2024

A GLOBAL SYNTHESIS OF THE RELATIVE IMPACTS OF HABITAT AMOUNT, FRAGMENTATION, AND MATRIX QUALITY ON FOREST BIODIVERSITY

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A Thesis Submitted to the
Graduate School of
John Carroll University
in Partial Fulfillment of the Requirements
for the Degree of
Master of Science

By

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2024

I, Antoinette Esposito, wrote this document in partial fulfillment of the requirements for the degree of Master of Science. Throughout this manuscript, the editorial "we" is used in place of "I" as this document is formatted for publication in a peer reviewed journal after final submission to the Graduate School at John Carroll University.

A global synthesis of the relative impacts of habitat amount, fragmentation, and matrix quality on forest biodiversity

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Abstract

Aim To assess the relative impact of different landscape variables on species richness and to determine whether species richness declines more rapidly below an extinction threshold of remaining habitat. The results of this study will help to better inform future conservation strategies.

Location Global

Time period 1997 – 2013

Major taxa studied Amphibians, birds, invertebrates, mammals, and reptiles

Methods Data from 71 studies published in the global BioFrag database were used to determine species richness across multiple landscapes and biomes. The Hansen dataset was used to collect data on habitat amount (forest area), fragmentation (patch density), and matrix quality (mean % tree cover in the matrix) within the local landscape of each plot. Multi-model inference and meta-analysis were used to compare the relative impacts of standardized predictor variables on species richness. Break point and linear regression models of percent forest cover and species richness were used to test for the presence of extinction thresholds.

Results Of the 29 studies included in multi-model inference, habitat amount had a greater regression coefficient than patch density in 15 studies and matrix quality in 21 studies. Patch density had a greater regression coefficient than habitat amount in 4 studies and matrix quality in 16 studies. The meta-analysis found habitat amount to have the greatest effect size with a |Fisher's z-score| ~1.7x greater than that of patch density and ~2.6x greater than matrix quality. The breakpoint regression model was significant and outperformed the linear regression model in 7 out of 71 studies.

Main conclusions Habitat amount had the greatest relative impact on species richness followed by patch density and matrix quality. We did not find support for the extinction threshold hypothesis.

INTRODUCTION

Human-modified forest landscapes (HMFLs), where both natural and anthropic land cover types coexist, dominate terrestrial ecosystems on Earth (Ellis, 2011). For decades, island biogeography theory (IBT), which considers habitat patches to be analogous to oceanic islands (Haila, 2002), was widely accepted as the conceptual framework for studying biodiversity in fragmented landscapes. This analogy has been challenged by those who argue that, unlike islands, habitat patches do not act as discrete spatial units (Bueno & Peres, 2019). Rather, biodiversity patterns may be driven by mechanisms operating on a larger scale (Kupfer et al., 2006). Following a review of the current literature, Arroyo-Rodríguez et al., 2020 constructed hypothetical optimal landscape scenarios for preserving forest biodiversity in HMFLs. The authors listed increasing/preserving forest cover as being the highest priority, with an optimal landscape containing ≥ 40% forest cover, with 10% being in a continuous patch, and the remaining 30% embedded in a high-quality matrix (e.g., low contrast with forest patches and inclusion of semi-natural corridors and single standing trees). In this study, we treat these recommendations as predictions about landscapes where we expect to see the highest species diversity, and tested those predictions using existing spatial and species occurrence data from HMFLs across the globe.

Habitat Amount

Landscape heterogeneity can be described in terms of composition (types and amounts of land cover present) and configuration (how land cover is spatially arranged). The habitat amount hypothesis (HAH) states that species richness increases with increasing habitat amount in the local landscape (i.e., the area in which individuals are likely to travel), regardless of its configuration (e.g., number and size of patches comprising that habitat) (Fahrig, 2013). In other words, the habitat amount hypothesis predicts that degree of fragmentation, or breaking apart of habitat into numerous smaller patches, has no effect on the number of species in a sample plot. Indeed, a recent meta-analysis confirmed the major predictions of the habitat amount hypothesis and found that across eight taxonomic groups from 35 studies around the world, the mean effect size for habitat amount on species density was greater than the mean effect of patch size or isolation in 33 of the studies (Watling et al., 2020). Increasing forest cover has been consistently found to have strong positive effects on species diversity, population abundance and distribution, as well as genetic diversity across taxa (Gibbs, 2001; Fahrig, 2003; Arroyo-Rodríguez et al., 2016; Betts et al., 2017; Galán-Acedo et al., 2019; Watling et al., 2020). A study on birds in the Lacandona rainforest in Mexico found that diversity was positively and more strongly related to variation in landscape forest cover than to variation in edge density and number of forest patches, and that this pattern was especially true for forest specialists (Carrara et al., 2015). Another study on small mammals in Brazil found habitat amount to have consistently large and positive effects on species richness, while patch size and isolation had no effects after habitat amount was controlled for (Melo et al., 2017). Habitat is of principal importance to wildlife because it is closely related to resource availability as well as various ecosystem processes which maintain

community dynamics such as niche differentiation and species interactions (Zanette et al., 2000; Kupfer et al., 2006; Morante-Filho et al., 2018). However, the relationship between species occurrence or abundance and habitat amount is not necessarily linear. Some species have minimum habitat requirements for population persistence to occur, so they may have a nonlinear relationship with habitat amount, with a sharp decrease in occurrence or abundance below a certain value (the extinction threshold). When several species in an area manifest this pattern at a similar extinction threshold, overall species richness may show a similar non-linear response to habitat loss. Simulation and empirical studies have found that when thresholds are apparent, most species require 10-30% of habitat in the landscape to persist (Andrén, 1994; Swift & Hannon, 2010). However, it has been suggested that tropical species may have greater minimum habitat requirements due to lower reproductive rates, smaller geographic ranges, and smaller population sizes (Purvis et al., 2000; Fahrig, 2001; Vance et al., 2003; Holland et al., 2005; Swift & Hannon, 2010).

Fragmentation

Fragmentation describes a form of landscape configuration where habitat is distributed in multiple patches. Deforestation often causes both habitat loss and an increase in fragmentation. In many previous studies, the effects of fragmentation were studied without controlling for differences in habitat amount. Island biogeography theory (IBT) was originally developed to explain species richness patterns on oceanic islands, whereby island size and isolation influence rates of colonization and extinction (Macarthur & Wilson, 1967). When applying IBT to terrestrial landscapes, authors often failed to consider that wildlife in HMFLs may move more easily between habitat patches, and so, unlike islands, patches may not be discrete spatial units. According to IBT, the species area relationship (the relationship between habitat area and the number of species found within that area) can be explained by "island effects" in which plots within larger and less isolated forest patches contain greater species diversity (Haddad et al., 2017; Bueno & Peres, 2019). However, the HAH predicts no effects of patch area and isolation because patches are not seen as discrete spatial units. Rather, all habitat in the local landscape is considered to be available to wildlife. According to the HAH, the species-area relationship can be explained by the sample area effect in which sample sites in larger and less isolated patches harbor more species because larger habitat areas sample more individuals, and therefore species, than smaller habitat areas (Fahrig, 2013).

