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SPECIES RESPONSES TO HABITAT EDGES AND FRAGMENTATION PER SE: A CROSS TAXA META-ANALYSIS

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SPECIES RESPONSES TO HABITAT EDGES AND FRAGMENTATION *PER SE*: A CROSS
TAXA META-ANALYSIS

A Thesis Submitted to the
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By
Rachel K. Snyder
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I, Rachel Snyder, 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.

ABSTRACT

Aim
We examined the scale equivalency of fragmentation effects at the patch scale and landscape scale to determine if patch level effects scale up to landscape level effects. First, we examined species responses to fragmentation effects at the patch scale and landscape scale. Second, we evaluated whether there is a difference in response between taxonomic groups and across latitudes. Finally, we analyzed the data at the level of individual species in order to determine how species respond to edge effects and fragmentation effects.

Location
Data for 71 studies were gathered from the BioFrag database. Studies used were located in 48 unique landscapes across the globe.

Major taxa studied
Our global dataset comprised 7619 species from 5 different taxonomic groups (1212 birds, 279 herps, 3490 invertebrates, 136 mammals, and 2502 plants).

Methods
We used vote counting in tandem with a meta-analysis comparing effect sizes of local-scale edge effects to landscape-scale fragmentation effects. We analyzed data at the species level using random placement models to determine how species individually respond to edge effects and fragmentation effects.

Results
Negative edge effects and fragmentation effects were not the most prevalent in our study landscapes. Nonsignificant responses to edges and fragmentation were more common than either negative or positive responses. Negative edge effects also do not scale up to negative fragmentation effects. Negative effects of fragmentation *per se* also do not predominate with species abundance permutations. Our abundance results show that species with significant negative responses were in the minority, indicating that individual species responses are not overwhelmingly negative.

Main conclusions
Overall, our results suggest that patch scale effects of fragmentation (edge effects) should not be extrapolated to landscape scale effects of fragmentation (fragmentation *per se* effects). In contrast to much of the literature, species responses were largely nonsignificant across both scales and individual species responses do not show a variation from this trend. Based on the results of our study, we suggest that researchers strongly consider the scale at which a study is conducted and recommend that researchers avoid untested extrapolation across scales.

INTRODUCTION

  Habitat loss is the primary threat to biodiversity across the globe (Jaureguiberry et al. 2022). In 2021, the tropics lost 11.1 million hectares of tree cover and temperate zones lost 3.1 million hectares (Global Forest Watch 2021). The trend of declining cover of natural habitats also applies to non-forested habitats, which can hold comparable amounts of biodiversity (Overbeck et al. 2015). Habitat loss can lead to habitat fragmentation, the process by which large continuous habitat is broken up into smaller patches (Fahrig 2003). Habitat fragmentation is often thought to have negative effects on biodiversity independently of habitat loss (Haddad et al. 2015; Pfeifer et al. 2017). The idea that habitat fragmentation has largely negative effects on biodiversity stems from the theory of island biogeography, which suggests that larger islands have more species than smaller islands (MacArthur & Wilson 1967). This theory has long been applied to terrestrial landscapes, in which habitat patches are likened to oceanic islands, and the surrounding matrix is viewed as similar to the inhospitable ocean (Diamond 1975; Haila 2002). The theory of island biogeography is also largely the reason that habitat loss and habitat fragmentation have become almost synonymous in the scientific literature over the last six decades (Haila 2002; Fahrig 2003). As such, it is widely accepted that habitat fragmentation is 'bad' for biodiversity.

  Fragmentation has long been recognized as a landscape-scale process because it describes the breaking up of continuous habitat areas into multiple smaller patches (Fahrig 2003). The physical fragmentation of continuous forest into smaller patches often results in species declines in those small patches because they generally contain fewer individuals (Debinski & Holt 2000; Matthews et al. 2016), decreased habitat diversity (Gibbs 1998), and a higher proportion of edge (Conor & McCoy 2013) than larger patches. Despite the apparent correlation between patch size, number of individuals, and habitat diversity, patch size effects depend on the landscape context

3

of the patch (Fahrig 2003). When small patches are examined together as part of a larger landscape, they often contain as many species as one large fragment as postulated by the habitat amount hypothesis (HAH; Fahrig 2013). The HAH stipulates that the number of species present in a patch is more influenced by habitat amount in the surrounding landscape (regardless of the number, size, or distance of habitat patches from one another) than by patch size or isolation itself, implying that habitat fragmentation is largely unimportant for understanding species diversity (Fahrig 2013). The HAH explains why species diversity may be largely unaffected by habitat fragmentation when there are suitable amounts of habitat (Fahrig 2013). However, empirical tests of the HAH have led to different conclusions regarding its validity, with some researchers citing support for the HAH (Melo et al. 2017, Watling et al. 2020) and other researchers arguing against it (Hanski 2015; Haddad et al. 2017; Saura 2021).

The effect of edges on species responses within forest fragments is a less debated subject (Murcia 1995). Edges can affect species by causing changes in the biotic and abiotic conditions in forests (Murcia 1995). Changes in both the abiotic and the biotic environment near edges means that forest species often experience a decreased likelihood of occurrence with decreasing distance to the nearest edge in habitat fragments or patches (Gonzalez et al. 1998; Fletcher 2005). Such a relationship would constitute a 'negative' edge effect, because the variable of interest is declining with proximity to the edge. Exposure to multiple edges may exacerbate such declines. For example, a study examining the impact of multiple edges on bobolink (*Dolichonyx oryzivorus*) populations in ten distinct, small temperate grasslands patches found that multiple edges (measured using distance to the edge) can intensify negative edge effects on bird populations (Fletcher 2005). Despite the preponderance of negative edge effects documented in the literature, not all edge effects are negative (Fahrig 2017). Species can also exhibit positive

responses close to edges (Fahrig 2017). The focus on negative effects of habitat edges in the literature may partially explain the perceived negative effects of habitat fragmentation, because edge effects often negatively affect species at the patch scale (Puttker et al. 2020). However, negative edge effects at the patch scale may not inherently lead to negative fragmentation effects at the landscape scale.

