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Geometric effects of fragmentation are likely to mitigate diversity loss following habitat destruction in real-world landscapes

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Abstract

Aim: Habitat conversion is the number one threat to biodiversity. The loss of biodiversity due to habitat loss might be exacerbated if species are harmed by fragmentation per se—the breaking apart of natural habitat that remains (hereafter *fragmentation*). However, the evidence that species are harmed by habitat fragmentation is mixed. Studies at the patch scale tend to show that fragmentation reduces diversity due to negative demographic effects on species' dispersal, survival and fecundity. In contrast, studies at the landscape scale tend to show that fragmentation increases diversity. This discrepancy may be partly due to geometric effects, defined as greater species turnover between patches in more fragmented landscapes. Although these effects have been demonstrated theoretically and are expected to be stronger across larger spatial extents, it is unclear whether they are likely to occur in real-world settings with both realistic landscape patterns and communities. Here, we investigated the possibility of geometric effects using simulations combined with real-world landscape and community data.

Location: New Jersey, northeastern USA.

Time period: Current.

Taxa studied: Bees.

Methods: We focused on landscape sizes within the typical range for protected areas (36–576 ha), simulated forest loss using real landscape patterns, and simulated forest-bee communities based on field data we collected.

Results: We found weak but positive effects of fragmentation: immediately following forest destruction, the most fragmented forests harboured up to 7.3% more species than the least fragmented forests of the same area, in agreement with observational studies of biodiversity along fragmentation gradients. In contrast to expectations, however, the overall effects of fragmentation did not change with spatial extent.

Conclusions: Our results suggest that fragmentation can mitigate biodiversity loss immediately following habitat destruction, but that the benefits do not vary strongly with spatial extent in real-world landscapes and at extents relevant to land management.

KEYWORDS
deforestation, edge density, forest patch, fragmentation, geometric effects, habitat amount, habitat configuration, habitat loss, land-use change, SLOSS

1 | INTRODUCTION

The conversion of Earth's natural habitats to human use is the largest threat to biodiversity: as the area of forests, wetlands, and grasslands disappears, so do the individuals and species that depend on these habitats (Julliard et al., 2003; Kattan et al., 2003; Newbold et al., 2015; Sala et al., 2000; Sodhi et al., 2004). However, these losses may be mediated by the spatial pattern of remaining habitat. For example, the effects of forest loss might differ if the remaining forest is scattered in pieces versus being left in one piece. This process of breaking a fixed area of habitat into pieces is called fragmentation per se and is distinct from the process of habitat loss (Fahrig, 2003, 2017). It has long been recognized that fragmentation per se (hereafter, *fragmentation*) can potentially affect biodiversity independently of habitat area (Fahrig, 2019). However, there has been a long-standing debate about the strength and direction of its effects, that is, whether fragmentation exacerbates biodiversity loss following habitat destruction (Chase et al., 2020; Fletcher et al., 2018; Haddad et al., 2017; Hanski, 2015), mitigates it (Collinge & Forman, 1998; Fahrig, 2003, 2019; Riva & Fahrig, 2023), or has no effect whatsoever (Watling et al., 2020).

Much of this debate has centred on the long-term, demographic effects of fragmentation (sensu May et al., 2019), with researchers asking whether populations in more fragmented habitats have lower rates of survival, fecundity, dispersal, and demographic rescue. Evidence from patch-scale studies suggests that they do (Cook et al., 2005; Townsend & Levey, 2005), with some studies suggesting the negative effects are exacerbated over time (Haddad et al., 2017). Conversely, studies at the landscape scale find that fragmented landscapes usually have as many or more species than continuous landscapes with the same total area of habitat (Fahrig, 2013, 2017; Riva & Fahrig, 2023; Watling et al., 2020), with no evidence that the effects of fragmentation become exacerbated over time (Fahrig, 2020). These studies suggest that the net effect of habitat fragmentation in natural systems is to mitigate species loss. One explanation for these discrepancies could be that, in landscape-scale studies, generalist or disturbance-tolerant species replace specialist, disturbance-sensitive species (Mckinney & Lockwood, 1999; Vellend, 2017), causing an increase or no net change in biodiversity with fragmentation. However, landscape-scale studies of habitat specialists also consistently find positive or neutral effects of fragmentation on biodiversity, suggesting that the replacement of specialists with generalists cannot entirely explain the observed patterns (Fahrig, 2020; Watling et al., 2020).