By not controlling for habitat amount, many studies which claimed to report large negative effects of fragmentation were likely actually observing the large negative effects of habitat loss. A comprehensive review of the available literature found that when the effects of habitat loss are controlled for, the effects of fragmentation are usually non-significant (Fahrig, 2003). Fragmentation per se (that is, the degree of fragmentation controlling for habitat amount) has been found to have much weaker effects on biodiversity than habitat amount and can have negative, neutral, and positive effects across different taxa (Fahrig, 2003; Fahrig, 2019; Watling et al., 2020). A review of 118 studies reporting 381 significant ecological responses to

fragmentation per se found that most responses were positive regardless of the taxonomic group, degree of specialization, or conservation status of the studied species (Fahrig, 2017). Possible causes for positive responses to fragmentation include positive edge effects (e.g., greater availability of foraging and refuge resources), increased functional connectivity, reduced competition, and higher habitat diversity (Fahrig, 2017). Moreover, possible causes for negative responses to fragmentation include negative edge effects (e.g., changes in microclimate, increased presence of invasive species, and altered species interactions), as well as reduced structural connectivity of the landscape (Kupfer et al., 2006). Some researchers have hypothesized that there is a threshold below which fragmentation effects become significantly negative at low levels of remaining habitat due to increased isolation of habitat patches (fragmentation threshold hypothesis) (Andrén, 1994; Swift & Hannon, 2010). However, the previously mentioned literature review did not find any support for this prediction (Fahrig, 2017).

Matrix Quality

Landscape composition also includes the land cover types surrounding habitat patches, referred to as the matrix. Different land uses create matrices of differing quality depending on how well wildlife can use and move through them. In the early literature, the matrix has often been regarded as one-dimensional non-habitat area, similar to an ocean separating isolated islands of habitat (i.e., island biogeography theory). However, more recent approaches recognize the matrix as being a heterogenous part of the functional landscape, comprised of a variety of land-use types which may provide a variety of species-specific uses. Previous studies have found increased use of the matrix by forest wildlife (i.e., higher matrix quality) with increased tree cover and increased similarity to habitat patches (Anderson et al., 2007; Collinge & Palmer, 2002; Harvey et al., 2005). A high-quality matrix can increase the resource base of the local landscape and improve connectivity by allowing wildlife to move between habitat patches (Kupfer et al., 2006; Ricketts, 2001; Watling et al., 2010). Long term (up to 19 year) studies of birds, frogs, small mammals, and ants in central Amazonia detected a large proportion (40-80%) of forest species from each taxon within the matrix. In addition, vertebrate species which used the matrix had a greater tendency for populations to remain stable or increase than those which avoided the matrix (Gascon et al., 1999). Forest species across taxa have been found to use the matrix for foraging, reproduction, and movement (Gascon et al., 1999; Baguette et al., 2000; Collinge & Palmer, 2002; Harvey et al., 2005; Anderson et al., 2007). On four cattle farms in Costa Rica and Nicaragua, birds within live fences (i.e., rows of trees planted to keep cattle in or out) were recorded actively seeking food, perching, using live fences as display posts, and traveling along live fences (Harvey et al., 2005). Matrix quality has also been found to influence patterns of species richness and abundance (Gascon et al., 1999; Cook et al., 2002; Benchimol & Peres, 2013). A study of a fragmented landscape in Kansas, USA, found that diversity patterns did not follow island biogeography theory when species which use the matrix were included in their analysis (Cook et al., 2002). It has been theorized that higher matrix quality may reduce

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minimum habitat requirements and therefore postpone the extinction threshold (matrix threshold hypothesis) (Fahrig, 2001; Swift & Hannon, 2010; Boesing et al., 2018). A study using field data from 23 landscapes in the Brazilian Atlantic Forest compared the extinction thresholds for birds in landscapes with low matrix quality (homogenous pastures) and high matrix quality (heterogeneous coffee farms). Landscapes with high matrix quality were found to have lower extinction thresholds than landscapes with low matrix quality, requiring only 19% forest cover as opposed to 35% (Boesing et al., 2018).

Hypotheses

Based on the above literature review, we hypothesize that (1) habitat amount will be the greatest predictor of species richness followed by matrix quality and degree of fragmentation. We also hypothesize that (2) across landscapes, species richness will sharply decline below an extinction threshold of 30% remaining forest cover. We predict that (3) this value will be higher in the tropics and (4) in landscapes with low matrix quality.

METHODS

Data Collection

Data from 71 studies published in the global BioFrag database were used to determine species richness across multiple landscapes and biomes (Pfeifer et al., 2014). The BioFrag database contains georeferenced count data of various taxa sampled at the plot scale within studies. Count data of mammal, bird, amphibian, non-avian reptile, and arthropod species from partially forested landscapes were used. Habitat amount, degree of fragmentation, and matrix quality within each local landscape were determined using ArcGIS10 (ESRI, version 10.8.1) and R (R Core Team, version 2.15.1).

Forest cover maps at the time of each BioFrag study (one year prior to the start of data collection) were obtained using the Global Forest Change Dataset (Hansen et al., 2013). Preparation of the forest cover data was completed in ArcMap (ESRI, version 10.8.1), using the global year 2000 percent tree cover raster and the global forest loss raster, which defines forest as >50% tree cover and indicates the year in which forest pixels were lost (Hansen et al., 2013). Seven studies began prior to the year 2000, the earliest in 1997, and so for those studies, forest cover in the year 2000 was used. The 2000 percent tree cover layer was converted to a forest cover layer using a threshold of >50% tree cover is forest. Forest cover at the end of other years was determined by first reclassifying the forest loss layer: forest lost prior to the year of interest was not forest (0) and forest lost after the year of interest was still forest (1). Forest that was never lost was then added to the reclassified forest loss layer to obtain total forest cover for the year of interest. Forest that was never lost was determined by subtracting all loss from the 2000 forest cover layer. Forest cover maps for each study were projected using the equal area Mollweide projection.

Data collection was performed using program R (R Core Team, version 2.15.1). Local landscapes were delineated by constructing buffers around each study plot with radii of 200, 500, 1000, 2000, 3000, and 6000 m. Although imperfect, calculating habitat amount in landscapes of approximately 13 to 11,309 ha should bracket much of the variation in the scale of habitat use for species included in this study. Scale of effect was determined using linear regression between total forest area and species richness; the buffer size with the highest *r* value was selected as the local landscape size for each study (Fahrig, 2013; Watling et al., 2020). All response variables were measured within the local landscape of each plot. Habitat amount was defined as total forest area, which was determined by counting the number of forest pixels within the local landscape and multiplying by pixel width^2. Percent forest cover was calculated as total forest area divided by the total area of the local landscape. Degree of fragmentation was defined as the number of forest patches present within the local landscape (determined using the num_patches function from the Landscape Metrics R package) divided by the area of the landscape (i.e., patch density). Unlike other common measures of fragmentation, such as mean patch size or isolation, patch density is independent of habitat amount (Fahrig, 2003). Matrix quality was measured as the mean percentage of tree cover in non-forest areas, with a possible range of 0-50%. Plots with no matrix were excluded from analysis.

Analysis

Data analysis was performed using program R (R Core Team, version 2.15.1). All predictor variables (habitat amount, patch density, and matrix quality) were standardized prior to analysis to allow for direct comparison of regression coefficients. In addition, forest area, percent forest cover, and species richness were log transformed to meet the normality assumption.