Response to habitat edge can vary by taxonomic group and latitude, which may indicate varying effects of landscape-scale fragmentation (Schlaepfer et al. 2018). Differential effects of habitat fragmentation can occur for a variety of reasons including differences in mobility (Debinski & Holt 2000), ecological specialization (e.g. habitat use or diet; Bregman et al. 2014), body size (Cardillo et al. 2005), and reproductive capacity (Polishchuk 2002). For example, epigeic insect (ants, ground-, and rove-beetles) assemblages differ across heavily degraded forest fragments due to differences in the distribution of habitat generalists and habitat specialists across these landscapes (Ramalingam and Rajan 2021). The diversity of taxonomic groups and functional feeding guilds were higher in smaller fragments compared to larger fragments, which suggests that species from forest fragments, the surrounding matrix, and edge specialist species occupied these smaller patches with high edge density (e.g. more edge per unit area; Ramalingam and Rajan 2021). Habitat quality and structure as well as the surrounding matrix quality can influence fragmentation effects (Andren 1994; Ricketts 2001). Similarly, latitude can influence how taxa are affected by fragmentation, with negative effects on species in tropical landscapes more likely than negative effects in temperate landscapes due to tropical forest species' limited mobility as compared to their temperate counterparts (Cerezo et al. 2010).

The nature of fragmentation effects has been debated for years (Fahrig 2017; Fletcher et al. 2018; Fahrig 2019; Fahrig et al. 2019). Although researchers may assume that observations of

negative effects at the patch scale 'scale up' to the landscape scale, other researchers highlight that because fragmentation *per se* (fragmentation examined separately from and accounting for habitat amount) is a landscape scale process, it may be unreliable to infer landscape scale responses from patch scale studies (Fahrig 2019). A review of 118 studies from the published literature found that greater than 70% of ecological responses to habitat fragmentation *per se* were non-significant (Fahrig 2017). Of the significant responses, approximately 76% were positive, meaning that species richness, abundance, and occurrence increase with habitat fragmentation *per se* (Fahrig 2017). Such results from the synthesis of multiple studies stand in contrast to the results from many individual studies that claim to demonstrate negative effects of habitat fragmentation.

Fragmentation effects have long been thought of as negative for species biodiversity, but more recent research points to its potential positive effects on species (Fahrig 2017; Fahrig et al. 2019). Researchers cite several possible explanations for positive fragmentation effects including increased functional connectivity, positive edge effects, reduced inter-and intra-specific competition, increased movement success, spreading of risk, stabilization of predator-prey or host-parasite interactions, increased landscape complementation, and higher habitat diversity (Fahrig et al. 2019). Functional connectivity is most often cited as the explanation for positive responses to habitat fragmentation (Fahrig 2017). Fragment connectivity and function can vary based on matrix quality (Santos-Barrera & Urbina-Cardona 2011; Reider et al. 2018) where patches surrounded by relative low-quality matrix are effectively more isolated than patches surrounded by relative high-quality matrix (Ricketts 2001). A study in a fragmented, agricultural landscape in Germany used 23 pairs of organic and conventional farming plots to examining wasp movement across fragmented landscapes (Holzschuh et al. 2010). Researchers

hypothesized that the observed positive fragmentation effects may be due to the connectivity provided by different habitat types and higher edge densities (Holzschuh et al. 2010). Positive edge effects are also used as a rationale to explain significant positive species response to fragmentation. A study examining responses of Amazonian bats to varying degrees of fragmentation indicated higher species abundance and richness in fragmented versus continuous forests (Klingbeil & Willig 2009). The findings were attributed to positive edge effects, such as higher forage availability and refuge from predation near forest edges (Klingbeil & Willig 2009).

A large portion of fragmentation literature measures biodiversity using species richness because it is a straightforward metric and is often correlated with species abundance and occupancy. However, some researchers have suggested that species richness may obscure predominantly negative area and isolation effects on species-level responses (Ewers & Didham 2006; MacDonald et al. 2021). A study used random-placement models to examine the relationship of butterfly species to island area and calculate expected species abundances and species richness on freshwater islands in Canada (MacDonald et al. 2021). Actual species abundance and species richness were compared to permutation models (MacDonald et al. 2021). Species abundance results indicated that abundance was lower on both smaller and more isolated islands, but these trends were not apparent in the analysis using species richness (MacDonald et al. 2021). The discrepancy among these inferences suggests that using an aggregate measure of species responses (e.g. species richness) may obscure individual species responses and lead to incorrect inferences (MacDonald et al. 2021). Another criticism of using species richness as a response variable is that individual species responses cannot be measured and generalist species can maintain biodiversity without considering species of conservation concern. The findings of a synthetic review of 23 habitat islands determined that studies which used species richness to

measure response to habitat loss may have underestimated the impact of habitat loss on specialist bird species, which tend to be species of conservation concern (Matthews et al. 2014). As a result, the researchers suggest that using species richness may lead to inaccurate interpretations of data as the sensitivity of different groups to habitat loss was highly variable (Matthews et al. 2014).

