [-0.06 to 0.04]	-0.02 [-0.08 to 0.03]	0.01 [-0.04 to 0.06]
Fst	0.01 [-0.11 to 0.16]	0.06 [-0.06 to 0.17]	0.02 [-0.11 to 0.15]	-0.01 [-0.13 to 0.09]
Mammal				
Allelic richness	-0.04 [-0.14 to 0.07]	0.03 [-0.06 to 0.12]	-0.01 [-0.08 to 0.06]	-0.02 [-0.09 to 0.05]
Ne	-0.01 [-0.19 to 0.18]	-0.03 [-0.13 to 0.08]	0.04 [-0.06 to 0.15]	0.02 [-0.08 to 0.13]
Gene diversity	0 [-0.09 to 0.08]	0.06 [0.01 to 0.11]	0.01 [-0.05 to 0.06]	-0.03 [-0.09 to 0.03]
Fst	-0.03 [-0.15 to 0.12]	-0.05 [-0.14 to 0.03]	0.04 [-0.04 to 0.13]	0.08 [-0.02 to 0.22]

Table S2. Multiple linear regression containing R^2 conditional and marginal values for each forest, species, and forest fragmentation intensity.

		R^2 Conditional; Marginal		
Fragmentation Type	**Response**	**Mammal**	**Bird**	**Amphibian**
Forest	Ne	0.22; 0.062	0.10; 0.028	0.07; 0.022
	Gene diversity	0.77; 0.088	0.92; 0.052	0.85; 0.16
	Allelic richness	0.64; 0.073	0.41; 0.08	0.76; 0.10
	Fst	0.45; 0.17	0.51; 0.12	0.63; 0.30
Species	Ne	0.70; 0.084	0.06; 0.027	0.08; 0.05
	Gene diversity	0.73; 0.011	0.88; 0.004	0.81; 0.043
	Allelic richness	0.61; 0.01	0.36; 0.014	0.69; 0.028
	Fst	0.27; 0.032	0.45; 0.049	0.42; 0.17
Intensity	Allelic richness	0.57; 0.007	0.30; 0.01	0.72; 0.074
	Ne	0.03; 0.012	0.37; 0.19	0.04; 0.016
	Gene diversity	0.74; 0.083	0.9; 0.045	0.86; 0.18
	Fst	0.37; 0.14	0.47; 0.18	0.6; 0.32

Table S3. Principal component regression containing R^2 conditional and marginal values for each forest, species, and forest fragmentation intensity.

		R^2 Conditional; Marginal		
Fragmentation Type	**Response**	**Mammal**	**Bird**	**Amphibian**
Forest	Gene diversity	0.70; 0.001	0.87; 0.002	0.72; 0.009
	Allelic richness	0.59; 0.001	0.33; 0.002	0.66; 0.003
	Fst	0.27; 0.003	0.39; 0.017	0.31; 0.010
	Ne	0.03; 0.002	0.07; 0.003	0.02; 0.001
Species	Gene diversity	0.72; 0.004	0.88; 0.001	0.78; 0.029
	Allelic richness	0.59; 0.002	0.35; 0.007	0.67; 0.007
	Fst	0.23; 0.012	0.33; 0.005	0.34; 0.036
	Ne	0.04; 0.003	0.03; 0.005	0.02; 0.002
Intensity	Gene diversity	0.67; 0.001	0.87; 0.003	0.73; 0.002
	Allelic richness	0.56; 0.001	0.33; 0.002	0.66; 0.001
	Fst	0.23; 0.002	0.4; 0.008	0.27; 0.002
	Ne	0.12; 0.006	0.12; 0.012	0.02; 0.002

Table S4. Forest fragmentation bivariate models containing parameter estimates.

Class	Response	Predictor	Parameter estimate [95% CI]	R^2 Conditional; Marginal
Amphibian	Allelic Richness	Habitat Amount	0.02 [-0.18 to 0.23]	0.69; 0.004
		Edge Density	-0.05 [-0.17 to 0.08]	0.70; 0.003
		Patch Distance	0 [0 to 0]	0.66; 0.013
		Patch Size	0 [0 to 0]	0.69; 0.012
	Fst	Patch Distance	0.04 [-0.16 to 0.31]	0.24; 0.003
		Habitat Amount	-0.02 [-0.37 to 0.35]	0.38; 0.014
		Edge Density	-0.03 [-0.26 to 0.2]	0.32; 0.006
		Patch Size	0 [0 to 0]	0.35; 0.059
	Gene Diversity	Habitat Amount	0.02 [-0.21 to 0.26]	0.72; 0.006
		Edge Density	-0.02 [-0.2 to 0.14]	0.73; 0.003
		Patch Size	0 [0 to 0]	0.72; 0.015
		Patch Distance	0 [0 to 0]	0.70; 0.004
	Ne	Patch Distance	0.02 [-0.1 to 0.13]	0.02; 0.002
		Habitat Amount	-0.02 [-0.13 to 0.08]	0.02; 0.002
		Edge Density	0.07 [-0.06 to 0.2]	0.04; 0.006
		Patch Size	-0.04 [-0.16 to 0.08]	0.02; 0.002
Bird	Allelic Richness	Patch Distance	-0.01 [-0.16 to 0.12]	0.32; 0.002
		Habitat Amount	0.03 [-0.15 to 0.22]	0.4; 0.004
		Edge Density	0 [-0.11 to 0.1]	0.37; 0.001
		Patch Size	0 [0 to 0]	0.38; 0.012
	Fst	Patch Distance	-0.14 [-0.66 to 0.37]	0.35; 0.035
		Habitat Amount	0.19 [-0.17 to 0.56]	0.44; 0.035
		Edge Density	0.09 [-0.12 to 0.31]	0.41; 0.01
		Patch Size	0.13 [-0.2 to 0.51]	0.37; 0.018
	Gene Diversity	Patch Size	-0.02 [-0.3 to 0.24]	0.87; 0.007
		Habitat Amount	-0.04 [-0.18 to 0.1]	0.89; 0.003
		Edge Density	-0.04 [-0.12 to 0.04]	0.87; 0.002
		Patch Distance	0 [0 to 0]	0.86; 0.003
	Ne	Patch Distance	-0.04 [-0.22 to 0.14]	0.07; 0.004
		Habitat Amount	-0.1 [-0.29 to 0.08]	0.11; 0.01

		Edge Density	-0.06 [-0.23 to 0.11]	0.13; 0.005
		Patch Size	-0.04 [-0.21 to 0.1]	0.09; 0.003
Mammal	Allelic Richness	Patch Distance	0.03 [-0.06 to 0.12]	0.57; 0.001
		Habitat Amount	0.01 [-0.11 to 0.13]	0.62; 0.002
		Edge Density	0.01 [-0.08 to 0.09]	0.58; 0.001
		Patch Size	0 [0 to 0]	0.62; 0.069
	Fst	Habitat Amount	0.01 [-0.12 to 0.13]	0.23; 0.002
		Patch Size	-0.02 [-0.14 to 0.09]	0.23; 0.002
		Patch Distance	0 [0 to 0]	0.3; 0.057
		Edge Density	0 [0 to 0]	0.24; 0.041
	Gene Diversity	Edge Density	-0.04 [-0.11 to 0.02]	0.67; 0.002
		Patch Distance	0 [0 to 0]	0.69; 0.009
		Patch Size	0 [0 to 0]	0.67; 0.006
		Habitat Amount	0 [0 to 0]	0.7; 0.02
	Ne	Patch Distance	0.17 [-0.21 to 0.56]	0.09; 0.032
		Habitat Amount	0.03 [-0.06 to 0.13]	0.02; 0.002
		Edge Density	-0.02 [-0.11 to 0.07]	0.02; 0.001
		Patch Size	0.03 [-0.08 to 0.14]	0.03; 0.002

Table S5. Species fragmentation bivariate models containing parameter estimates.

Class	Response	Predictor	Parameter estimates [95% CI]	R^2 Conditional; Marginal
Amphibian	Allelic Richness	Edge Density	-0.07 [-0.23 to 0.10]	0.70; 0.005
		Habitat Amount	0.11 [-0.12 to 0.35]	0.70; 0.014
		Patch Distance	-0.04 [-0.19 to 0.06]	0.66; 0.002
		Patch Size	0.06 [-0.18 to 0.32]	0.68; 0.006
	Fst	Edge Density	-0.09 [-0.35 to 0.19]	0.31; 0.012
		Habitat Amount	-0.23 [-0.66 to 0.17]	0.34; 0.054
		Patch Distance	0.08 [-0.13 to 0.30]	0.30; 0.008
		Patch Size	-0.20 [-0.72 to 0.21]	0.29; 0.034
	Gene Diversity	Edge Density	0.01 [-0.20 to 0.21]	0.74; 0.004
		Habitat Amount	0.22 [-0.09 to 0.53]	0.74; 0.047
		Patch Distance	-0.07 [-0.22 to 0.08]	0.75; 0.005
		Patch Size	0.22 [-0.08 to 0.6]	0.73; 0.041
	Ne	Edge Density	0.08 [-0.05 to 0.21]	0.04; 0.007
		Habitat Amount	0.04 [-0.08 to 0.18]	0.03; 0.003
		Patch Distance	0.03 [-0.18 to 0.30]	0.02; 0.004
		Patch Size	-0.02 [-0.15 to 0.10]	0.02; 0.002
Bird	Allelic Richness	Edge Density	0 [-0.11 to 0.11]	0.37; 0.003
		Habitat Amount	0.09 [-0.05 to 0.20]	0.39; 0.008
		Patch Distance	-0.04 [-0.15 to 0.05]	0.34; 0.002
		Patch Size	0.02 [-0.16 to 0.16]	0.39; 0.003
	Fst	Edge Density	0.08 [-0.02 to 0.17]	0.32; 0.007
		Habitat Amount	0 [-0.28 to 0.28]	0.41; 0.008
		Patch Distance	0.04 [-0.07 to 0.15]	0.29; 0.019
		Patch Size	0.04 [-0.18 to 0.3]	0.35; 0.006
	Gene Diversity	Edge Density	-0.03 [-0.07 to 0.02]	0.88; 0.001
		Habitat Amount	-0.01 [-0.12 to 0.10]	0.87; 0.001
		Patch Distance	0 [-0.05 to 0.05]	0.87; 0
		Patch Size	-0.07 [-0.21 to 0.05]	0.89; 0.005
	Ne	Edge Density	-0.11 [-0.36 to 0.12]	0.12; 0.014

		Habitat Amount	0.22 [-0.1 to 0.54]	0.21; 0.049
		Patch Distance	-0.04 [-0.16 to 0.08]	0.02; 0.003
		Patch Size	0.33 [-0.27 to 0.89]	0.41; 0.1
Mammal	Allelic Richness	Edge Density	0.02 [-0.05 to 0.09]	0.59; 0.001
		Habitat Amount	0.04 [-0.07 to 0.16]	0.62; 0.003
		Patch Distance	-0.03 [-0.1 to 0.03]	0.58; 0.001
		Patch Size	0.01 [-0.06 to 0.08]	0.59; 0.001
	Fst	Edge Density	-0.01 [-0.10 to 0.09]	0.20; 0.013
		Habitat Amount	-0.20 [-0.31 to -0.08]	0.22; 0.039
		Patch Distance	0.09 [-0.05 to 0.29]	0.25; 0.030
		Patch Size	-0.11 [-0.21 to -0.01]	0.20; 0.012
	Gene Diversity	Edge Density	-0.01 [-0.09 to 0.05]	0.69; 0.001
		Habitat Amount	0.13 [0.04 to 0.22]	0.70; 0.016
		Patch Distance	-0.05 [-0.16 to 0.03]	0.72; 0.002
		Patch Size	0.07 [0.01 to 0.13]	0.69; 0.005
	Ne	Edge Density	-0.02 [-0.12 to 0.07]	0.02; 0.001
		Habitat Amount	0.05 [-0.04 to 0.14]	0.02; 0.003
		Patch Distance	0.24 [-0.39 to 0.84]	0.53; 0.068
		Patch Size	0.04 [-0.06 to 0.14]	0.02; 0.002

Table S6. Intensity of forest fragmentation bivariate models containing parameter estimates.