Generalized least squares regression

Variance inflation factors (VIF) were calculated to assess collinearity among predictor variables. Generalized least squares (GLS) regression with coordinate data as the correlation matrix was used to account for spatial autocorrelation (Dormann et al., 2007). Candidate models were constructed representing univariate effects (1. Habitat Amount, 2. Patch Density, and 3. Matrix Quality), fragmentation per se (4. Habitat Amount + Patch Density), the fragmentation threshold hypothesis (5. Habitat Amount*Patch Density), the matrix threshold hypothesis (6. Habitat Amount*Matrix Quality), and a complete model of the effects of all predictor variables (7. Habitat Amount + Patch Density + Matrix Quality) on species richness. We used model averaging of candidate GLS models weighted by their Akaike weights to obtain mean slopes +/- standard error (SE) for each predictor variable. The mean slope of each predictor variable represents the direction and magnitude of its effect on species richness. We used z-tests to compare the proportion of studies with positive vs. negative slopes. The direction of effect was recorded as neutral if the slope +/- SE contained zero, such studies were excluded from z-test comparisons. Within studies, we compared the magnitude of each variable's effect +/- SE. If

there was overlap between the absolute value of the slope of one variable +/- SE and that of another variable, there was concluded to be no difference in relative importance. Only studies which had low to moderate variable collinearity (VIF < 7), and a top model that significantly outperformed the null model (determined using AIC and ANOVA) were included in model averaging.

Univariate and fragmentation per se GLS models were also used to calculate mean slopes and obtain counts of studies with significant positive/negative slopes. All 71 studies were used for the univariate models, whereas only studies with a VIF < 7 were used for the fragmentation per se model.

Linear mixed effects meta-analysis

A meta-analysis was conducted using all 71 BioFrag studies to estimate average global trends in the relative effects of habitat amount, matrix quality, and fragmentation per se on forest biodiversity. The correlation coefficients (r) between each variable and species richness were calculated for each study and converted to Fisher's Z (measure of effect size). The combined data were then used to run univariate linear mixed effects models to determine the weighted mean effect size of each predictor variable. Study weights were calculated as the inverse of the sum of within-study variance and random effects by landscape. Within-study variance was calculated as $1/(N-3)$ where N is the number of plots.

Break point regression

The presence of an extinction threshold was tested for by running break point and linear regression models between percent forest cover and species richness. If the break point model was significant, and had a lower AIC than the linear model, then an ANOVA was used to determine whether the break point model significantly outperformed the linear model, indicating the presence of an extinction threshold.

RESULTS

Generalized least squares regression

Twenty nine of 71 BioFrag studies were included in model averaging. Twenty-seven studies were excluded from model averaging due to a high correlation among predictor variables (VIF > 7) and 15 studies were excluded due to not having a top model which significantly outperformed the null model. When comparing the absolute value of the mean slope (hereafter |mean slope|) +/- SE of habitat amount and patch density, 15 studies showed habitat amount to have a greater slope than patch density, 4 studies showed patch density to have a greater slope than habitat amount, and 10 studies showed no detectable difference. When comparing the |mean

slope| +/- SE between habitat amount and matrix quality, 21 studies showed habitat amount to have a greater slope than matrix quality, 5 studies showed matrix quality to have a greater slope than habitat amount, and 3 studies showed no detectable difference. When comparing the |mean slope| +/- SE of matrix quality and patch density, 6 studies showed matrix quality to have a greater slope than patch density, 16 studies showed patch density to have a greater slope than matrix quality, and 7 studies showed no detectable difference. The direction of effect for habitat amount was positive in 19 studies, negative in 4 studies, and neutral in 6 studies (Table 1). The proportion of studies showing a positive effect of habitat amount was significantly greater than the proportion of studies showing a negative effect of habitat amount (χ^2 = 17.04, p-value < 0.001, N = 23). The direction of effect for patch density was positive in 6 studies, negative in 15 studies, and neutral in 8 studies (Table 1). The proportion of studies showing a negative effect of patch density was significantly higher than the proportion of studies showing a positive effect of patch density (χ^2 = 6.1, p-value = 0.01, N = 21). However, there was no significant difference in the proportion of negative and positive responses to patch density among studies taken place in the neotropics (χ^2 < 0.001, p-value = 1, N = 11). The direction of effect for matrix quality was positive in 5 studies, negative in 6 studies, and neutral in 18 studies (Table 1). There was no significant difference between the proportion of studies showing a positive vs. a negative effect of matrix quality (χ^2 < 0.001, p-value = 1, N = 11).

Univariate GLS regression models showed that 31 out of 71 BioFrag studies had a significant effect of forest area on species richness, 26 of which were positive and 5 were negative (Table S1). The mean slope of forest area across all studies was 26.7 (+/- 7.4 SE) (Table 2). Eighteen studies had a significant effect of patch density, 15 of which were negative and 3 were positive (Table S1). The mean slope of patch density across all studies was -5.3 (+/- 1.9 SE) (Table 2). Fourteen studies had a significant effect of matrix quality, 10 of which were positive and 4 of which were negative (Table S1). The mean slope of matrix quality across all studies was 1.96 (+/- 0.7 SE) (Table 2). The fragmentation per se multiple GLS regression model (habitat amount + patch density) and species richness showed 24 studies had a significant effect of habitat amount, and a VIF < 7, 20 of which were positive and 4 were negative. Eleven studies had a significant effect of patch density, and a VIF < 7, 8 of which were negative and 3 were positive. The mean slope of forest area in the fragmentation per se model across all studies was 27.1 (+/- 10.7 SE), while the mean slope of patch density in the fragmentation per se model across all studies was -1.33 (+/- 1.9 SE)(Table 2).

Linear mixed effects meta-analysis

The meta-analysis using univariate linear mixed effects models yielded a mean effect size (Fisher's z) of 0.253 (+/- 0.05 SE, σ^2 = 0.0009, p-value < 0.001, t-value(df) = 5.89 (70)) for habitat amount, -0.145 (+/- 0.05 SE, σ^2 = 0.0007, p-value = 0.002, t-value(df) = -3.27(70)) for patch density, and 0.099 (+/- 0.04 SE, σ^2 = 0.0001, p-value = 0.007, t-value(df) = 2.76 (70)) for matrix quality (Figure 1). There were no apparent trends in Fisher's *z* based on taxon (Figure 2).

Break point regression

The breakpoint regression model between percent forest cover and species richness was significant in 15 of 71 BioFrag studies, 7 of which significantly outperformed the linear regression model. Of those 7, the estimated break point ranged from 35 – 99% remaining forest cover. There was no pattern between region or matrix quality and the estimated break point value (Table 3).

DISCUSSION

Our synthesis of spatial and species occurrence data from fragmented landscapes across the globe found habitat amount to be the greatest predictor of species richness, followed by fragmentation, and then matrix quality. This finding supports the recommendation made by Arroyo-Rodríguez et al., 2020 that preservation and restoration of forest cover, regardless of its configuration, should be the highest priority of conservation management plans. Of the 29 studies included in model averaging, habitat amount had a greater |mean slope| +/- SE than patch density in 15 studies, whereas the inverse was true in only 4 studies. Similarly, habitat amount had a greater |mean slope| +/- SE than matrix quality in 21 studies, whereas the inverse was true in only 3 studies (Table 1). In the univariate and fragmentation per se models, habitat amount generally had a strong positive relationship with species richness, while patch density generally had a much weaker negative relationship; habitat amount had a |mean slope| ~5-20x greater than that of patch density (Table 2). The univariate models also resulted in 58% more significant responses of habitat amount than patch density (Table S1). The meta-analysis found habitat amount to have the greatest effect size with a |Fisher's z-score| ~1.7x greater than that of patch density and ~2.6x greater than matrix quality (Figure 1). These results underscore the importance of preserving all forest, regardless of patch size or degree of fragmentation in the landscape. The widespread misconception that small forest patches have little to no ecological value has influenced the decisions of conservation managers regarding which forest patches should receive protection (Margules & Pressy, 2000). Increasing the preservation and restoration of forest patches in HMFLs is predicted to have a range of benefits for biodiversity conservation and human well-being. Landscapes with greater forest cover have been found to have greater species richness, species density, and abundance across taxa (i.e., plants, fungi, gastropods, insects, amphibians, reptiles, birds, and mammals) (Fahrig, 2003; Watling et al., 2020). Local forests also facilitate a variety of ecosystem services such as pollination and pest control, reduced ambient air temperature, and maintenance of clean drinking water (MEA, 2005; Grass et al., 2019; Yin et al., 2022). In addition, exposure to natural spaces has been found to have a significantly positive effect on happiness, altruism, and desire to conserve biodiversity (Soga et al., 2016; Joye et al., 2020; Ribeiro et al., 2021).