In this paper we will examine the scale equivalency of fragmentation effects at the patch scale and landscape scale to determine if patch level effects scale up to landscape level effects. We predict that (1) negative edge effects will predominate using distance to edge analysis, with decreased species richness in plots closer to edges (negative edge effects). Similarly, we also predict that fragmentation *per se* analysis will show a predominance of studies showing negative effects of habitat fragmentation (negative fragmentation effects) on species richness. In other words, studies with negative edge effects will also have negative fragmentation effects. We will evaluate these predictions using both a vote counting approach as well a meta-analysis comparing effect sizes of local-scale edge effects to landscape-scale fragmentation effects. We will also evaluate whether there is a difference in response between taxonomic groups and across latitudes. We recognize that numerous researchers have suggested that measuring species richness may obscure negative effects on individual species. In recognition of the fact that species richness does not differentiate species of conservation concern from generalist species, we will also analyze the data at the species level to determine how species individually respond to edge effects and fragmentation effects. To evaluate the extent to which individual species are responding to edge effects and fragmentation *per se*, we will use random placement models based on MacDonald et al. (2021) to calculate expected probability of species abundance in each study landscape. We expect (2) a large proportion of individual species to show negative effects

in these permutation analyses, which will reflect the results of the vote counting and meta-analysis approaches.

MATERIALS AND METHODS

Species data

Our global dataset comprised 7619 species from 5 different taxonomic groups (1212 birds, 279 herps, 3490 invertebrates, 136 mammals, and 2502 plants). Data for 71 studies were gathered from the BIOFRAG database (Pfeifer et al. 2014). Species were located in 48 unique landscapes across the globe (Figure 1). Species richness and abundance for each study was calculated from the count data. Species richness data were standardized for comparison across studies.

Habitat classification

We used forest cover raster layers from the Hansen dataset for each study area. Forest cover shapefiles were created from the forest cover raster layers. Forest habitat was defined as any forest cover greater than 60% while matrix was defined as forest cover less than 60% (DiGregorio 2022). The cell size of the forest cover map was 30 x 30 m^2, which means that the smallest patches that could be detected were 0.09 ha. For all studies, the forest cover shapefiles were used to estimate habitat amount, distance to the nearest edge, and number of patches in each landscape. Data were standardized by subtracting the mean for each observation and dividing by the standard deviation to allow for comparison of variables measured on different scales. We calculated species richness for each plot within each study using count data for each study from the BioFrag database. We used plot shapefiles and forest cover shapefiles to calculate distance to the nearest edge for each plot within each study. Standardized distance to edge was compared to plot species richness using a regression analysis. Distance to edge was the metric used to qualify edge effects. To measure the effects of fragmentation *per se*, a 1 km buffer was created around each plot in each study which acted as a measure of the landscape around each

individual plot (e.g. Pfeifer et al. 2017; Betts et al. 2019). We used a 1 km buffer to create the

landscapes for all taxa, regardless of differences in dispersal capability because data to determine

dispersal ability for the taxa and landscapes in our study do not exist. We calculated habitat

amount (hectares) and number of patches in each buffer using forest cover shapefiles.

Statistical analysis

Prediction 1: Negative edge effects and fragmentation effects will predominate. Negative edge

effects will translate to negative fragmentation effects.

Vote counting

We examined the influence of edge effects on species using a regression model

comparing plot species richness to standardized distance to the edge. We measured the effect of

fragmentation *per se* on species richness using a regression model comparing plot species

richness to standardized habitat amount + standardized number of patches. We used number of

patches (patch density) as a metric of fragmentation because it is a straightforward metric that

clearly describes fragmentation (Fahrig 2003). Patch density is easy to compare across multiple

studies, with increased patch density (e.g. more patches per unit area) describing greater

fragmentation. Variance Inflation Factors (VIFs) for each study were calculated, and studies with

VIF > 5 were excluded from the fragmentation *per se* analysis to avoid collinearity in our

samples (Hair et al. 2009). The number of studies with negative, positive, and non-significant

relationships were counted for both edge effect and fragmentation *per se*. Proportions of

negative, positive, and non-significant studies were compared using Z-test of proportions.

Meta-analysis

We conducted a meta-analysis on three multiple regression models to compare effect

sizes across different predictor variables. The different models tested were the Local vs.

Landscape Model , Scale-Dependent Taxa Response Model, and the Latitudinal Gradient Model.

The Local vs. Landscape Model examined effect sizes across the two different scales (edge effect vs. fragmentation effect). The Scale Dependent Taxa Response Model examined the effect sizes across the 5 different taxonomic groups for each scale. The Latitudinal Gradient Model examined the effect sizes for each scale and among tropical and temperate latitudes. Tropical latitudes were defined as the area between the Tropic of Cancer (23.4°N) and Tropic of Capricorn (23.4°S). Temperate latitudes were defined as latitudes above 23.4°N and below 23.4°S. The models were mixed effects models where a random effect of the uniqueness of the landscape was included in each model, which allowed us to account for variation from studies of different taxonomic groups collected in the same landscape.

Effect size and variance for multiple regression models were calculated based on equations from Aloe & Becker (2012). The effect size equation was $r_{sp} = \frac{t_f \sqrt{(1-R_Y^2)}}{\sqrt{(n-p-1)}}$ where t_f is the t test of the regression coefficient, R_Y^2 is the squared multiple correlation for the full model without the predictors, n is sample size, and p is the number of predictors in the model (Aloe & Becker 2012). The equation for variance was $\hat{\sigma}^2(r_{sp}) = \frac{r_Y^4 - 2r_Y^2 + r_{Y(f)}^2 + 1 - r_{Y(f)}^4}{n}$ where r_Y^4 is the squared R^2 value of the full model, r_Y^2 is the R^2 value of the full model, $r_{Y(f)}^2$ is the R^2 value of the full model without predictor variables (null model for edge effect and HA only for fragmentation effect), $r_{Y(f)}^4$ is the squared R^2 value of the full model without predictor variables (null model for edge effect and HA only for fragmentation effect), and n is sample size (Aloe & Becker 2012).