Class	Response	Predictor	Parameter estimates [95% CI]	R^2 Conditional; Marginal
Amphibian	Allelic Richness	Edge Density	0 [-0.08 to 0.07]	0.65; 0.001
		Habitat Amount	-0.03 [-0.17 to 0.06]	0.66; 0.001
		Patch Distance	0 [-0.08 to 0.07]	0.65; 0.001
		Patch Size	0.01 [-0.07 to 0.1]	0.66; 0.001
	Fst	Edge Density	0.11 [-0.08 to 0.37]	0.28; 0.009
		Habitat Amount	0.34 [-0.07 to 0.78]	0.36; 0.094
		Patch Distance	-0.02 [-0.16 to 0.1]	0.26; 0.001
		Patch Size	-0.04 [-0.17 to 0.1]	0.29; 0.030
	Gene Diversity	Edge Density	-0.09 [-0.23 to 0]	0.73; 0.035
		Habitat Amount	-0.19 [-0.47 to 0.05]	0.75; 0.032
		Patch Distance	0.03 [-0.04 to 0.14]	0.71; 0.001
		Patch Size	0.11 [-0.07 to 0.31]	0.72; 0.011
	Ne	Edge Density	0.01 [-0.1 to 0.13]	0.02; 0.002
		Habitat Amount	0.02 [-0.1 to 0.15]	0.02; 0.002
		Patch Distance	-0.01 [-0.13 to 0.1]	0.02; 0.002
		Patch Size	0.05 [-0.1 to 0.22]	0.03; 0.003
Bird	Allelic Richness	Edge Density	0.02 [-0.07 to 0.11]	0.3; 0.001
		Habitat Amount	0.01 [-0.09 to 0.11]	0.3; 0.001
		Patch Distance	0 [-0.15 to 0.13]	0.3; 0.001
		Patch Size	-0.01 [-0.11 to 0.1]	0.3; 0.001
	Fst	Edge Density	0.02 [-0.11 to 0.16]	0.3; 0.002
		Habitat Amount	0.04 [-0.07 to 0.14]	0.31; 0.039
		Patch Distance	-0.02 [-0.17 to 0.11]	0.28; 0.001
		Patch Size	0.01 [-0.09 to 0.11]	0.28; 0.001
	Gene Diversity	Edge Density	-0.02 [-0.09 to 0.05]	0.87; 0.001
		Habitat Amount	-0.03 [-0.08 to 0.02]	0.86; 0.005
		Patch Distance	0.03 [-0.04 to 0.11]	0.86; 0.001
		Patch Size	-0.01 [-0.05 to 0.05]	0.86; 0
	Ne	Edge Density	0.01 [-0.12 to 0.13]	0.07; 0.002
		Habitat Amount	0.01 [-0.14 to 0.15]	0.07; 0.002

		Patch Distance	-0.33 [-1.38 to 0.73]	0.24; 0.137
		Patch Size	-0.01 [-0.15 to 0.14]	0.07; 0.002
Mammal	Allelic Richness	Edge Density	-0.01 [-0.07 to 0.05]	0.56; 0
		Habitat Amount	0.03 [-0.05 to 0.1]	0.56; 0.001
		Patch Distance	-0.03 [-0.13 to 0.07]	0.56; 0.001
		Patch Size	-0.01 [-0.06 to 0.05]	0.56; 0
	Fst	Edge Density	0.02 [-0.05 to 0.1]	0.23; 0.001
		Habitat Amount	-0.04 [-0.11 to 0.04]	0.22; 0.001
		Patch Distance	-0.03 [-0.14 to 0.1]	0.23; 0.002
		Patch Size	0.04 [-0.05 to 0.14]	0.23; 0.002
	Gene Diversity	Edge Density	0.01 [-0.05 to 0.06]	0.67; 0
		Habitat Amount	0.04 [-0.01 to 0.09]	0.67; 0.002
		Patch Distance	0 [-0.09 to 0.08]	0.67; 0.001
		Patch Size	-0.02 [-0.07 to 0.04]	0.67; 0
	Ne	Edge Density	0.04 [-0.06 to 0.14]	0.02; 0.002
		Habitat Amount	-0.02 [-0.11 to 0.07]	0.01; 0.001
		Patch Distance	-0.01 [-0.2 to 0.17]	0.01; 0.002
		Patch Size	0 [-0.09 to 0.1]	0.01; 0.001

Table S7. Principal component regression parameter estimates of forest fragmentation (*Forest*), intensity of forest fragmentation (*Forest fragmentation intensity*) and species fragmentation *(Species).*

		Parameter Estimate [95% Credible Interval Range]		
Class	**Response**	**Forest**	**Species**	**Forest fragmentation intensity**
Amphibian	Allelic Richness	0.05 [-0.07 to 0.19]	0.08 [-0.05 to 0.22]	0.01 [-0.05 to 0.08]
	Fst	-0.06 [-0.37 to 0.21]	-0.18 [-0.43 to 0.07]	0.03 [-0.1 to 0.14]
	Gene Diversity	0.09 [-0.1 to 0.3]	0.17 [-0.03 to 0.37]	-0.04 [-0.13 to 0.06]
	Ne	0 [-0.12 to 0.11]	0.04 [-0.09 to 0.16]	-0.01 [-0.12 to 0.11]
Bird	Allelic Richness	0.01 [-0.13 to 0.13]	0.08 [-0.02 to 0.18]	0 [-0.14 to 0.14]
	Fst	-0.12 [-0.42 to 0.18]	-0.03 [-0.23 to 0.16]	0.07 [-0.15 to 0.29]
	Gene Diversity	0.05 [-0.06 to 0.16]	0.01 [-0.06 to 0.08]	-0.06 [-0.13 to 0.01]
	Ne	0.03 [-0.13 to 0.2]	0.08 [-0.06 to 0.24]	0.11 [-0.03 to 0.24]
Mammal	Allelic Richness	-0.01 [-0.12 to 0.1]	0.03 [-0.07 to 0.14]	0.02 [-0.04 to 0.09]
	Fst	-0.05 [-0.17 to 0.09]	-0.11 [-0.22 to -0.01]	-0.05 [-0.12 to 0.03]
	Gene Diversity	0.03 [-0.07 to 0.11]	0.06 [-0.01 to 0.14]	0.02 [-0.03 to 0.08]
	Ne	-0.04 [-0.15 to 0.07]	0.05 [-0.06 to 0.17]	-0.07 [-0.22 to 0.09]

Table S8. Forest fragmentation principal component regression with habitat amount categories (High: >60%; Moderate: 60% < 30%; Low: 30%<) as an interactive effect parameter estimate.

		Parameter Estimate [95% Credible Interval Range]		
Class	**Response**	**High**	**Moderate**	**Low**
Amphibian	Allelic Richness	0.06 [-0.08 to 0.21]	0.04 [-0.12 to 0.21]	-0.02 [-0.15 to 0.07]
	Fst	0.12 [-0.13 to 0.35]	-0.19 [-0.47 to 0.07]	-0.01 [-0.22 to 0.16]
	Gene Diversity	0.08 [-0.12 to 0.3]	0.05 [-0.17 to 0.26]	0.03 [-0.16 to 0.22]
	Ne	-0.07 [-0.3 to 0.17]	-0.05 [-0.3 to 0.21]	-0.27 [-0.5 to -0.04]
Bird	Allelic Richness	0.15 [-0.25 to 0.55]	-0.1 [-0.51 to 0.31]	-0.08 [-0.27 to 0.06]
	Fst	-0.49 [-1 to 0.03]	0.15 [-0.36 to 0.65]	0.22 [-0.14 to 0.58]
	Gene Diversity	0.3 [0.07 to 0.53]	-0.09 [-0.31 to 0.12]	-0.08 [-0.22 to 0.06]
	Ne	0.08 [-0.5 to 0.67]	-0.64 [-1.23 to -0.04]	-0.03 [-0.19 to 0.17]
Mammal	Allelic Richness	-0.06 [-0.29 to 0.18]	-0.08 [-0.29 to 0.13]	0.1 [-0.02 to 0.23]
	Fst	-0.21 [-0.5 to 0.09]	-0.12 [-0.38 to 0.15]	-0.12 [-0.25 to 0]
	Gene Diversity	0.12 [-0.08 to 0.31]	0.04 [-0.13 to 0.22]	0.08 [-0.01 to 0.19]
	Ne	0.4 [0.03 to 0.76]	0.01 [-0.32 to 0.34]	0.02 [-0.11 to 0.14]

Table S9. Species Fragmentation principal component regression with habitat amount categories (High: >60%; Moderate: 60% < 30%; Low: 30%<) as an interactive effect parameter estimate.

		Parameter Estimate [95% Credible Interval Range]		
Class	**Response**	**High**	**Moderate**	**Low**
Amphibian	Allelic Richness	-0.2 [-0.38 to -0.03]	0 [-0.2 to 0.2]	0.03 [-0.09 to 0.19]
	Fst	0.14 [-0.19 to 0.49]	0.1 [-0.24 to 0.47]	-0.07 [-0.35 to 0.26]
	Gene Diversity	-0.2 [-0.48 to 0.09]	-0.07 [-0.35 to 0.21]	-0.01 [-0.29 to 0.25]
	Ne	0.07 [-0.24 to 0.35]	-0.06 [-0.37 to 0.25]	0.2 [-0.01 to 0.44]
Bird	Allelic Richness	-0.05 [-0.26 to 0.17]	-0.03 [-0.23 to 0.17]	0.06 [-0.06 to 0.19]
	Fst	0.11 [-0.12 to 0.34]	-0.09 [-0.31 to 0.11]	0.01 [-0.12 to 0.15]
	Gene Diversity	-0.08 [-0.18 to 0.02]	0.03 [-0.06 to 0.12]	-0.02 [-0.07 to 0.04]
	Ne	0.03 [-0.23 to 0.29]	-0.09 [-0.4 to 0.23]	0.07 [-0.09 to 0.22]
Mammal	Allelic Richness	0.04 [-0.09 to 0.16]	0.05 [-0.09 to 0.18]	0.14 [0.03 to 0.26]
	Fst	0 [-0.17 to 0.17]	-0.11 [-0.3 to 0.07]	-0.06 [-0.21 to 0.09]
	Gene Diversity	0.01 [-0.09 to 0.12]	0.07 [-0.05 to 0.18]	0.03 [-0.06 to 0.13]
	Ne	-0.26 [-0.59 to 0.08]	-0.11 [-0.45 to 0.23]	-0.06 [-0.4 to 0.27]

Table S10. Principal component regression with habitat amount as an interactive effect parameter estimates of forest fragmentation intensity**.**