When significant, we found a greater prevalence of negative fragmentation effects than positive (Table 2). This challenges the prediction that significant fragmentation per se effects are more often positive than negative (Fahrig, 2017). However, considering previous research we

caution against generalizing the effects of fragmentation per se. While habitat amount has been found to have consistently positive effects on species richness, the effects of fragmentation per se are more variable. A meta-analysis of 13 tests of the HAH found that patch size and isolation effects independent of habitat amount do exist, some negative and some positive, although their overall effect is weak (Martin, 2018). Similarly, a study of vascular plant diversity on lake islands found evidence of both negative and positive fragmentation effects after controlling for habitat amount; while habitat isolation negatively impacted species richness, SLOSS-based analyses indicated that several small islands harbored more species than a single large island of equal total area (Macdonald et al., 2018). Bueno & Peres, 2019 proposed that island effects and the sample area effect may both be taking place to different degrees in fragmented landscapes. The authors predict that island effects may be most relevant when describing species richness patterns in highly fragmented landscapes, in which forest patches are embedded in a hostile matrix and the focal taxa have low dispersal ability. Given that the effects of habitat configuration appear to be relatively weak as well as highly context and taxa specific, the HAH serves as an effective null model to guide conservation management decisions. Rather than an absolute to be taken literally, the assumption that habitat configuration has no effect on species richness serves as a simplifying assumption which is likely to be met to varying degrees in the real world. We support the recommendation that an optimal HMFL should contain some continuous forest (~10% of the landscape as one forest patch) along with a mosaic of smaller forest patches throughout (~30% of the landscape).

We were unable to find consistent evidence for an extinction threshold, suggesting that further research is needed to assess how much forest cover needs to be maintained to support species persistence in HMFLs. Most studies showed greater support for a linear relationship between percent tree cover and species richness even though many studies had plots which contained a wide range of percent tree cover (Table S2). Of the 7 out of 71 studies which did show support for a break point relationship, there was no consistency in where the estimated break point occurred (Table 3). Most of the estimated break points were at very high levels of percent forest cover. This may reflect support for the initial intrusion hypothesis, whereby habitat loss in intact landscapes causes a sharper decline in species richness than habitat loss in less intact landscapes (Betts et al., 2017), although the small number of studies limits the generality of this observation.

Unexpectedly, matrix quality was found to have the lowest impact on species richness. Patch density had a greater |mean slope| +/- SE than matrix quality in 16 studies, with the inverse being true in only 6 studies (Table 1). In the meta-analysis, matrix quality had the smallest effect size (|Fisher's z|), which was ~1.5x less than that of patch density (Figure 1). Matrix quality also did not appear to have a clear direction of effect (Table 1, Table 2). We may have failed to detect a relationship between mean % tree cover in the matrix and species richness because many other factors exist which may affect matrix quality. The presence of shrubs, cover objects, and food sources all contribute to matrix benefits i.e., increased connectivity between habitat patches and access to resources (Ricketts, 2001; Kupfer et al., 2006; Watling et al., 2010). Whereas mortality from roadkill, hunting, exposure to pesticides, and changes in microclimate all contribute to matrix hostility (Åström & Pärt, 2013; Benchimol & Peres, 2013; Schiesari et al., 2013; Rendall

et al., 2021). A study on neotropical primates found that matrix type was a good predictor of species richness when only non-hunted sites were considered (Benchimol & Peres, 2013). Further research is needed to develop more accurate ways of measurably estimating matrix quality in HMFLs.

In conclusion, our findings support the recommendations made by Arroyo-Rodríguez et al., 2020 that preserving and restoring habitat amount regardless of configuration should be the highest conservation priority, with an optimal landscape containing many smaller forest patches and some continuous forest. Preserving and restoring as much habitat as possible is the best strategy for conserving biodiversity, as well as maintaining economically and culturally beneficial ecosystems. Further research is needed to explore the potential value of increasing matrix quality for global biodiversity conservation. The results of this study join a growing body of empirical research showing that the effects of habitat loss outweigh the effects of fragmentation per se across taxa and biomes.

Table 1: Summary of relative effect sizes between habitat amount, patch density, and matrix quality (with the direction of effect for each variable in parentheses) for included BioFrag studies. Inclusion criteria included having a VIF < 7 in the complete regression model and having a top model (lowest AIC) which outperformed the null model. Candidate generalized least squares regression models[a] were averaged and the absolute value of the mean slope +/- SE was used to measure effect size for each standardized variable. If the mean slope +/- SE included zero, then the effect size and direction of effect was considered zero.

Study	PID	Primary researcher's last name	Taxa	Region	Relative effect sizes of habitat amount vs. patch density (direction of effect)	Relative effect sizes of habitat amount vs. matrix quality (direction of effect)	Relative effect sizes of matrix quality vs. patch density (direction of effect)
5	PID0006	Banks-Leite	Birds	Neotropic	HA(+) = PD(-)	HA(+) > MQ(0)	MQ(0) < PD(-)
6	PID0007	Banks-Leite	Birds	Neotropic	HA(+) > PD(+)	HA(+) > MQ(-)	MQ(-) = PD(+)
10	PID0015	Ewers	Arthropods	Australasia	HA(+) > PD(-)	HA(+) > MQ(0)	MQ(0) < PD(-)
11	PID0017	Young	Herps	Neotropic	HA(0) = PD(0)	HA(0) < MQ(-)	MQ(-) > PD(0)
13	PID0021	Eigenbrod	Herps	Nearctic	HA(+) = PD(-)	HA(+) > MQ(0)	MQ(0) < PD(-)
15	PID0026	Duguay	Mammals	Nearctic	HA(0) < PD(-)	HA(0) = MQ(0)	MQ(0) < PD(-)
16	PID0028	Wood	Birds	Nearctic	HA(+) = PD(+)	HA(+) > MQ(0)	MQ(0) < PD(+)
20	PID0039	Slade	Arthropods	Palaearctic	HA(+) > PD(-)	HA(+) > MQ(0)	MQ(0) < PD(-)
22	PID0041	Somarriba	Herps	Neotropic	HA(+) > PD(+)	HA(+) > MQ(0)	MQ(0) < PD(+)
25	PID0044	Somarriba	Herps	Neotropic	HA(0) = PD(0)	HA(0) < MQ(+)	MQ(+) > PD(0)
28	PID0048	Robinson	Birds	Australasia	HA(0) < PD(-)	HA(0) < MQ(+)	MQ(+) > PD(-)
31	PID0054	Kormann	Birds	Neotropic	HA(+) > PD(0)	HA(+) > MQ(0)	MQ(0) = PD(0)
32	PID0055	Ewers	Arthropods	Australasia	HA(-) = PD(-)	HA(-) = MQ(-)	MQ(-) = PD(-)
37	PID0063	Gardner	Herps	Neotropic	HA(+) > PD(-)	HA(+) > MQ(+)	MQ(+) < PD(-)
41	PID0068	Gardner	Arthropods	Neotropic	HA(+) = PD(+)	HA(+) > MQ(0)	MQ(0) < PD(+)
42	PID0069	Gardner	Mammals	Neotropic	HA(+) = PD(-)	HA(+) > MQ(0)	MQ(0) < PD(-)
43	PID0073	Robinson	Herps	Australasia	HA(0) < PD(-)	HA(0) < MQ(-)	MQ(-) = PD(-)
44	PID0075	Robinson	Arthropods	Australasia	HA(-) > PD(0)	HA(-) = MQ(+)	MQ(+) > PD(0)
45	PID0076	Robinson	Arthropods	Australasia	HA(-) = PD(-)	HA(-) > MQ(0)	MQ(0) < PD(-)
46	PID0077	Robinson	Arthropods	Australasia	HA(+) > PD(0)	HA(+) > MQ(0)	MQ(0) = PD(0)