Prediction 2: A large proportion of individual species will show negative effects in species abundance permutation analyses, consistent with the results of the vote counting and meta-analysis approaches.

Species Abundance Models

We calculated the number of species with negative, positive, or nonsignificant relationships to edge effect or fragmentation effect using abundance permutation models. The equation for expected species abundance we used was $E\left(n_{ij}\right) = n_i\left(\frac{a_j}{A_T}\right)$ where a_j is the area of the jth patch, A_T is the total area of all patches, and n_i is the abundance of species i summed across all patches. (MacDonald et al. 2021). We calculated the regression between abundance and area and calculated the residuals (unexplained variance in abundance after accounting for area). We measured the effects of fragmentation *per se* on the residuals using regression models to examine if the variance in abundance of individual species after accounting for patch area is related to fragmentation *per se*. The number of species in studies with negative, positive, and non-significant relationships were counted. Proportions of negative, positive, and non-significant studies were compared using Z-test of proportions.

We completed all calculations and analysis in R version 4.2.0. (R Core Team 2022).

RESULTS

Vote counting

We predicted that negative edge effects would predominate, with decreased species richness in plots closer to edges. Although there was a significant difference in the proportion of studies reporting negative, positive, and nonsignificant edge effects ($\chi^2 = 41.87$, df = 2, p-value < 0.001; Figure 2) most studies (n=44) were nonsignificant (70%). In contrast, only 25% (n=18) of studies showed the expected decline in species richness near edges. When nonsignificant studies are removed, there was no difference in proportion of studies that are negative or positive ($\chi^2 = 2.93$, df = 1, p-value = 0.087).

We also predicted that the fragmentation *per se* analysis would show a predominance of studies with negative effects of habitat fragmentation on species richness. We found a significant difference in proportion of studies that have negative, positive, and nonsignificant fragmentation effects ($\chi^2 = 30.11$, df = 2, p = 2.891e-07; Figure 2). Again, most studies were nonsignificant (n=33). When nonsignificant studies were removed, we found no difference in proportion of studies that were negative or positive ($\chi^2 = 0.06$, df = 1, p = 0.804).

Of the 18 studies that had negative edge effects, four studies also had negative fragmentation effects (Figure 2). Seven studies switched from a negative edge effect to a nonsignificant fragmentation effect and one switched to a positive fragmentation effect. Five studies with a negative edge effect had a VIF value > 5 and had to be excluded from the fragmentation effect analysis.

Meta-analysis

Overall, we found no difference in effect sizes between edge effects and fragmentation effects ($F_{1,122}$) = 0.09, p = 0.763; Figure 3). The mean effect size for edge effects at the patch scale was -0.12 ± 0.001 (SE) and mean effect estimate for fragmentation effects at the landscape scale was 0.02 ± 0.001 (SE). In general, edge effects do not have a larger effect than fragmentation effects.

We found a significant interaction between scale and taxon ($F_{9,114}$ = 5.16, p < 0.001; Figure 4). Among birds, the mean effect estimate for edge effect was -0.22 ± 0.003 (SE) and the mean effect estimate for fragmentation was -0.01 ± 0.004 (SE). The mean effect estimate for edge effect among herps was -0.19 ± 0.006 (SE) and the mean effect estimate for fragmentation among herps was 0.16 ± 0.008 (SE). The mean effect estimate for edge effect on mammals was -0.06 ± 0.005 (SE) and the mean effect estimate for fragmentation on mammals was 0.01 ± 0.010 (SE). Among invertebrates, the mean effect estimate for edge effect was -0.05 ± 0.003 (SE) and the mean effect estimate for fragmentation was 0.06 ± 0.003 (SE). The mean effect estimate for edge effect among plants was -0.11 ± 0.006 (SE) and the mean effect estimate for fragmentation among plants was -0.14 ± 0.006 (SE).

We found a significant interaction between scale and latitude ($F_{3,120}$ = 4.14, p = 0.008; Figure 5). For studies in temperate regions, the mean effect estimate for edge effect was -0.03 ± 0.002 (SE) and the mean effect estimate for fragmentation was 0.003 ± 0.002 (SE). For studies in tropical regions, the mean effect estimate for edge effect was -0.22 ± 0.002 (SE) and the mean effect estimate for fragmentation was 0.04 ± 0.003 (SE).

Species abundance models

We expected a large proportion of individual species to show negative effects in the species abundance permutation analyses. With the abundance models, we found significant differences in the proportion of species in each category. However, the proportion of species that show significant negative effects of fragmentation *per se* on abundance distributions never exceeds 12% (Table 1). Most species (87%, n=1241) in studies with a negative edge effect and a non-significant fragmentation effect responded positively (Table 1). Of the significant negative edge effects, species most often had positive (47%, n=3483) or non-significant (43%, n=3483) responses (Table 1). Significant positive edge effects yielded similar results with 53% (n=2620) positive species responses and 47% nonsignificant species responses. Significant negative and positive fragmentation effects showed similar trends to the significant edge effects with the majority of species showing positive or non-significant responses to fragmentation. We do not see evidence of a preponderance of negative effects (as opposed to positive or non-significant effects) at either the patch or the landscape scale.