		Parameter Estimate [95% Credible Interval Range]		
Class	**Response**	**High**	**Moderate**	**Low**
Amphibian	Allelic Richness	-0.03 [-0.12 to 0.06]	0.06 [-0.16 to 0.28]	0.1 [-0.07 to 0.26]
	Fst	0.1 [-0.04 to 0.26]	-0.14 [-0.47 to 0.19]	0.1 [-0.16 to 0.37]
	Gene Diversity	-0.13 [-0.24 to -0.03]	0.15 [-0.05 to 0.36]	0 [-0.17 to 0.16]
	Ne	0.02 [-0.12 to 0.16]	0.18 [-0.23 to 0.59]	-0.06 [-0.35 to 0.23]
Bird	Allelic Richness	0.02 [-0.1 to 0.13]	-0.12 [-0.45 to 0.2]	0.05 [-0.13 to 0.23]
	Fst	-0.04 [-0.17 to 0.08]	0.4 [0.06 to 0.74]	0 [-0.19 to 0.2]
	Gene Diversity	0.01 [-0.08 to 0.1]	-0.22 [-0.38 to -0.06]	-0.03 [-0.13 to 0.08]
	Ne	0.01 [-0.16 to 0.17]	-0.01 [-0.49 to 0.46]	0.06 [-0.2 to 0.32]
Mammal	Allelic Richness	-0.01 [-0.08 to 0.06]	-0.04 [-0.22 to 0.15]	0.14 [-0.01 to 0.3]
	Fst	0 [-0.1 to 0.09]	-0.07 [-0.31 to 0.16]	0.07 [-0.16 to 0.3]
	Gene Diversity	-0.01 [-0.07 to 0.05]	0.12 [-0.04 to 0.27]	0.05 [-0.09 to 0.19]
	Ne	0.03 [-0.08 to 0.14]	0 [-0.29 to 0.3]	0.03 [-0.21 to 0.27]

Table S11. Description of landcover classes from the European Space Agency Climate Change Initiative landscape cover maps.

CLASS CODE	DESCRIPTION
0	No Data
10	Cropland, rainfed
11	Herbaceous cover
12	Tree or shrub cover
20	Cropland, irrigated or post-flooding
30	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)
40	Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%)
50	Tree cover, broadleaved, evergreen, closed to open (>15%)
60	Tree cover, broadleaved, deciduous, closed to open (>15%)
61	Tree cover, broadleaved, deciduous, closed (>40%)
62	Tree cover, broadleaved, deciduous, open (15-40%)
70	Tree cover, needleleaved, evergreen, closed to open (>15%)
71	Tree cover, needleleaved, evergreen, closed (>40%)
72	Tree cover, needleleaved, evergreen, open (15-40%)
80	Tree cover, needleleaved, deciduous, closed to open (>15%)
81	Tree cover, needleleaved, deciduous, closed (>40%)
82	Tree cover, needleleaved, deciduous, open (15-40%)
90	Tree cover, mixed leaf type (broadleaved and needleleaved)
100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)
110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)
120	Shrubland
130	Grassland
140	Lichens and mosses
150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)
160	Tree cover, flooded, fresh or brakish water
170	Tree cover, flooded, saline water
180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water
190	Urban areas
200	Bare areas
210	Water bodies
220	Permanent snow and ice

Table S12 Landcover classes from the European Space Agency Climate Change Initiative landscape cover maps converted to forest cover.

CLASS CODE	DESCRIPTION	CATEGORY
0	No Data	Non-Forest
10	Cropland, rainfed	Non-Forest
11	Herbaceous cover	Non-Forest
12	Tree or shrub cover	Non-Forest
20	Cropland, irrigated or post-flooding	Non-Forest
30	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)	Non-Forest
40	Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%)	Non-Forest
120	Shrubland	Non-Forest
50	Tree cover, broadleaved, evergreen, closed to open (>15%)	Forest
60	Tree cover, broadleaved, deciduous, closed to open (>15%)	Forest
61	Tree cover, broadleaved, deciduous, closed (>40%)	Forest
62	Tree cover, broadleaved, deciduous, open (15-40%)	Forest
70	Tree cover, needleleaved, evergreen, closed to open (>15%)	Forest
71	Tree cover, needleleaved, evergreen, closed (>40%)	Forest
72	Tree cover, needleleaved, evergreen, open (15-40%)	Forest
80	Tree cover, needleleaved, deciduous, closed to open (>15%)	Forest
81	Tree cover, needleleaved, deciduous, closed (>40%)	Forest
82	Tree cover, needleleaved, deciduous, open (15-40%)	Forest
90	Tree cover, mixed leaf type (broadleaved and needleleaved)	Forest

Figures

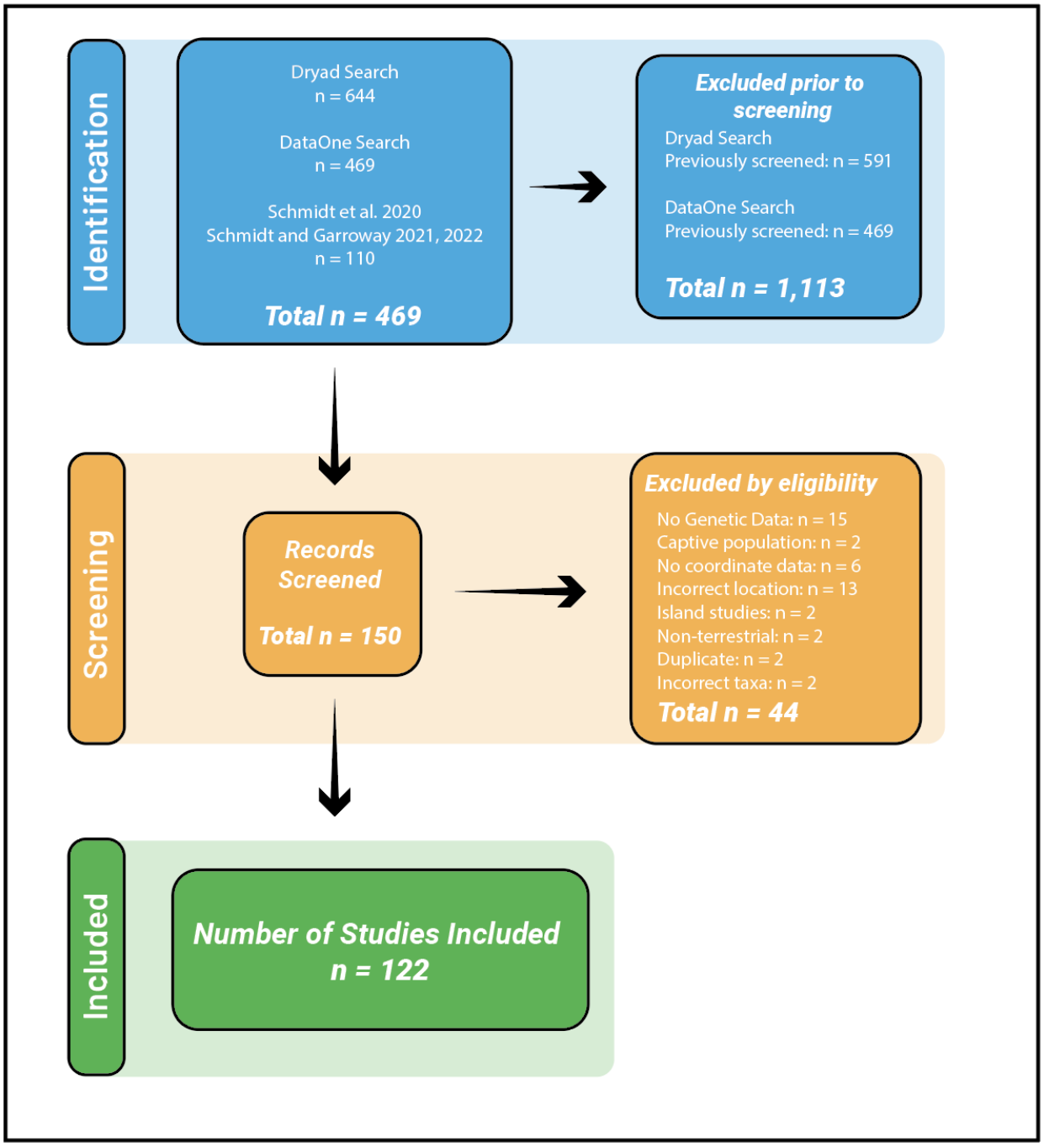

Figure S1. PRISMA diagram for study eligibility.

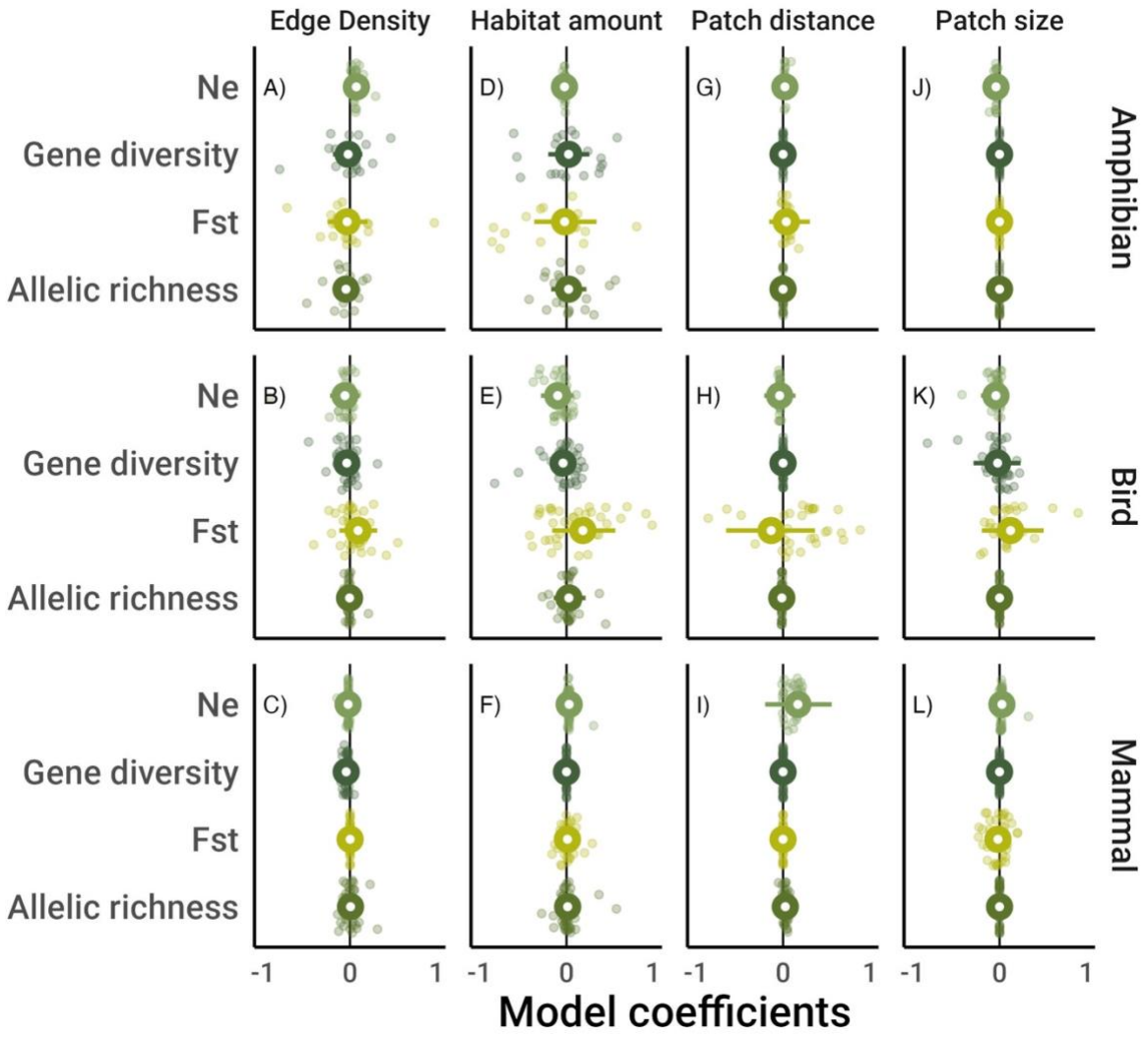

Figure S2. Orchard plot of forest fragmentation bivariate models with species as a random effect. Circles with a white circle inside represent the slope parameter estimates and lighter circles represent the species level slope parameter estimates; protruding lines are 95% credible intervals and black vertical lines at 0 are reference lines. There are forty-eight total models with sixteen attributed to each: amphibians, birds, and mammals. Models used anywhere from 20 to 40 species and 349 to 853 sites. The X axis represents the parameter estimates (i.e., 'Model coefficients'). All data was standardized to a mean of 0. Response variables are on the left Y axis (effective population size [Ne], gene diversity, fixation index [Fst] and allelic richness) and are modeled separately across fragmentation metrics: edge density (A-C), habitat amount (D-F), patch distances (G-I) and patch size (J-L).