48	PID0082	Lakeman-Fraser	Arthropods	Australasia	HA(+) > PD(0)	HA(+) > MQ(-)	MQ(-) > PD(0)
54	PID0091	Arroyo-Rodríguez	Birds	Neotropic	HA(+) > PD(-)	HA(+) > MQ(0)	MQ(0) < PD(-)
55	PID0092	Arroyo-Rodríguez	Mammals	Neotropic	HA(+) > PD(+)	HA(+) > MQ(0)	MQ(0) < PD(+)
57	PID0095	Arroyo-Rodríguez	Arthropods	Neotropic	HA(+) > PD(0)	HA(+) > MQ(0)	MQ(0) = PD(0)
59	PID0099-PID0111	Possingham	Birds	Australasia	HA(-) > PD(-)	HA(-) > MQ(0)	MQ(0) < PD(-)
68	PID0124	Marsh	Arthropods	Neotropic	HA(+) > PD(-)	HA(+) > MQ(0)	MQ(0) < PD(-)
69	PID0125	Marsh	Arthropods	Neotropic	HA(0) = PD(+)	HA(0) < MQ(-)	MQ(-) > PD(+)
70	PID0131	Wearn	Mammals	Indomalayan	HA(+) > PD(0)	HA(+) > MQ(+)	MQ(+) = PD(0)
71	PID0133	Watling	Herps	Neotropic	HA(+) < PD(-)	HA(+) > MQ(0)	MQ(0) < PD(-)

[a]Candidate models: 1) Habitat Amount, 2) Patch Density, 3) Matrix Quality, 4) Fragmentation per se (Habitat Amount + Patch Density), 5) Fragmentation Threshold (Habitat Amount*Patch Density), 6) Matrix Threshold (Habitat Amount*Matrix Quality), 7) Complete (Habitat Amount + Patch Density + Matrix Quality

Table 2: Summary of results from generalized least squares regression models in 71 BioFrag studies. Counts of studies with significant ($p < 0.05$) positive and negative slopes as well as the mean slope (standard error) across all studies are shown for univariate models (habitat amount, patch density, and matrix quality) as well as the fragmentation per se model (habitat amount + patch density) with species richness as the response variable. All significant results in the fragmentation per se model (habitat amount + patch density) had a VIF < 7.

	Habitat Amount Model (SE)	Patch Density Model (SE)	Matrix Quality Model (SE)	Habitat Amount in Fragmentation per se Model (SE)	Patch Density in Fragmentation per se Model (SE)
Significant positive slopes	26	3	10	20	3
Significant negative slopes	5	15	4	4	8
Mean slope (SE)	26.7 (7.4)	-5.3 (1.9)	1.96 (0.7)	27.1 (10.7)	-1.3 (1.9)

Table 3: Summary of studies which showed a significant break point regression between percent forest cover (log transformed) and species richness (log transformed) as well as significantly outperformed the linear regression model. Matrix quality was measured as the mean percentage of tree cover in the matrix.