DISCUSSION

Our results do not support our predictions. Negative edge effects and fragmentation effects were not the most prevalent in our study landscapes. In both cases, nonsignificant responses to edges and fragmentation were more common than either negative or positive responses. We found no evidence that negative edge effects scale up to negative fragmentation effects, as only four out of 53 studies had both negative edge effects and negative fragmentation effects. Negative effects of fragmentation *per se* also do not predominate with species abundance permutations. Our abundance results show that species with significant negative responses were in the minority, indicating that individual species responses are not overwhelmingly negative. The Taxa Response Model indicated that declines in richness near habitat edges are more severe than responses to fragmentation *per se*, and the Latitudinal Gradient Model showed a stronger negative edge effect in the tropics than the temperate zones. Based on the analysis, there is no reason to think that using species richness as a response causes us to miss important species responses in these landscapes. We suggest that patch scale effects of fragmentation (edge effects) should not be extrapolated to landscape scale effects of fragmentation (fragmentation *per se* effects).

Previously, negative edge effects have been assumed to translate into negative fragmentation effects (Fletcher et al. 2018) and others have pointed out the lack of evidence to support this idea. Our results do not support the assumption that patch scale species responses to edges will translate to landscape scale fragmentation responses. Negative edge effects do not mean negative fragmentation effects. We therefore suggest that researchers should exercise caution when extrapolating patch scale studies to landscape scale effects in the future.

We found that neither negative edge effects nor fragmentation effects predominate. Most studies showed non-significant relationships between species richness and edge or fragmentation effects. Overall, our results align with the findings of Fahrig (2017) that >70% of responses to habitat fragmentation *per se* were non-significant. However, our results did not support the finding that most significant results were positive, as we found no difference in the proportion of significant positive and negative results at either scale (Fahrig 2017). Our abundance results show that species with significant negative responses were in the minority, indicating that individual species responses are not overwhelmingly negative. Furthermore, our species abundance results supported our findings from the species richness analyses. These results stand in contrast to the results of a study on island butterfly assemblages which found that species abundance was a better predictor of species response than species richness (MacDonald et al. 2021).

Fahrig (2017) offers some possible explanations for varying species responses to habitat fragmentation such as increased functional connectivity, habitat diversity, positive edge effects, stability of predator–prey/host–parasitoid systems, reduced competition, spreading of risk, and landscape complementation. The most common explanation for positive responses to fragmentation is increased functional connectivity (Fahrig 2017). More fragmented landscapes often have a higher number of small patches with smaller distances between them, thereby increasing patch encounter rate and leading to higher patch immigration and reduced emigration from the landscape (Ricketts 2001; Santos-Barrera & Urbina-Cardona 2011). Theoretical studies support the idea that a positive effect of habitat patchiness facilitates movement success (Bowman et al. 2002; Saura et al. 2014). Positive edge effects may also influence species relationships to fragmentation. Edges can be high quality habitats for many species and may

offer higher forage ability and refuge from predation than habitat interiors (Klingbeil & Willig 2009). A study located in lowland Amazonian rainforest found that bat abundance and richness were higher in moderately fragmentated forest than continuous forest (Klingbeil & Willig 2009). Authors suggest that edges are more productive and offer higher forage ability and refuge from predation than forest interiors (Klingbeil & Willig 2009). Reduced intra- and interspecific competition has also been discussed as a possible explanation for positive effects of fragmentation (Fahrig 2017). A study of gray-tailed voles (*Microtus canicaudus*) in artificially fragmented habitat in the Pacific Northwest suggest that fragmentation allows for better defense of territories for small mammals and that patch edges are used by species as territory boundaries (Wolff et al. 1997). Multiple mechanisms may also be interacting to result in positive or variable responses to fragmentation *per se* (Prevedello et al. 2016). We suggest that the explanations for positive effects of fragmentation could be at work in our studies as well, but result in a mostly nonsignificant effect of fragmentation in these landscapes.

The significant interaction of taxa and scale indicates that the effect of scale on effect size varies by taxonomic group. Declines in richness near habitat edges tend to be more severe than responses to fragmentation *per se*, which generally vary from weakly negative to positive. The exception was plants, which showed negative responses to both edges and fragmentation. Plants show a small difference in effect size between the local and landscape scale. A study in deciduous forest patches in Germany determined that plants with limited dispersal are likely to be adversely affected by fragmentation (Kolb & Diekmann 2005). Plants may be the most dispersal limited group as they often rely on external biotic and abiotic sources for dispersal. Another study examining plant species richness across multiple spatial scales in mountain landscapes in China found that species richness varies by scale and dispersal mode (Li et al.

19

2020). Plants in this study responded positively to local scale variables, they responded negatively at the landscape scale (Li et al. 2020). Additionally, landscapes with less vegetation (shrubs and bare land) negatively affect the migration, colonization, and species richness of plant species with biotic and abiotic dispersal methods (Li et al. 2020). Plant species may therefore show distinct and complex response patterns to a variety of environmental gradients occurring at different spatial scales.

The significant interaction of latitude and scale indicates that the effect of scale on species response is not the same across high and low latitudes. The results of our study suggest that species in the tropics experience much stronger negative edge effects than species in temperate zones. This is in agreement with previous literature which suggests that the effects of edges can be variable, with species in the tropics experiencing more negative edge effects than those in temperate zones (Betts et al. 2019). Temperate species may be more adaptable to a wide variety of environmental conditions, while species in the tropics may not have such tolerance for great extremes due to their narrower niche requirements (Granot & Belmaker 2020). Additionally, species at both temperate and tropical latitudes demonstrate negative responses to edges but positive responses to fragmentation *per se*. However, species in the tropics had stronger negative responses to edges and stronger positive responses to fragmentation than species in temperate zones. Our results support those of Fahrig (2017) which found overwhelmingly positive effects of fragmentation *per se* on tropical and subtropical species.