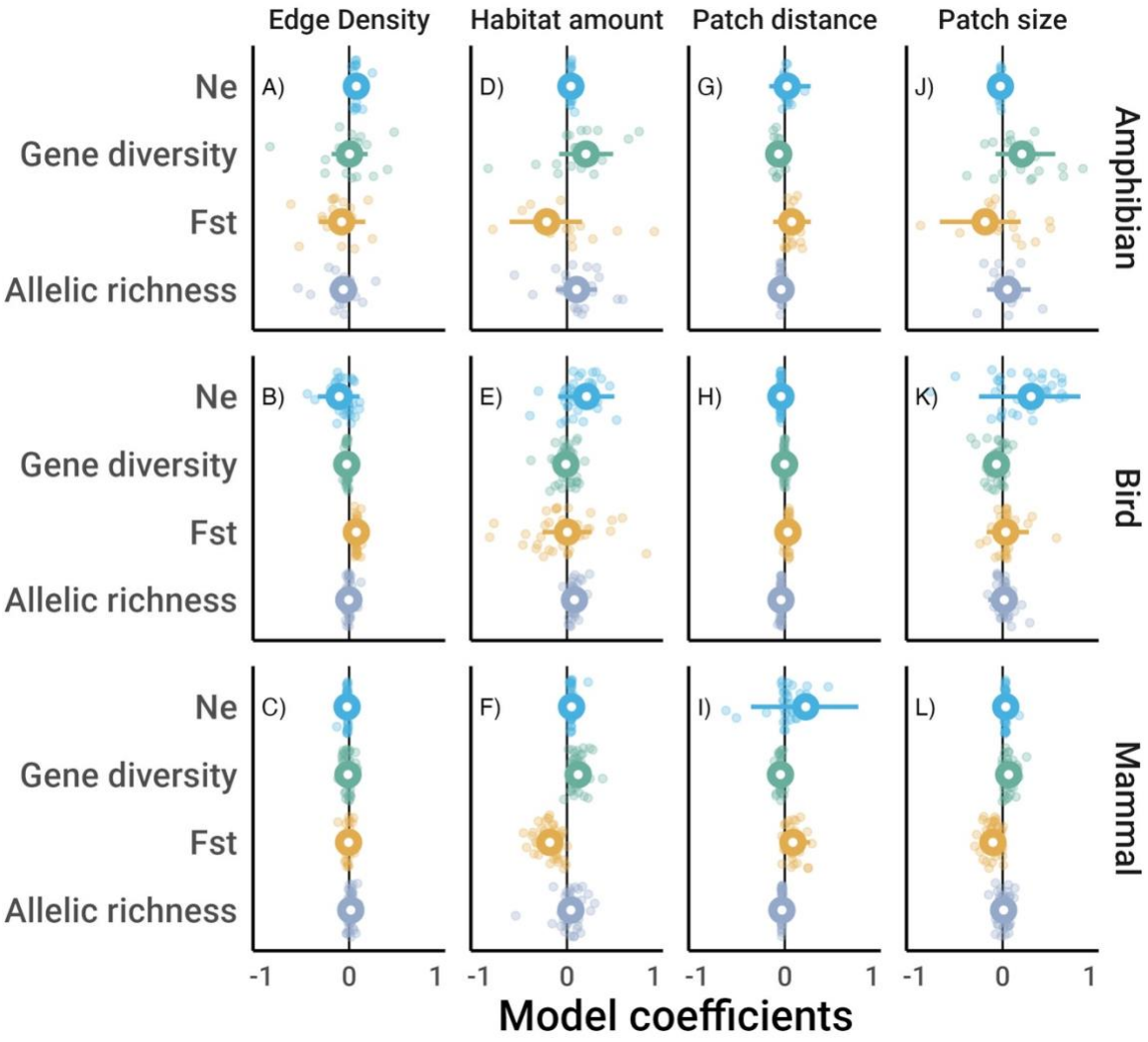

Figure S3. Orchard plot of species fragmentation bivariate models with species as a random effect. Circles with a white circle inside represent the slope parameter estimates and lighter circles represent the species level slope parameter estimates; protruding lines are 95% credible intervals and black vertical lines at 0 are reference lines. There are forty-eight total models with sixteen attributed to each: amphibians, birds, and mammals. Models used anywhere from 19 to 42 species and 378 to 811 sites. The X axis represents the parameter estimates (i.e., 'Model coefficients'). All data was standardized to a mean of 0. Response variables are on the left Y axis (effective population size [Ne], gene diversity, fixation index [Fst] and allelic richness) and are modeled separately across fragmentation metrics: edge density (A-C), habitat amount (D-F), patch distances (G-I) and patch size (J-L).

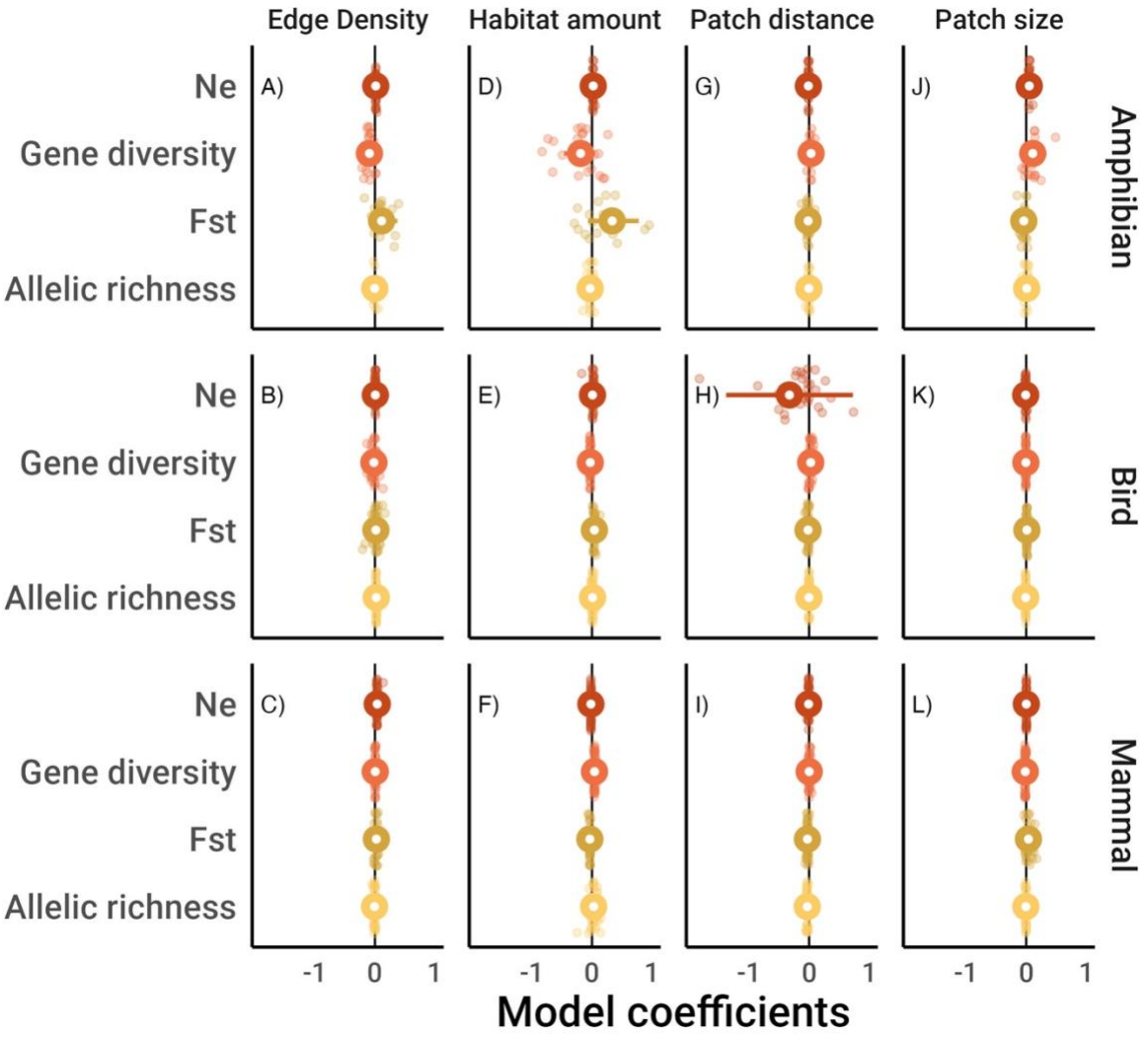

Figure S4. Orchard plot of forest fragmentation intensity bivariate models with species as a random effect. Circles with a white circle inside represent the slope parameter estimates and lighter circles represent the species level slope parameter estimates; protruding lines are 95% credible intervals and black vertical lines at 0 are reference lines. There are forty-eight total models with sixteen attributed to each: amphibians, birds, and mammals. Models used anywhere from 20 to 40 species and 319 to 650 sites. The X axis represents the parameter estimates (i.e., 'Model coefficients'). All data was standardized to a mean of 0. Response variables are on the left Y axis (effective population size [Ne], gene diversity, fixation index [Fst] and allelic richness) and are modeled separately across fragmentation metrics: edge density (A-C), habitat amount (D-F), patch distances (G-I) and patch size (J-L).