Study	PID	Primary researcher's last name	Taxa	Region	Range of % forest cover among plots	Mean matrix quality among plots	Break point (% forest cover)
1	PID0001	Phalan	Birds	Afrotropic	40 - 100	38.7	72.6
6	PID0007	Banks-Leite	Birds	Neotropic	28 - 100	10.1	97.9
16	PID0028	Wood	Birds	Nearctic	2 - 89	7.3	44.5
45	PID0076	Robinson	Arthropods	Australasia	2 - 92	35.9	35.1
47	PID0081	Pilia	Arthropods	Palaearctic	19 - 76	3.2	55.6
57	PID0095	Arroyo Rodriguez	Arthropods	Neotropic	41 - 100	16.8	98.9
70	PID0131	Wearn	Mammals	Indomalayan	0 - 100	10.8	96.4
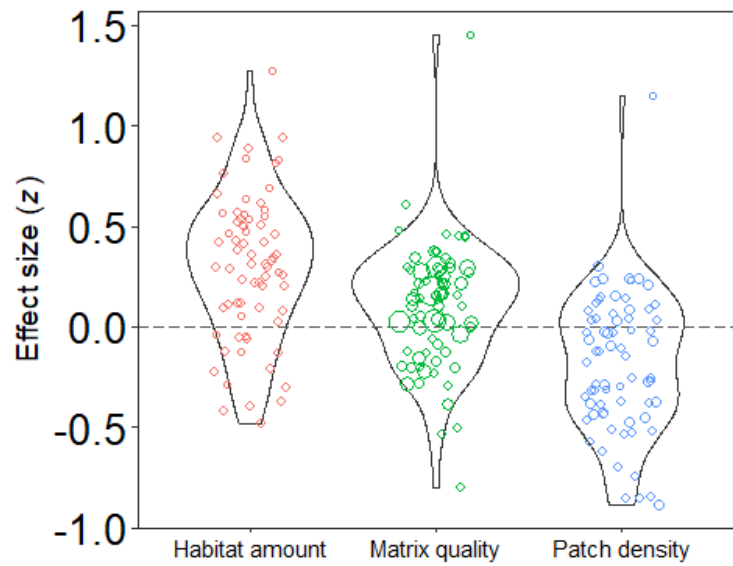
Figure 1: Effect sizes (Fisher's z) of habitat amount, matrix quality, and patch density in 71 BioFrag studies. Point size is proportional to the number of plots surveyed in the study.
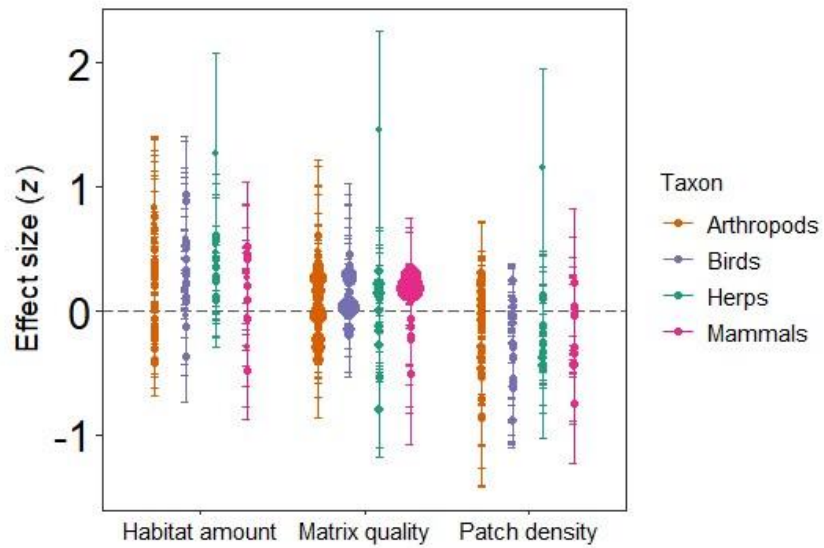
Figure 2: Effect sizes of habitat amount, matrix quality, and patch density in 71 BioFrag studies by taxon. Point size is proportional to the number of plots surveyed in the study. Error bars represent 95% confidence intervals around the effect size estimates.
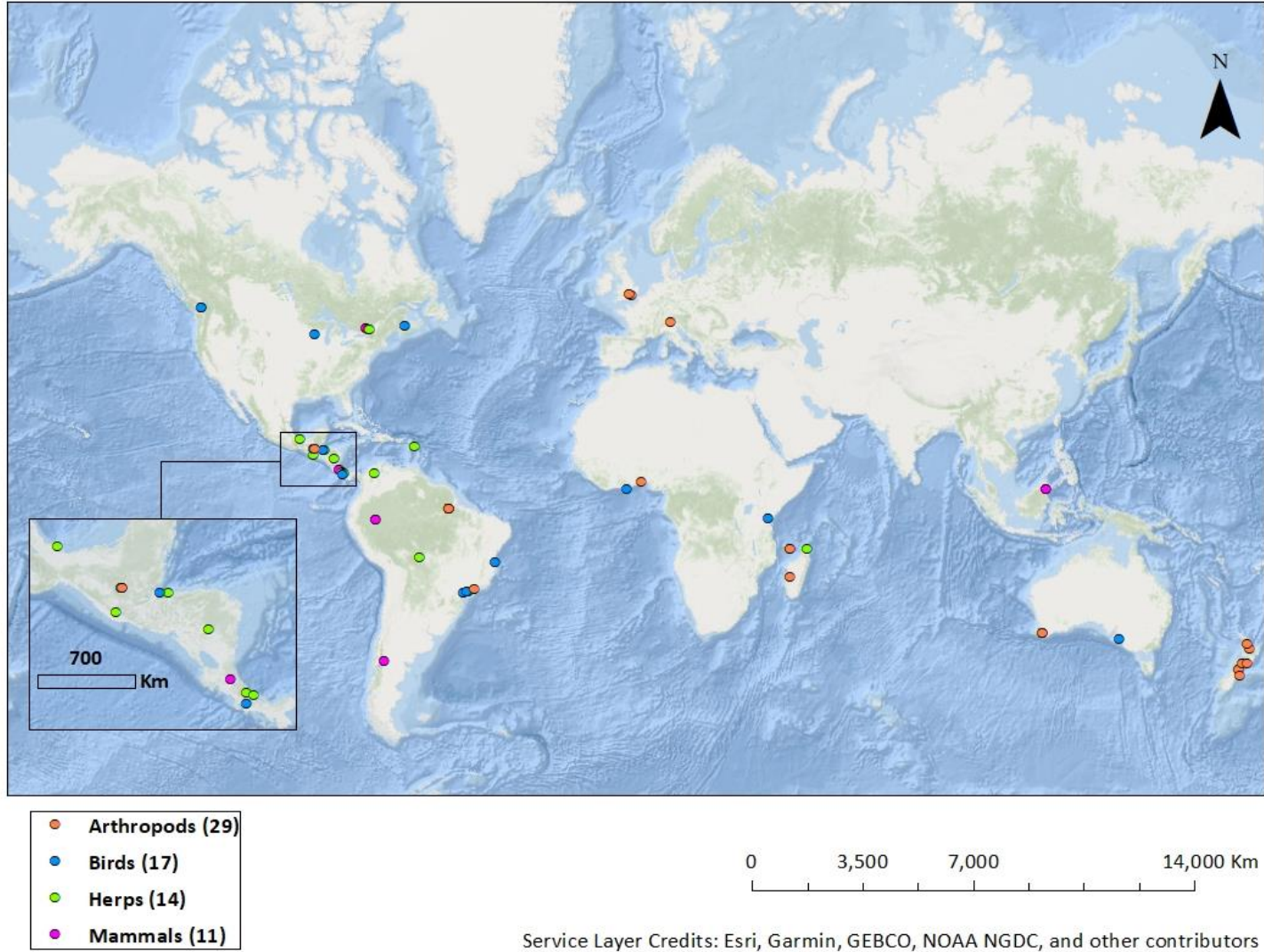
Figure 3: Locations of the 71 BioFrag studies used in data analysis with point color representing the taxon surveyed. The number of studies included for each taxon is stated in parenthesis in the legend.

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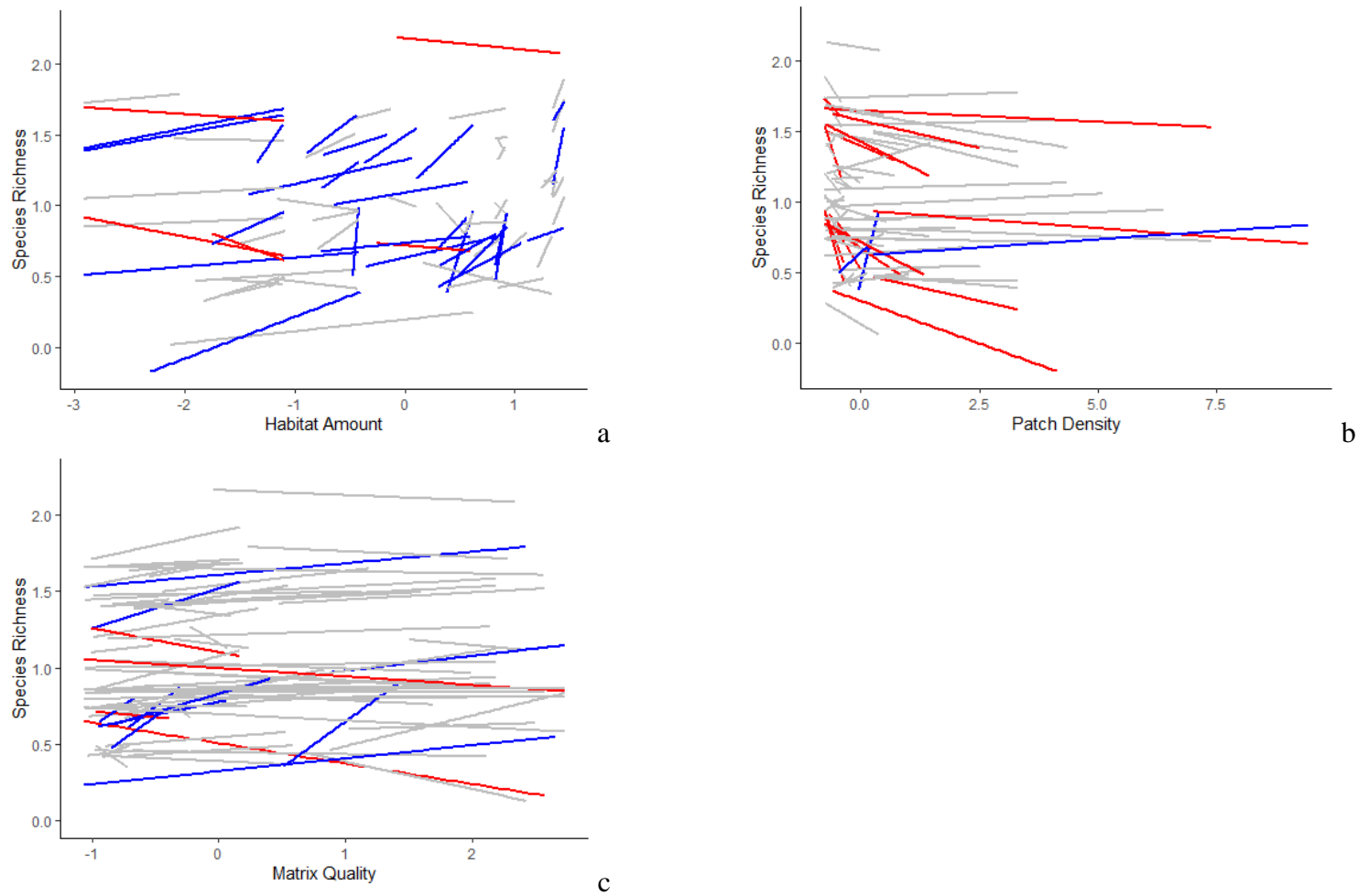
Figure S1: Univariate generalized least squares regression models a) habitat amount (total forest area in hectares), b) patch density (patches/m^2), and c) matrix quality (mean % of tree cover) with species richness as the response variable in 71 BioFrag studies. Patch density, habitat amount, and matrix quality data were standardized. Habitat amount data and species richness data were log-transformed. Negative slopes are shown in red, positive slopes are shown in blue, and non-significant slopes are shown in grey.