Assumptions and limitations

There are several factors that limit the inferences that can be made regarding the effect of edges vs. fragmentation on species in this study. First, we acknowledge that we used forest cover as a proxy for forest habitat, but habitat is a multidimensional description of the abiotic and

biotic requirements of a species to maintain fitness. Equating land cover with habitat may therefore be an oversimplification. However, due to the nature of the species data and land cover dataset, we were unable to determine the preferred habitat for these species and compare it to the land cover accurately. Secondly, we used a 1 km buffer size for all studies regardless of taxonomic group or scale of the study. We recognize that ideal buffer may vary by taxonomic group or species, but because of the nature of the database, data to determine dispersal ability for the taxa and landscapes in our study do not exist. Additionally, the sample size for herps (n=7), mammals (n=7), and plants (n=8) are relatively small for the fragmentation *per se* analysis. Thus, the meta-analysis Scale Dependent Taxa Response Model may need to be interpreted with caution. However, we deemed it necessary to remove studies with potential collinearity from the fragmentation *per se* analysis so as not to confound the data (Hair et al. 2009). We also made no effort to filter out non-forest species from our final analyses, so there may be some non-forest species in analysis. Removing non-forest species was not possible to do for all studies because of limited species information or varying data collection and entry methods between studies.

CONCLUSION

In this paper we present evidence to support the idea that negative edge effects at the patch scale do not reliably translate to negative fragmentation effects at the landscape scale. In addition, negative edge effects and fragmentation effects were not the most prevalent in our study landscapes. Nonsignificant responses to edges and fragmentation were more common than either negative or positive responses. Additionally, we found that negative effects of fragmentation *per se* also do not predominate with species abundance permutations. In fact, species with significant negative responses were in the minority, indicating that individual species responses are not overwhelmingly negative. Overall, we suggest that patch scale effects

of fragmentation (edge effects) should not be extrapolated to landscape scale effects of fragmentation (fragmentation *per se* effects). Contrary to much of the edge and fragmentation literature, species responses are overwhelmingly nonsignificant and individual species responses do not show a variation from this trend. Based on the results of our study, we suggest that future research take into account the scale at which a study is conducted and advise against untested extrapolation across scales.

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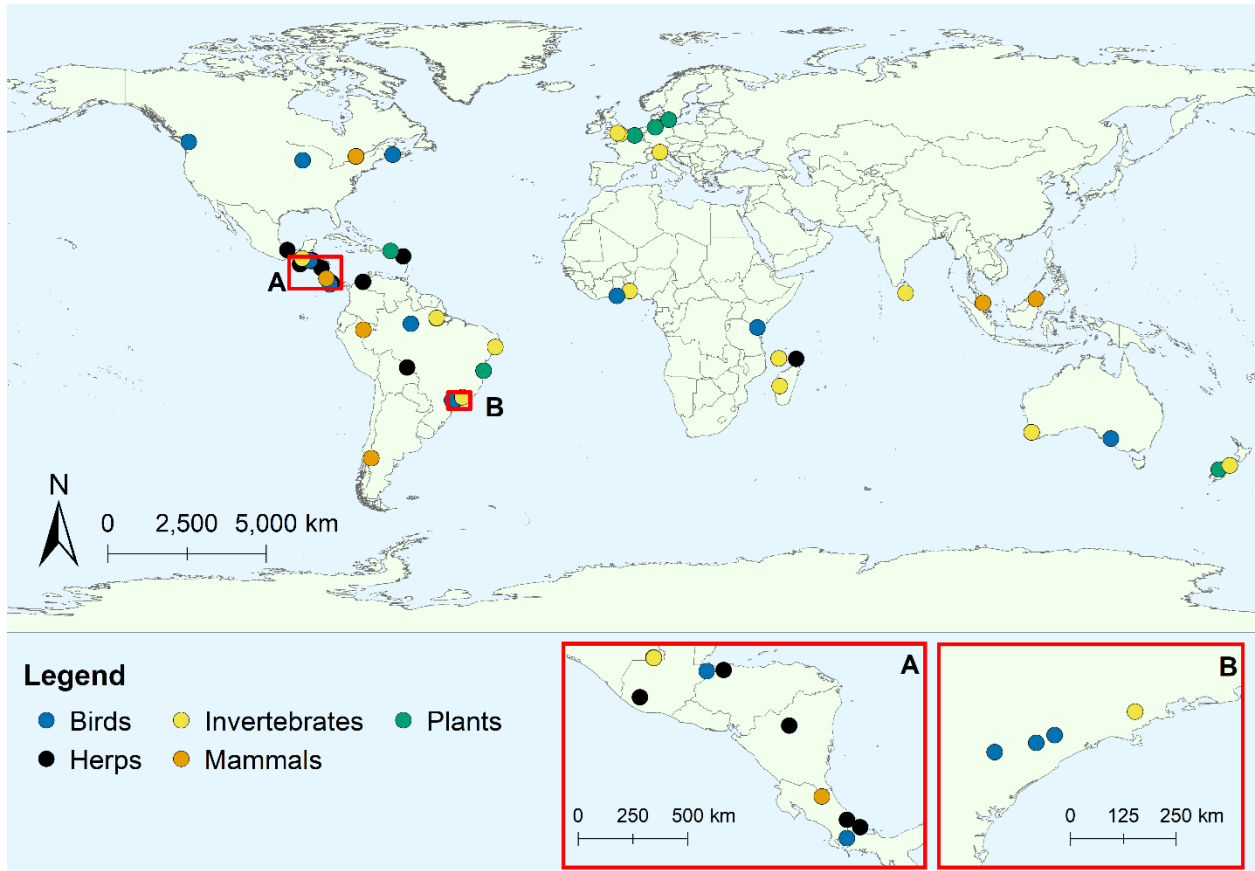
Appendix