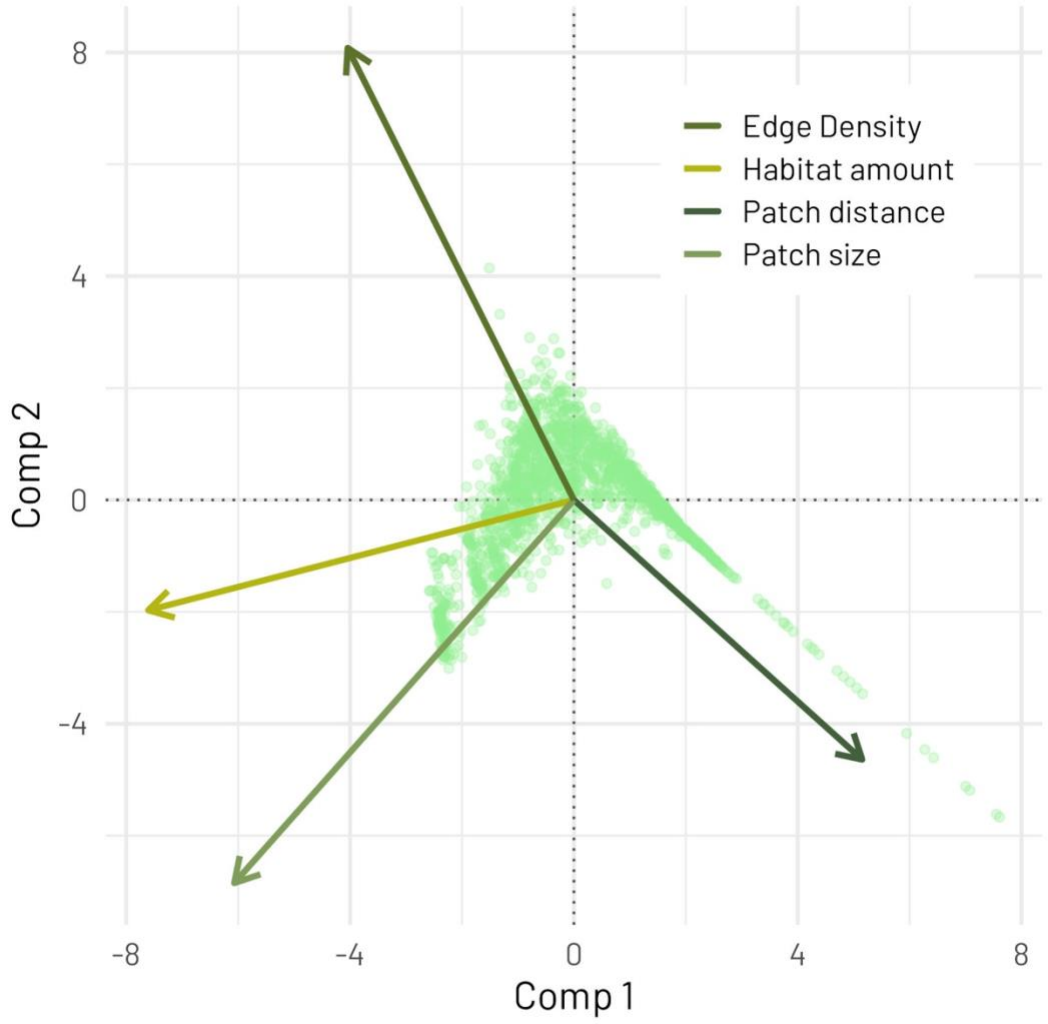

Figure S5. Forest fragmentation PCA biplot of populations (points) and standardized landscape metrics (arrows). Arrow length indicates the strength of each metric's loading; arrow direction shows increasing values. Arrows are colored by landscape metrics: edge density, habitat amount, patch distance, and patch size.

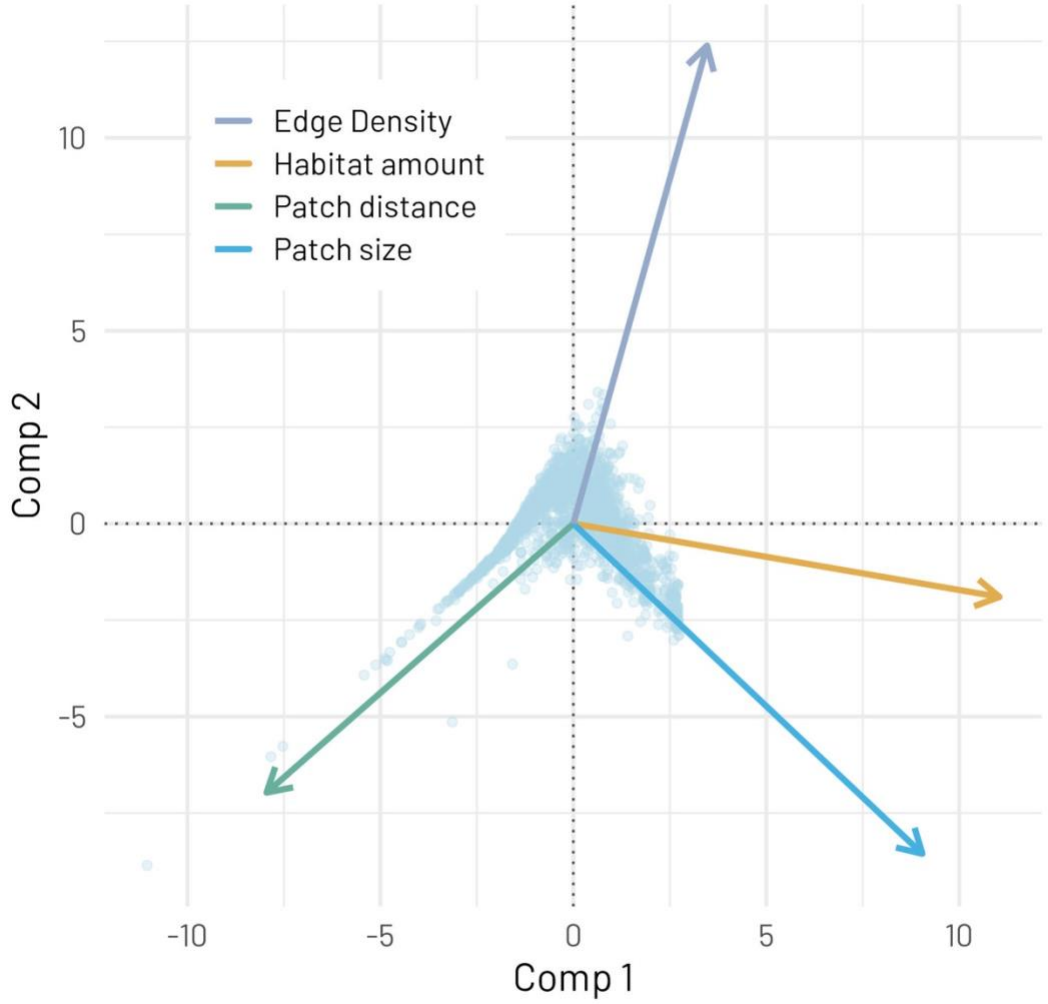

Figure S6. Species fragmentation PCA biplot of populations (points) and standardized landscape metrics (arrows). Arrow length indicates the strength of each metric's loading; arrow direction shows increasing values. Arrows are colored by landscape metrics: edge density, habitat amount, patch distance, and patch size.

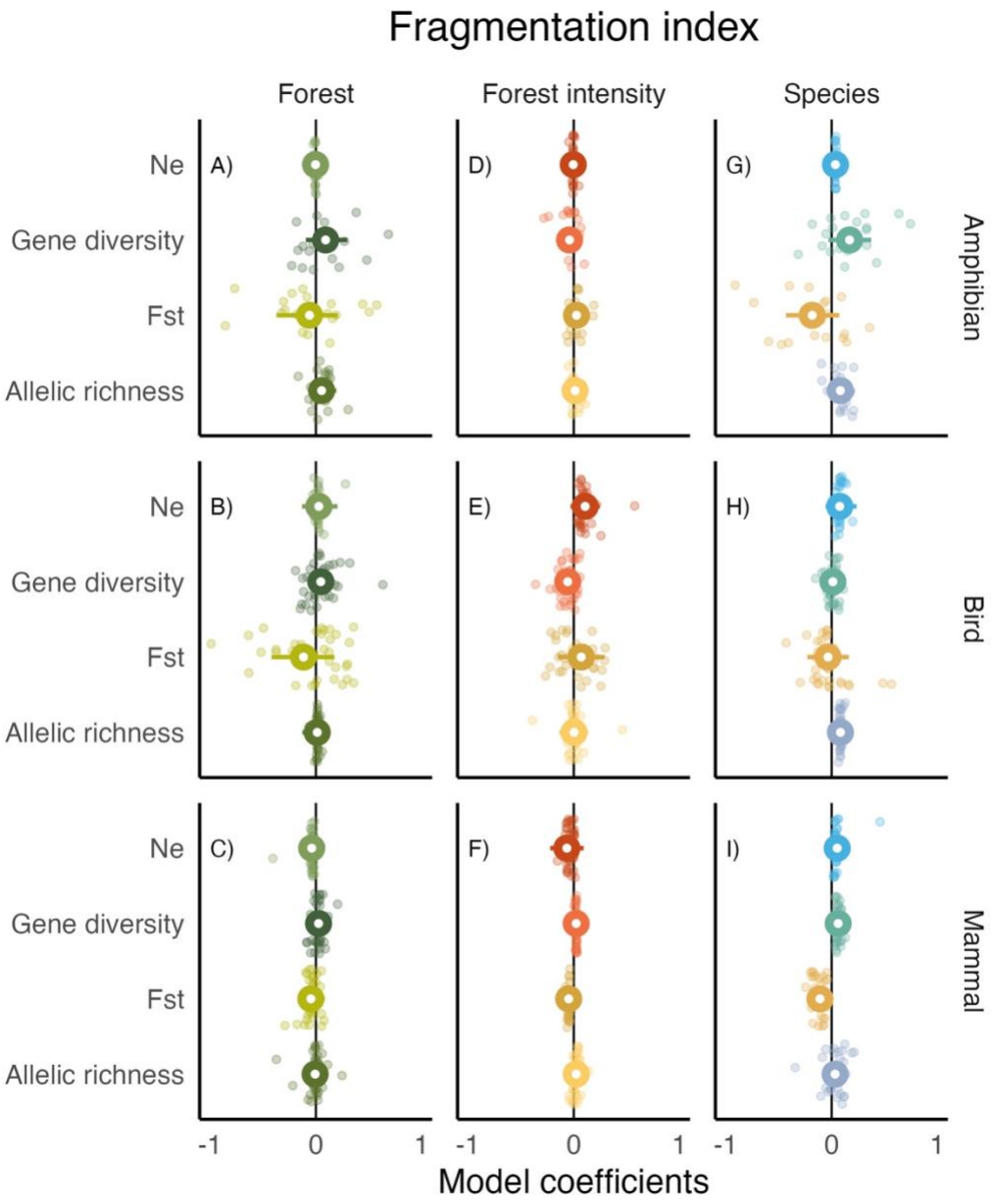

Figure S7. Orchard plot of principal component regression bivariate models with species as a random effect. Circles with a white circle inside represent the slope parameter estimates and lighter circles represent the species level slope parameter estimates; protruding lines are 95% credible intervals and black vertical lines at 0 are reference lines. There are forty-eight total models with sixteen attributed to each: forest fragmentation (Forest; A-C), intensity of forest fragmentation (Forest fragmentation intensity; D-F) and species fragmentation (Species: G-I). Models used anywhere from 20 to 40 species and 319 to 650 sites. The X axis represents the parameter estimates (i.e., 'Model coefficients'). All data was standardized to a mean of 0. Response variables are on the left Y axis (effective population size [Ne], gene diversity, fixation index [Fst] and allelic richness).