Table S1: Summary of regression coefficients from univariate generalized least squares regression models. Significance of regression coefficients is indicated with asterisks where non-significant: no asterisk, p<0.05 : *, p<0.01 : **, p<0.001 : ***. Studies which had a VIF < 7 in the complete regression model (habitat amount + patch density + matrix quality) are bolded. Studies which did not have a top model that outperformed the null model are highlighted in grey.

Study	PID	Primary researcher's last name	Taxa	Region	Habitat amount	Patch density	Matrix quality
1	PID0001	Phalan	Birds	Afrotropic	5.04*	-0.61	0.34
2	**PID0003**	**Marsh**	**Birds**	**Afrotropic**	**-5.99**	**-0.08**	**-0.61**
3	**PID0004**	**Marsh**	**Arthropods**	**Afrotropic**	**-5.6**	**-2.41**	**-0.14**
4	**PID0005**	**Ewers**	**Arthropods**	**Palaearctic**	**9.66**	**4.58**	**9.26****
5	**PID0006**	**Banks-Leite**	**Birds**	**Neotropic**	**16.14***	**-5.82**	**4.93**
6	**PID0007**	**Banks-Leite**	**Birds**	**Neotropic**	**30.39*****	**-7.98***	**3.04**
7	**PID0008**	**Banks-Leite**	**Birds**	**Neotropic**	**19.07**	**-2.03**	**6.56**
8	**PID0012**	**Urbina Cardona**	**Herps**	**Neotropic**	**12.95*****	**-5.80*****	**5.13**
9	PID0013	Mezger	Arthropods	Afrotropic	109.1	-7.05	-1.51
10	**PID0015**	**Ewers**	**Arthropods**	**Australasia**	**14.54*****	**0.1**	**9.16***
11	**PID0017**	**Young**	**Herps**	**Neotropic**	**-2.67**	**0.21**	**-0.67***
12	**PID0019**	**Lens**	**Birds**	**Afrotropic**	**1**	**-3.54**	**2.38**
13	**PID0021**	**Eigenbrod**	**Herps**	**Nearctic**	**1.80*****	**-2.49*****	**0.8**
14	**PID0025**	**Rytwinski**	**Mammals**	**Nearctic**	**-0.49**	**-0.04**	**-0.17**
15	**PID0026**	**Duguay**	**Mammals**	**Nearctic**	**0.78**	**-0.39*****	**-0.26**
16	**PID0028**	**Wood**	**Birds**	**Nearctic**	**5.68***	**2.64**	**2.91**
17	**PID0029**	**Ribeiro**	**Arthropods**	**Neotropic**	**21.46**	**-1.14**	**14.83**
18	**PID0033**	**D'Cruze**	**Herps**	**Afrotropic**	**25.26****	**12.51***	**6.10****
19	**PID0038**	**Medina Rangel**	**Herps**	**Neotropic**	**-0.25**	**0.57**	**-0.94**
20	**PID0039**	**Slade**	**Arthropods**	**Palaearctic**	**11.83****	**-3.46**	**8.07**
21	**PID0040**	**Lantschner**	**Mammals**	**Neotropic**	**0.43**	**0.06**	**0.61**
22	**PID0041**	**Somarriba**	**Herps**	**Neotropic**	**139.12***	**12.12**	**-0.75**
23	**PID0042**	**Somarriba**	**Herps**	**Neotropic**	**3.6**	**-2.03**	**-0.61**

24	PID0043	Somarriba	Herps	Neotropic	46.69	-8.75	3.33
25	**PID0044**	**Somarriba**	**Herps**	**Neotropic**	**7.16**	**-0.76**	**2.23***
26	PID0045	Somarriba	Herps	Neotropic	20.09	-6.22*	0.51
27	**PID0046**	**Cerezo**	**Birds**	**Neotropic**	**48.41***	**-10.66***	**0.87**
28	**PID0048**	**Robinson**	**Birds**	**Australasia**	**0.93**	**-0.21**	**2.66****
29	**PID0049**	**Lachat**	**Arthropods**	**Afrotropic**	**7.25**	**1.15**	**-6.18**
30	PID0050	Hawes	Arthropods	Neotropic	262.92	-70.16	-2.44
31	**PID0054**	**Kormann**	**Birds**	**Neotropic**	**53.07****	**-7.30****	**7.43**
32	**PID0055**	**Ewers**	**Arthropods**	**Australasia**	**-2.49****	**1.03**	**-4.55****
33	**PID0057**	**Gardner**	**Arthropods**	**Neotropic**	**6.34**	**-8.18**	**2.57**
34	PID0059	**Gardner**	Birds	Neotropic	330.98	-79.69	30.19
35	PID0061	Gardner	Arthropods	Neotropic	139.64**	-36.32**	5.02
36	PID0062	Gardner	Arthropods	Neotropic	218.62*	-53.95*	22.72*
37	**PID0063**	**Gardner**	**Herps**	**Neotropic**	**68.61***	**-18.18***	**1.91**
38	PID0064	Gardner	Arthropods	Neotropic	40.4	-11.87	-5.87*
39	**PID0065**	**Gardner**	**Arthropods**	**Neotropic**	**-38.56**	**6.64**	**-1.54**
40	PID0066	Gardner	Herps	Neotropic	46.6	-11	5.19
41	**PID0068**	**Gardner**	**Arthropods**	**Neotropic**	**30.84**	**-4.24**	**0.13**
42	**PID0069**	**Gardner**	**Mammals**	**Neotropic**	**54.13***	**-14.37***	**0.61**
43	**PID0073**	**Robinson**	**Herps**	**Australasia**	**0.26**	**-0.71**	**-0.68**
44	**PID0075**	**Robinson**	**Arthropods**	**Australasia**	**-1.86****	**-0.34**	**1.56**
45	**PID0076**	**Robinson**	**Arthropods**	**Australasia**	**-24.19***	**-9.73**	**-5.14**
46	**PID0077**	**Robinson**	**Arthropods**	**Australasia**	**0.65***	**0.1**	**0.4**
47	**PID0081**	Pilia	**Arthropods**	**Palaearctic**	**5.34***	**6.23**	**7.22***
48	**PID0082**	Lakeman-Fraser	**Arthropods**	**Australasia**	**1.23**	**-0.08**	**-0.24**
49	**PID0083**	Betts	**Birds**	**Nearctic**	**3.44**	**-0.21**	**0.08**
50	**PID0084**	Lakeman Fraser	**Arthropods**	**Australasia**	**1.36**	**1.48**	**4.04**
51	**PID0085**	Lakeman Fraser	**Arthropods**	**Australasia**	**1.4**	**4.58**	**4.69**