Figure 1. Map of 71 studies used in data analysis with colors indicating different taxa examined at each location. Inset maps are included to show detail of studies that are close in proximity to each other.
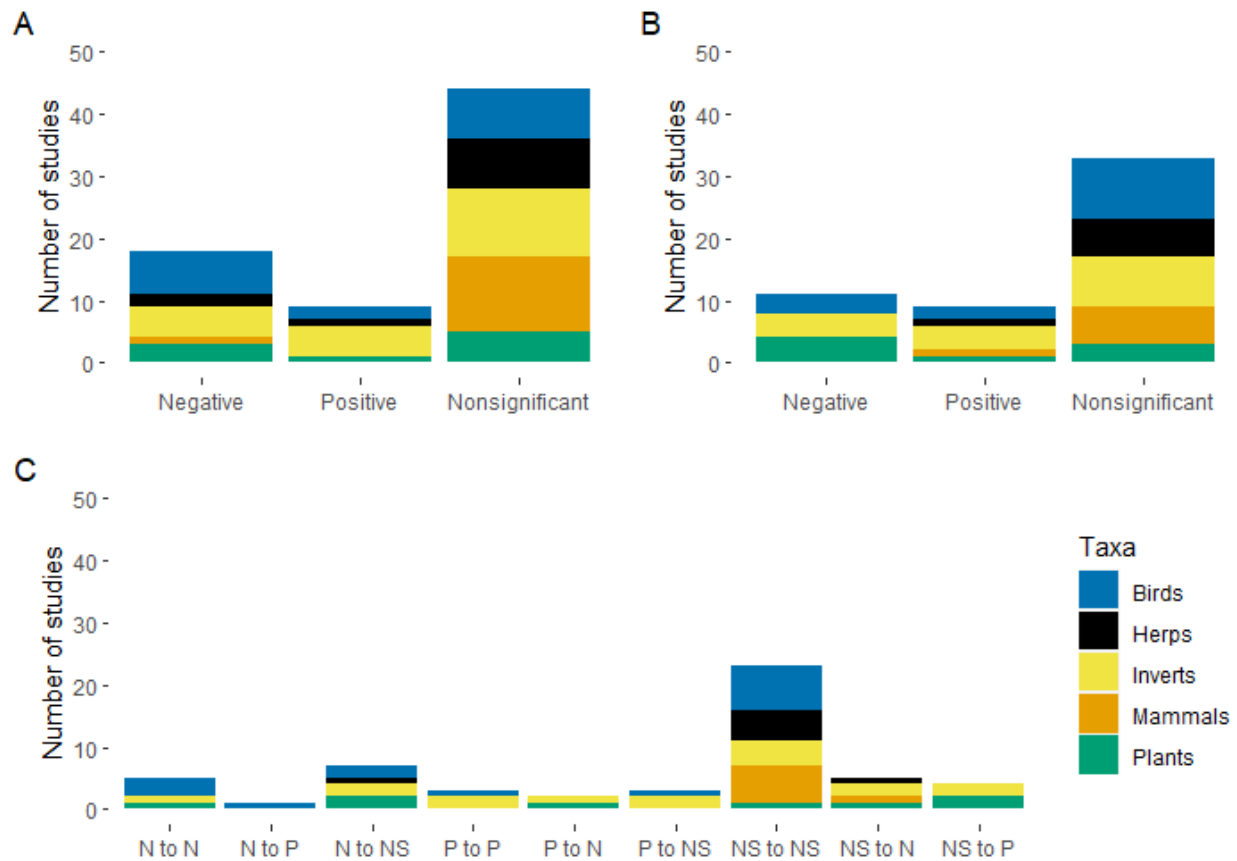
Figure 2. Vote counting data. Colors indicate the breakdown of different taxa within each group. A. Count data for the number of studies which had negative, positive, and nonsignificant edge effects. B. Count data for the number of studies which had negative, positive, and nonsignificant fragmentation effects. C. Count data for the change of studies between edge effect and fragmentation effect analyses. Groups are N to N (negative edge effects to negative fragmentation effects), N to P (negative edge effects to positive fragmentation effects), N to NS (negative edge effects to nonsignificant fragmentation effects), P to P (positive edge effects to positive fragmentation effects), P to N (positive edge effects to negative fragmentation effects, P to NS (positive edge effects to nonsignificant fragmentation effects), NS to NS (nonsignificant edge effects to nonsignificant fragmentation effects), NS to N (nonsignificant edge effects to negative fragmentation effects), and NS to P (nonsignificant edge effects to positive fragmentation effects).
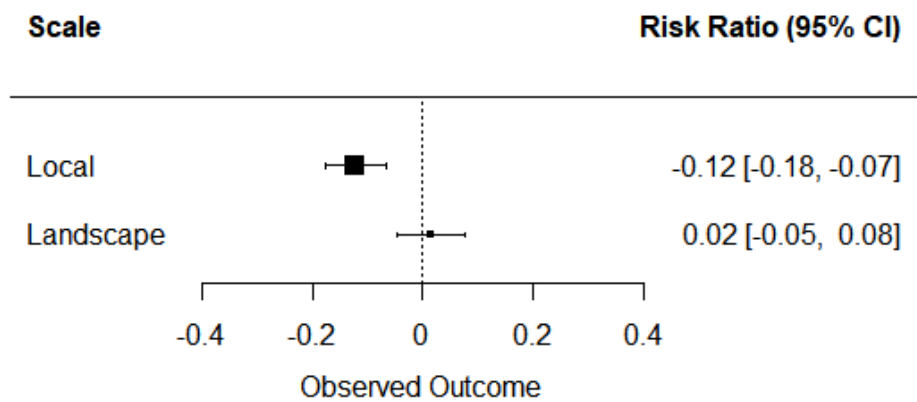
Figure 3. Forest plot of the Local vs. Landscape Model showing calculated effect size across local and landscape scales.