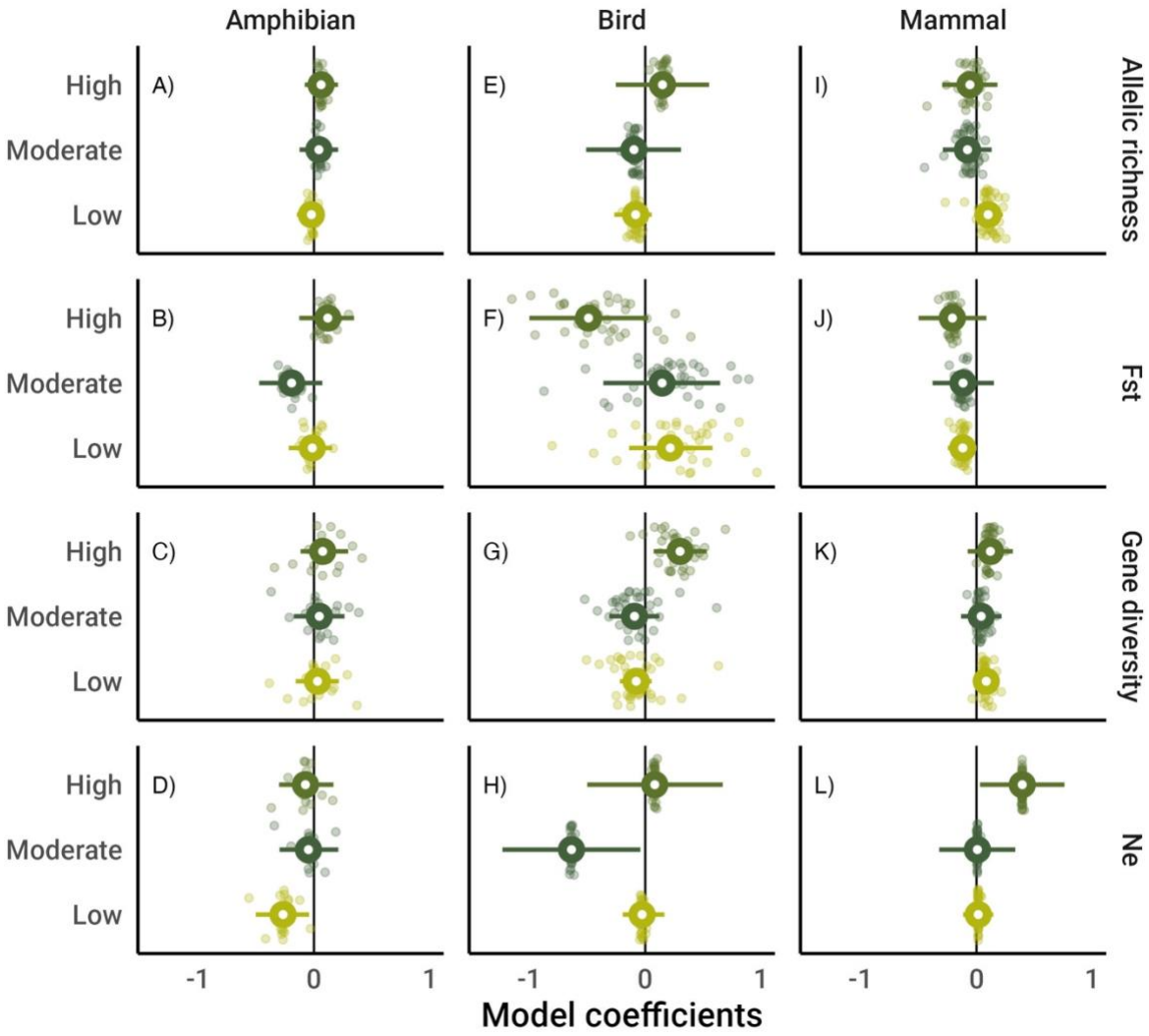

Figure S8. Orchard plot of forest fragmentation principal component regression with habitat amount (High: >60%; Moderate: 60% < 30%; Low: 30%<) as an interactive effect. Circles represent the parameter estimates; protruding lines are 95% credible intervals and black vertical lines at 0 are reference lines. There are four models with one attributed to each: Response variables are on the left Y axis (effective population size [Ne], gene diversity, fixation index [Fst] and allelic richness).

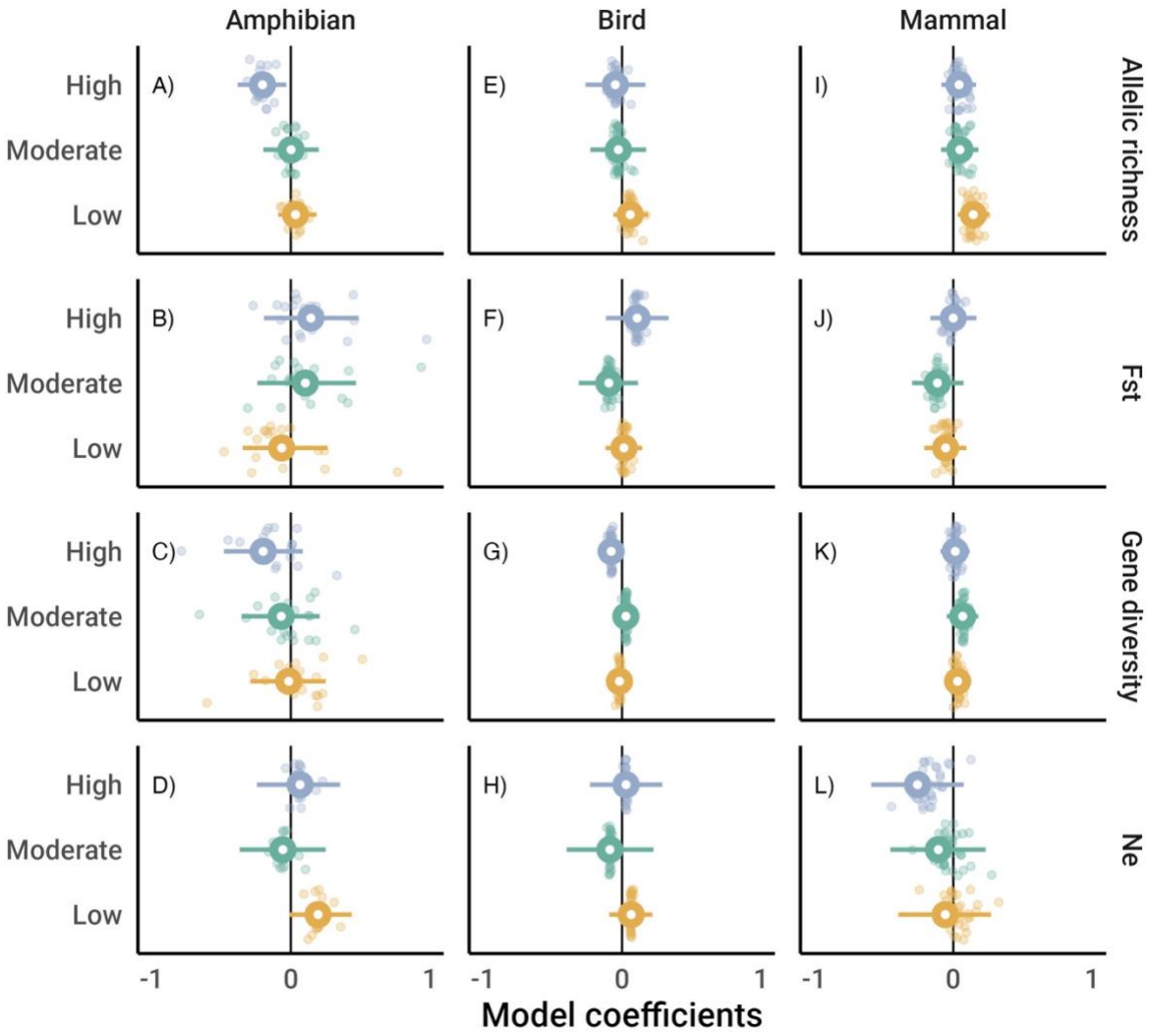

Figure S9. Orchard plot of species fragmentation principal component regression with habitat amount (High: >60%; Moderate: 60% < 30%; Low: 30%<) as an interactive effect. Circles represent the parameter estimates; protruding lines are 95% credible intervals and black vertical lines at 0 are reference lines. There are four models with one attributed to each: Response variables are on the left Y axis (effective population size [Ne], gene diversity, fixation index [Fst] and allelic richness).

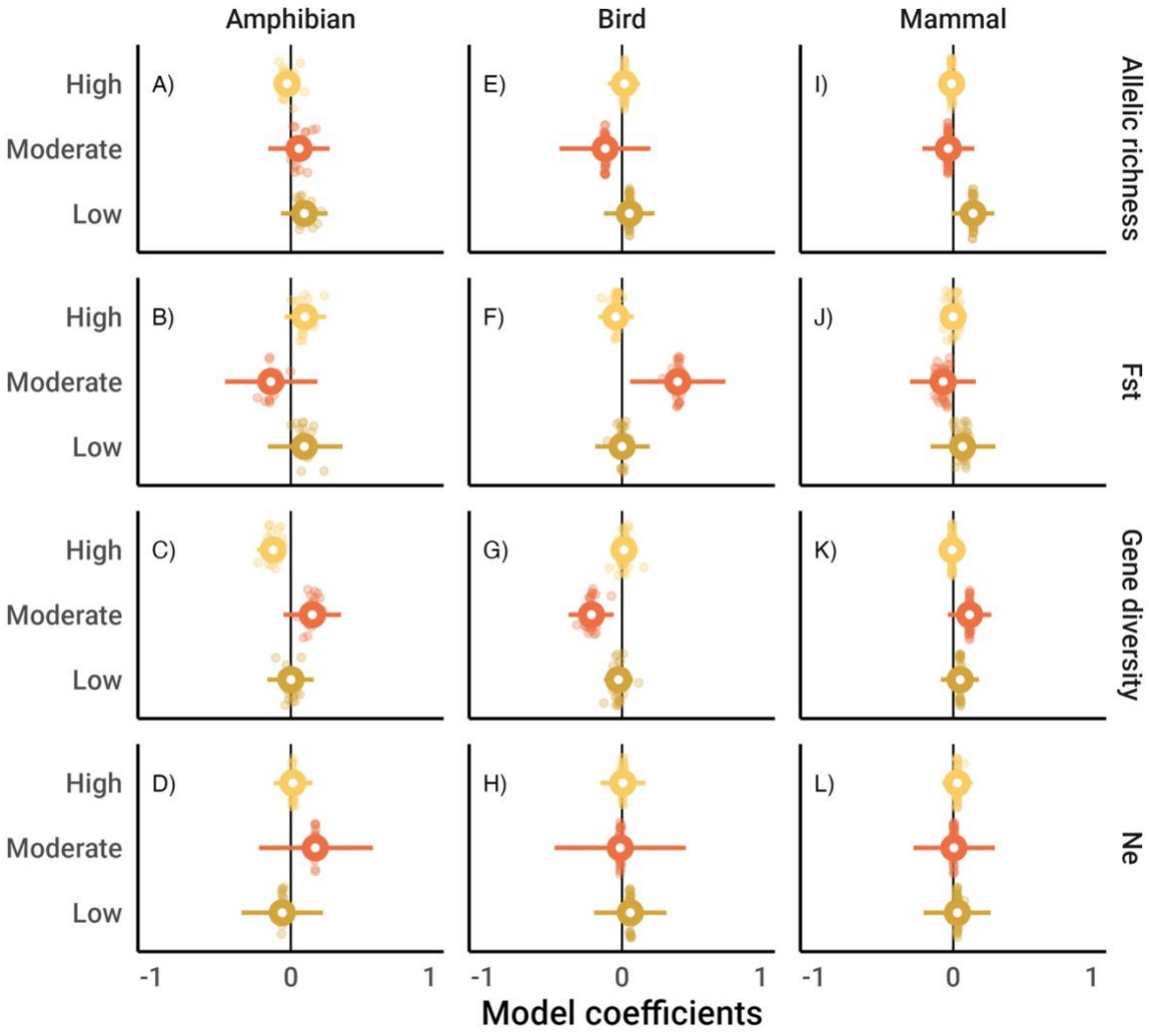

Figure S10. Orchard plot of intensity of forest fragmentation over time principal component regression with habitat amount (High: >60%; Moderate: 60% < 30%; Low: 30%<) as an interactive effect. Circles represent the parameter estimates; protruding lines are 95% credible intervals and black vertical lines at 0 are reference lines. There are four models with one attributed to each: Response variables are on the left Y axis: (effective population size [Ne], gene diversity, fixation index [Fst] and allelic richness).