52	PID0086	Lakeman Fraser	Arthropods	Australasia	-0.06	0	1.14
53	**PID0087**	**Lakeman Fraser**	**Arthropods**	**Australasia**	**-0.11**	**-0.34**	**-3.11**
54	**PID0091**	**Arroyo-Rodríguez**	**Birds**	**Neotropic**	**75.37****	**-4.8**	**2.92**
55	**PID0092**	**Arroyo-Rodríguez**	**Mammals**	**Neotropic**	**6.93**	**0.12**	**0.65**
56	**PID0093**	**Arroyo-Rodríguez**	**Mammals**	**Neotropic**	**35.32**	**-7.48**	**-16.28**
57	**PID0095**	**Arroyo-Rodríguez**	**Arthropods**	**Neotropic**	**20.71***	**-1.91**	**1**
58	PID0098	Wearn	Mammals	Indomalayan	10.45***	-2.32***	3.44***
59	PID0099-PID0111	**Possingham**	**Birds**	**Australasia**	**-4.63*****	**-1.08****	**-0.61**
60	**PID0112**	**Melles**	**Birds**	**Nearctic**	**3.59*****	**2.13***	**4.43****
61	**PID0113**	**Melles**	**Birds**	**Nearctic**	**1.11*****	**-0.17**	**0.12**
62	**PID0114**	**Klingbeil**	**Mammals**	**Neotropic**	**77.06**	**-29.33**	**-5.9**
63	**PID0115**	**Klingbeil**	**Mammals**	**Neotropic**	**-89.81**	**26.48**	**2.82**
64	PID0117	Cisneros	Mammals	Neotropic	-2.84	0.24	-3.45
65	PID0118	Marsh	Arthropods	Neotropic	-1.53	0.26	-0.99*
66	PID0119	Marsh	Arthropods	Neotropic	0.79	-0.18	0.06
67	PID0121	Morante-Filho & Faria	Birds	Neotropic	13.75	-5.43	4.8
68	**PID0124**	**Marsh**	**Arthropods**	**Neotropic**	**7.17****	**-0.47***	**0.01**
69	**PID0125**	**Marsh**	**Arthropods**	**Neotropic**	**-2.16***	**0.19***	**-0.34**
70	**PID0131**	**Wearn**	**Mammals**	**Indomalayan**	**1.59*****	**-0.57*****	**0.47****
71	**PID0133**	**Watling**	**Herps**	**Neotropic**	**3.74****	**-7.04**	**2.72**

Table S2: AIC values for linear and breakpoint regression models between percent forest cover and species richness. Estimated breakpoints, minimum and maximum values for percent forest cover across plots, and coordinates for plot one of every study are also shown. Significance is indicated with asterisks where no asterisk : non-significant, * : p<0.05, ** : p<0.01, *** : p<0.001.

Study	Linear Model AIC	Breakpoint Model AIC	Estimated Breakpoint (% Forest Cover)	Min % Forest Cover	Max % Forest Cover
1	82.81***	53.17*	72.61*	40	100
2	-58.39	-55.06	59.16	52	99
3	64.67	66.84	93.11	41	97
4	39.54**	37.63	38.64	20	40
5	-40.86	-41.54*	41.40*	10	49
6	-54.81***	-61.02***	97.95***	28	100
7	-34.74	-34.12	38.28	27	91
8	-26.48***	-27.42	59.16	38	84
9	-27.73*	-26.30	75.86	75	82
10	-113.06***	-146.94	35.81	0	100
11	42.70	45.12	85.11	70	100
12	-2.91	-0.51	61.66	6	100
13	-13.44***	-19.69	7.05	3	95
14	-8.45	-4.95	34.36	21	98
15	13.41	13.36	33.73	23	90
16	-124.90*	-130.92***	44.46***	2	89
17	-25.34	-21.97	36.73	18	54
18	-0.20**	2.03	33.73	23	44
19	-17.23	-17.23	None	0	100
20	-40.20**	-38.62	4.06	0	100
21	76.57	66.70	89.54	2	93
22	-27.58*	-27.58**	None**	86	99
23	-36.07	-32.91	73.28	32	98
24	-10.96	-14.34	84.72	82	98
25	-27.97	-28.99	80.35	46	89
26	-10.28*	-11.80	69.82	53	74

27	-274.66***	-275.29***	74.64***	25	100
28	-45.55	-42.33	87.10	0	100
29	-58.79	-55.75	87.10	0	7
30	-7.12	-3.89	96.83	76	100
31	-50.33***	-57.43	63.97	28	94
32	311.97	312.31	19.77	10	92
33	-21.91	-20.86	98.17	75	100
34	-19.10	-27.73	92.47	9	100
35	-41.14**	-38.66	76.38	76	100
36	-6.56*	-3.01*	95.72*	76	100
37	-0.52*	1.72	80.54	75	100
38	-19.47	-20.19	88.92	76	100
39	7.24	8.61	90.57	75	100
40	-12.53	-10.28	98.40	76	100
41	-24.88*	-22.99	92.47	75	100
42	88.94*	81.59	62.52	0	99
43	56.60	55.47	67.76	0	100
44	19.22***	19.19	2.94	0	100
45	-89.90	-102.44**	35.08**	2	92
46	-9.31	-5.81	68.71	0	100
47	-72.26***	-82.09***	55.59***	19	76
48	-161.77***	-161.77***	None***	13	100
49	-372.57	-373.40	95.72	34	100
50	-57.12	-58.66	51.88	24	71
51	-138.04***	-138.29	25.76	20	61
52	-74.54	-74.54	None	13	96
53	72.16***	72.16***	None***	3	74
54	-34.63***	-33.52	76.21	52	100
55	-25.01*	-23.76	49.89	36	100
56	-27.48	-24.58	77.45	57	85
57	-44.84***	-58.23**	98.86**	41	100
58	317.11***	314.86	99.31	30	100

59	-347.13***	-343.57***	89.54***	0	100
60	129.55***	123.19***	21.53***	5	36
61	-157.71***	-156.96	9.79	1	41
62	-21.49	-20.44	89.54	81	95
63	-26.27	-26.27	None	81	95
64	-22.72	-29.72	66.83	61	88
65	-90.72	-90.85	69.02	14	100
66	-72.68	-77.99	77.09	34	100
67	-97.01	-95.77	38.99	25	98
68	-110.42***	-132.67	40.09	6	100
69	161.95	164.21	19.36	6	100
70	2671.17***	2332.71***	96.38***	0	100
71	-63.16**	-63.66	2.47	2	39