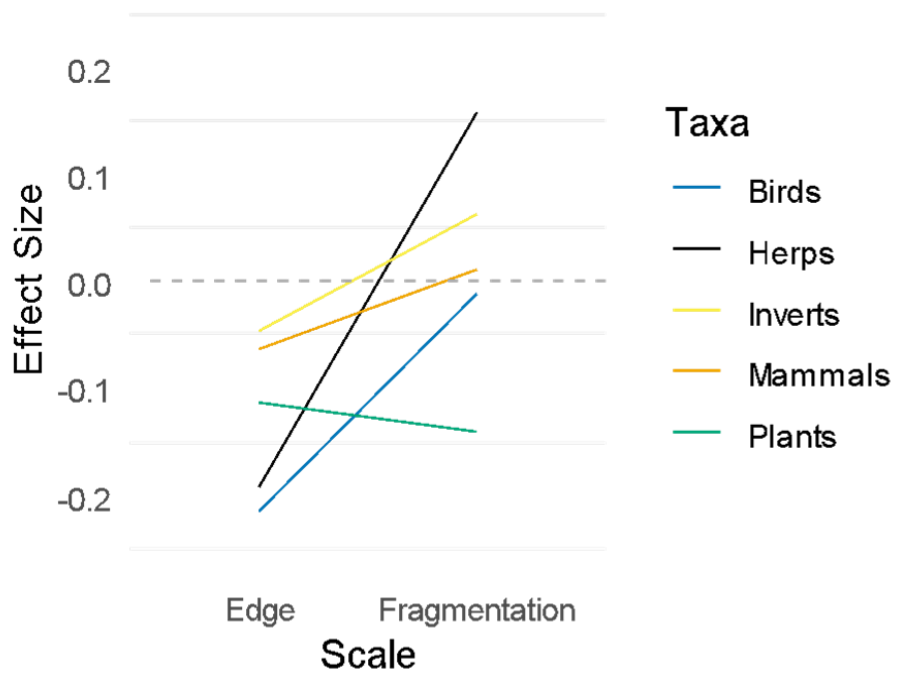
Figure 4. Interaction plot of the Scale Dependent Taxa Response Model.
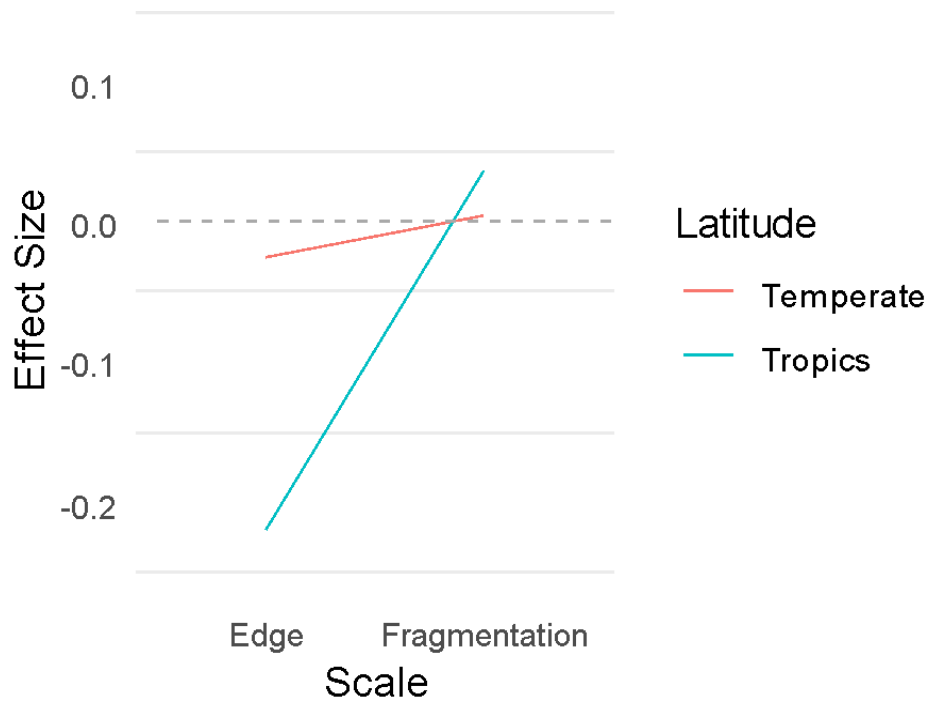
Figure 5. Interaction plot of the Latitudinal Gradient model.

Table 1. Count data of the number of species with negative, positive, or nonsignificant relationships to edge effect or fragmentation effect using abundance permutation models. Groups are split into overall (studies that switched from negative edge effects to non-significant fragmentation effects), negative and positive effect size using edge effect, negative and positive effect size using fragmentation effect, significant negative and positive effect size using edge effect, and significant negative and positive effect size using fragmentation effect. Asterisks indicate significance of the overall effect size in each column. Z-test results comparing each relationship indicated significant differences between each relationship across the board.

Relationship	Overall	Edge Effect		Fragmentation Effect		Significant Edge Effect		Significant Fragmentation Effect	
	Negative to NS*	N Effect Size*	P Effect Size*	N Effect Size*	P Effect Size*	N Effect Size*	P Effect Size*	N Effect Size*	P Effect Size*
N	31	375	3	322	56	349	1	319	31
P	1075	1924	1396	1597	1723	1633	1382	1569	1446
NS	135	2150	1771	1320	2601	1501	1237	944	1794
Total species	1241	4449	3170	3239	4380	3483	2620	2832	3271

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