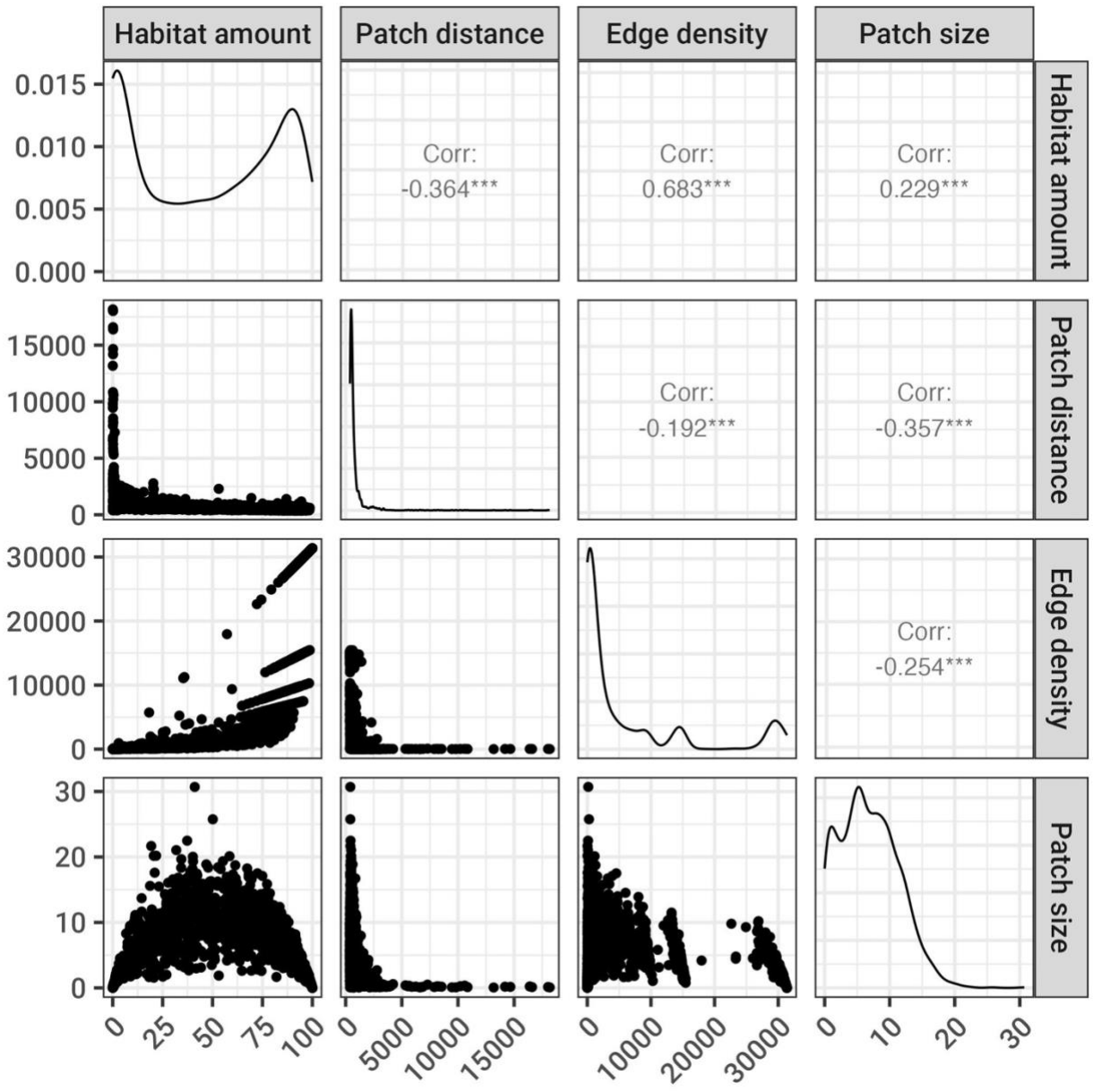

Figure S11. Forest fragmentation metric correlation.

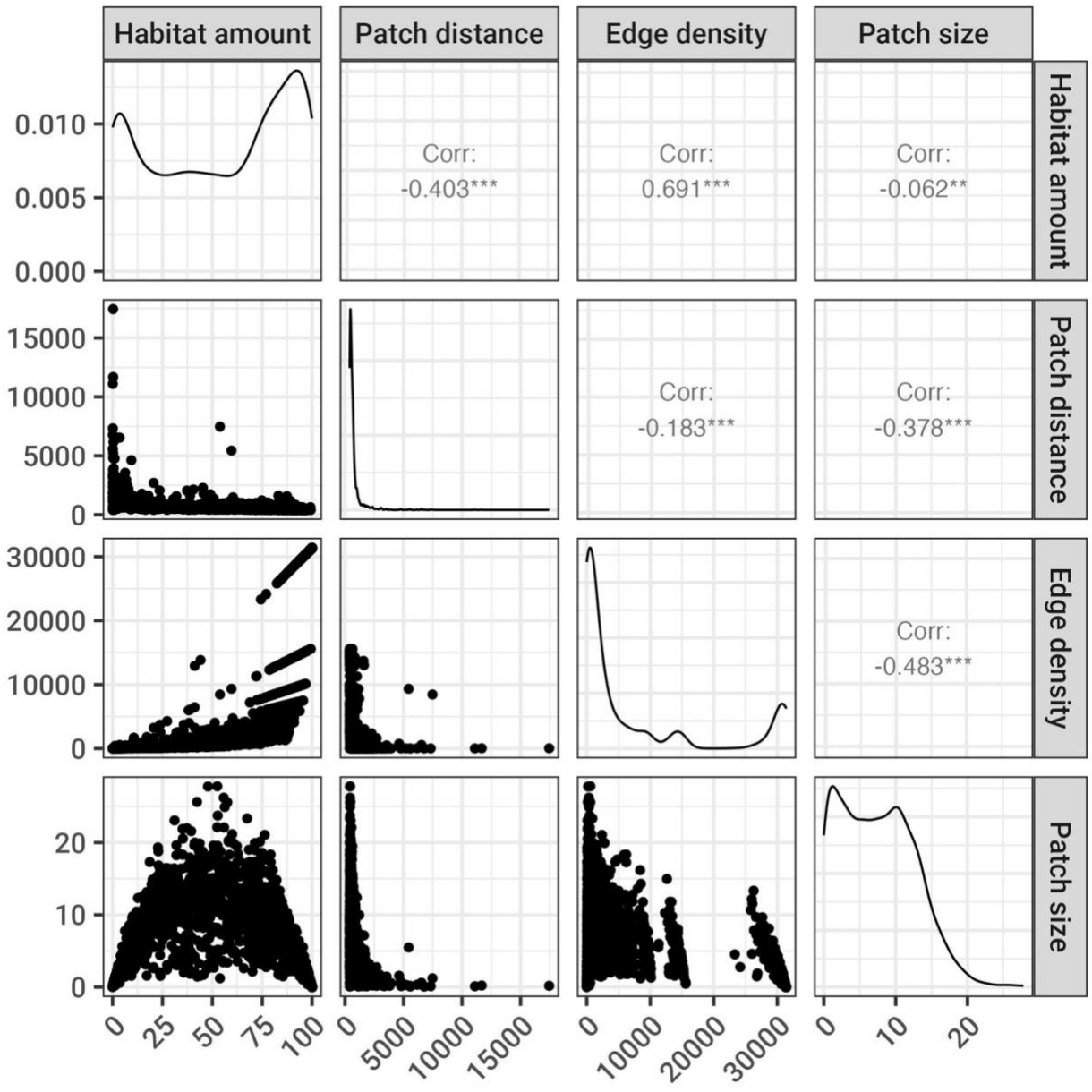

Figure S12. Species fragmentation correlation.

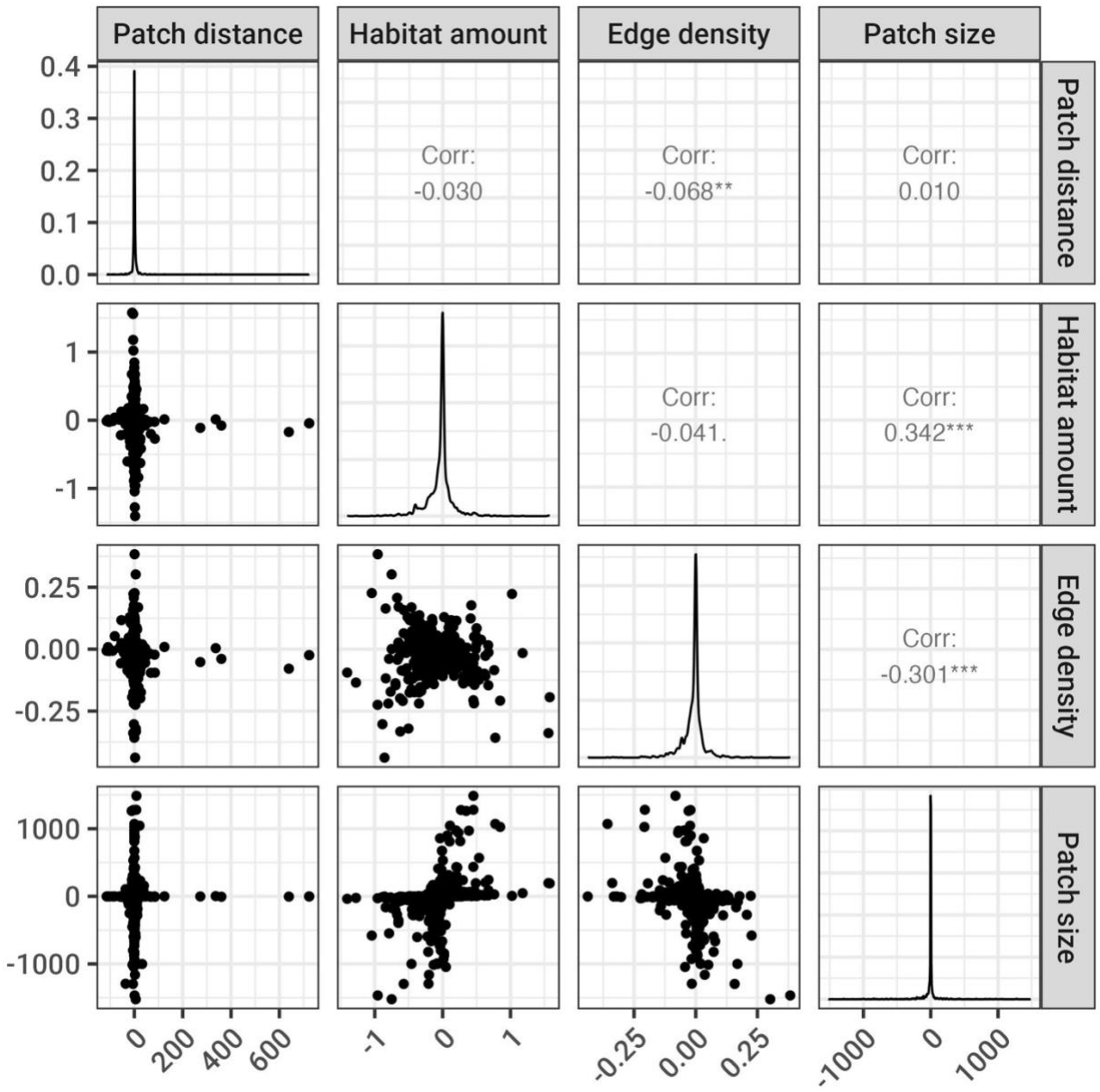

Figure S13. Forest fragmentation intensity metrics correlation.

Raw data sources

Species table

References of species with class (M–mammal; A–amphibian; B–bird), the repository that data was found in, and the search date of data collection.

Species	Class	Repository	Search Date	Reference
Alces alces	M	Dryad	February 2018	(1, 2)
Canis latrans	M	Dryad	February 2018	(3, 4)
Cervus elaphus nannodes	M	Dryad	February 2018	(5, 6)
Lasionycteris noctivagans	M	Dryad	February 2018	(7, 8)
Lasiurus cinereus	M	Dryad		
Lynx rufus	M	Dryad	February 2018	(9, 10)
Leopardus pardalis	M	Dryad		
Lynx rufus	M	Dryad	February 2018	(11, 12)
Lynx rufus	M	Dryad	February 2018	(13, 14)
Mephitis mephitis	M	Dryad	February 2018	(15, 16)
Procyon lotor	M	Dryad		
Microdipodops megacephalus	M	Dryad	February 2018	(17, 18)
Microdipodops pallidus				
Myotis lucifugus	M	Dryad	February 2018	(19, 20)
Myotis lucifugus	M	Dryad	February 2018	(21, 22)
Myotis lucifugus	M	Dryad	February 2018	(23, 24)
Myotis septentrionalis	M	Dryad		
Odocoileus hemionus	M	Dryad	February 2018	(25, 26)
Oreamnos americanus	M	Dryad	February 2018	(27, 28)
Ovis canadensis	M	Dryad	February 2018	(29, 30)
Peromyscus leucopus	M	Dryad	February 2018	(31, 32)
Peromyscus leucopus	M	Dryad	February 2018	(33, 34)
Peromyscus leucopus	M	Dryad	February 2018	(35, 36)
Peromyscus maniculatus	M	Dryad	February 2018	(37, 38)
Puma concolor	M	Dryad	February 2018	(39, 40)
Puma concolor	M	Dryad	February 2018	(41, 42)
Puma concolor	M	Dryad	February 2018	(43, 44)
Puma concolor	M	Dryad	February 2018	(45, 46)
Rangifer tarandus	M	Dryad	February 2018	(47, 48)
Rangifer tarandus	M	Dryad	February 2018	(49, 50)
Rangifer tarandus	M	Dryad	February 2018	(51, 52)
Rangifer tarandus	M	Dryad	February 2018	(53, 54)
Rattus rattus	M	Dryad	February 2018	(55, 56)
Taxidea taxus	M	Dryad	February 2018	(57, 58)

Taxidea taxus	M	Dryad	February 2018	(59, 60)
Taxidea taxus	M	Dryad	February 2018	(61, 62)
Ursus americanus	M	Dryad	February 2018	(63, 64)
Ursus americanus	M	Dryad	February 2018	(65, 66)
Ursus maritimus	M	Dryad	February 2018	(67, 68)
Ursus arctos	M	Dryad	February 2018	(69, 70)
Ursus maritimus	M	Dryad		
Ursus americanus	M	Dryad		
Ursus arctos	M	Dryad	February 2018	(71, 72)
Ursus maritimus	M	Dryad	February 2018	(73, 74)
Ursus maritimus	M	Dryad	February 2018	(75, 76)
Vulpes vulpes	M	Dryad	February 2018	(77, 78)
Vulpes lagopus	M	Dryad		
Vulpes vulpes	M	Dryad	February 2018	(79, 80)
Canis lupus	M	Dryad	February 2018	(81, 82)
Canis lycaon	M	Dryad		
Odocoileus_hemionus	M	Dryad	February 2018	(83, 84)
Tamiasciurus hudsonicus	M	Dryad	February 2018	(85, 86)
Tamiasciurus douglasii	M	Dryad		
Lepus americanus	M	Dryad	February 2018	(87, 88)
Martes americana	M	Dryad	February 2018	(89, 90)
Agelaius phoeniceus	B	Dryad	February 2018	(91, 92)
Aphelocoma californica	B	Dryad	February 2018	(93, 94)
Calidris alpina	B	Dryad	February 2018	(95, 96)
Charadrius melodus	B	Dryad	February 2018	(97, 98)
Charadrius montanus	B	Dryad		
Charadrius nivosus	B	Dryad		
Charadrius vociferus	B	Dryad		
Laterallus jamaicensis	B	Dryad	February 2018	(99, 100)
Selasphorus platycercus	B	Dryad	February 2018	(101, 102)
Poecile hudsonicus	B	Dryad	February 2018	(103, 104)
Poecile atricapillus	B	Dryad	February 2018	(105, 106)
Poecile atricapillus	B	Dryad	February 2018	(107, 108)
Setophaga caerulescens	B	Dryad	February 2018	(109, 110)
Sialis sialis	B	Dryad	February 2018	(111, 112)
Antilocapra americana	M	Dryad	May 2018	(113, 114)
Bison bison	M	Dryad	May 2018	(115, 116)
Odocoileus virginianus	M	Dryad	May 2018	(117, 118)
Otospermophilus beecheyi	M	Dryad	May 2018	(119, 120)
Ovis canadensis nelsoni	M	Dryad	May 2018	(121, 122)
Rangifer tarandus	M	Dryad	May 2018	(123, 124)
Sylvilagus transitionalis	M	Dryad	May 2018	(125, 126)
Anser albifrons	B	USGS	May 2018	(127)
Campylorhynchus	B	Dryad	May 2018	(128, 129)

brunneicapillus				
Clangula hyemalis	B	USGS	May 2018	(130)
Falco peregrinus	B	USGS	May 2018	(131)
Junco hyemalis	B	Dryad	May 2018	(132, 133)
Strix occidentalis	B	USGS	May 2018	(134)
Rallus obsoletus	B	USGS	May 2018	(135)
Vireo atricapilla	B	Dryad	May 2018	(136, 137)
Ursus americanus	M	Dryad	May 2018	(138, 139)
Lynx canadensis	M	Dryad	May 2018	(140, 141)
Lynx rufus	M	Dryad	May 2018	(142, 143)
Odocoileus hemionus	M	Dryad	May 2018	(144, 145)
Ursus americanus	M	Dryad	May 2018	(146, 147)
Ursus arctos	M	Dryad		
Lynx canadensis	M	Dryad	February 2018	(148, 149)
Glaucomys volans	M	Dryad		
Odocoileus hemionus	M	USGS	May 2018	(150)
Anser albifrons	B	USGS	May 2018	(151)
Branta canadensis	B	USGS		
Branta hutchinsii	B	USGS		
Chen canagica	B	USGS		
Ursus americanus	M	Dryad	May 2018	(152, 153)
Ursus maritimus	M	Dryad	May 2018	(154, 155)
Peromyscus maniculatus	M	Dryad	May 2018	(156, 157)
Pekania pennanti	M	Dryad	NA	(158, 159)
Tyto alba	B	NA	NA	(160)
Vireo atricapilla	B	Dryad	NA	(161, 162)
Cynomys leucurus	M	Dryad	November 2020	(163, 164)
Dipodomys ingens	M	Dryad	November 2020	(165, 166)
Myotis lucifugus	M	Dryad	November 2020	(167, 168)
Myotis septentrionalis	M	Dryad	November 2020	(167, 168)
Myotis thysanodes	M	Dryad	November 2020	(167, 168)
Canis latrans	M	Dryad	November 2020	(169-172)
Martes americana	M	Dryad	November 2020	(173, 174)
Taxidea taxus	M	Dryad	November 2020	(175, 176)
Vulpes vulpes	M	Dryad	November 2020	(177, 178)
Hydromantes platycephalus	A	Dryad	February 2019	(179, 180)
Hydromantes brunus	A	Dryad		
Rana draytonii	A	Dryad	February 2019	(181, 182)
Rana pretiosa	A	Dryad	February 2019	(183, 184)
Rana luteiventris	A	Dryad		
Rana cascadae	A	Dryad		
Lithobates pipien	A	Dryad		
Rana pretiosa	A	Dryad	February 2019	(185, 186)
Rana luteiventris	A			

Dicamptodon copei	A	Dryad	February 2019	(187, 188)
Ambystoma barbouri	A	Dryad	February 2019	(189, 190)
Desmognathus fuscus	A	Dryad	February 2019	(191, 192)
Plethodon albagula	A	Dryad	February 2019	(193, 194)
Ambystoma maculatum,	A	Dryad	February 2019	(195, 196)
Ambystoma maculatum	A	Dryad	February 2019	(197, 198)
Rana sylvatica	A	Dryad		
Ambystoma maculatum	A	Dryad	February 2019	(199, 200)
Lithobates sylvaticus	A	Dryad		
Ascaphus montanus	A	Dryad	February 2019	(201, 202)
Dicamptodon aterrimus	A	Dryad	February 2019	(203, 204)
Pseudacris streckeri	A	Dryad	February 2019	(205, 206)
Lithobates sylvaticus	A	Dryad	February 2019	(207, 208)
Plethodon cinereus	A	Dryad	February 2019	(209, 210)
Pseudacris crucifer	A	Dryad	February 2019	(211, 212)
Taricha granulosa	A	Dryad	February 2019	(213, 214)
Eumops floridanus	M	Dryad	October 2024	(215, 216)
Cervus nippon	M	Dryad	October 2024	(217, 218)
Athene cunicularia	B	Dryad	October 2024	(219, 220)
Poecile rufescens	B	Dryad	October 2024	(221, 222)
Zapus hudsonius	M	Dryad	October 2024	(223, 224)
Cyanocitta stelleri	B	Dryad	October 2024	(225, 226)
Plethodon hubrichti	A	Dryad	October 2024	(227, 228)
Plethodon cinereus	A	Dryad		
Perisoreus canadensis	B	Dryad	October 2024	(229, 230)
Pagophila eburnea	B	Dryad	October 2024	(231, 232)
Zonotrichia leucophrys	B	Dryad	October 2024	(233, 234)
Ammospiza maritima	B	Dryad	October 2024	(235, 236)
Ammospiza caudacuta	B	Dryad	October 2024	(237, 238)
Ascaphus truei	A	Dryad	October 2024	(239, 240)

References

1. Wilson RE, Farley SD, McDonough TJ, Talbot SL, Barboza PS (2015) A genetic discontinuity in moose (*Alces alces*) in Alaska corresponds with fenced transportation infrastructure. *Conserv Genet* 16(4):791–800.

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