Another way fragmentation could mitigate biodiversity loss at the landscape scale is through 'geometric effects' that result from the combined spatial patterns of habitat loss and species distributions (Kobayashi, 1985; May et al., 2019; Rosenzweig, 1995). Most populations have aggregated spatial distributions due to variability in habitat quality and because of neutral processes, such as dispersal limitation, in homogenous environments (Chave et al., 2002). As a result, habitat patches that are more evenly spaced across the landscape are more likely to harbour individuals of different species, even for a single habitat type (Fahrig et al., 2022). Because a greater number of habitat patches will tend to more evenly sample a landscape, more fragmented landscapes will have greater species turnover across remaining patches, resulting in more species preserved across the entire landscape (Chisholm et al., 2018; Kobayashi, 1985; Lasky & Keitt, 2013; May et al., 2019; Quinn & Harrison, 1988; Tscharntke et al., 2002). Such positive geometric effects of fragmentation would affect generalists and specialists alike and could mitigate the number of species lost immediately following habitat destruction. Furthermore, because geometric effects are inherently a landscape-scale process (Fahrig, 2003; McGarigal & Cushman, 2002) they could also help explain why landscape-scale studies find positive effects of fragmentation on biodiversity (Collinge & Forman, 1998; Fahrig, 2017) but patch-scale studies find negative effects (Haddad et al., 2015).

Even at the landscape scale, theory suggests that the strength of geometric effects of fragmentation depends on spatial extent, in particular, the spatial extent of habitat loss relative to the extent of population aggregations (Chisholm et al., 2018; Fletcher et al., 2023; May et al., 2019; Rosenzweig, 1995). This can matter because, at spatial extents larger than the level of population aggregations, there will be greater species turnover across the focal landscape. As a result, fragmentation across large extents should reduce species loss because such spatial patterns increase the chance that distant patches will contain different species, as discussed above (Chisholm et al., 2018; May et al., 2019). At the largest extents (e.g. an entire continent), there can be complete turnover among the most distant patches (Chisholm et al., 2018), although this is unlikely to occur at the scales at which real-world conservation decisions are typically made (e.g. most protected areas are <1000 ha; Volenec & Dobson, 2019). In contrast, fragmentation is expected to have no geometric effects or even negative geometric effects on biodiversity when the spatial extent is small relative to the level of species aggregations, in which individuals will be more randomly or regularly spaced (May et al., 2019). In studies that focus on larger spatial extents, it may therefore be more likely that any negative demographic effects of fragmentation will be offset by positive geometric effects that are not detectable at smaller spatial extents (Chase et al., 2020; May et al., 2019).

Despite these theoretical predictions, it is unclear what geometric effects to expect in real-world landscapes. The theoretical work assumes habitat patches to be uniform in size and shape (Chisholm et al., 2018; Deane et al., 2022), and it is unclear how more realistic distributions in patch size and shape affect the strength of geometric effects. Real-world geometric effects will also depend on the degree and pattern of fragmentation that occur in real-world systems, and on the spatial extent of habitat loss relative to that of species turnover. Thus, while it is clear from theory that geometric effects can occur, their ability to explain observed relationships between fragmentation and biodiversity, as well as their relevance to conservation policy, is yet unknown. To clarify these issues, it is therefore important to assess the strength and sign of geometric effects in realistic communities and landscapes, with relevant levels of population aggregation, habitat loss, and fragmentation.

Here, we investigate the geometric effects of fragmentation on biodiversity across a range of scales relevant to real-world land managers. To that end, we used spatially explicit simulations based on real-world bee communities and land cover in the northeastern USA. We focused on mixed deciduous forests and native, forest-specialist bees. To ensure the realism of our simulations of habitat and diversity loss, we used actual landscape patterns drawn from across the northeastern USA, and patterns of diversity that matched what we find in nature for forest-specialist bee species (Smith et al., 2021). We aimed to answer the following questions: (i) What are the expected geometric effects of fragmentation on forest bee diversity across the empirical range of forest fragmentation patterns found in the northeastern United States? And (ii) How do these geometric effects change with spatial extent? Across the empirical range of fragmentation patterns found in the northeastern USA, we find that more fragmented landscapes harbour up to 7.3% more species following forest loss, suggesting positive geometric effects of fragmentation. However, in contrast to theoretical predictions, we found no change in the strength of the effect with spatial extent.

2 | METHODS

Our analysis combined real-world data with simulations, as follows. First, we used GIS to sample real-world forests of the northeastern United States. We selected the most and least fragmented forest landscapes in the region across different levels of forest loss (Section 2.1). Then we simulated forest-specialist bee communities in fully forested landscapes, with parameters based on real-world bee communities (Sections 2.2 and 2.3). Finally, we simulated forest loss by superimposing the real-world, deforested landscapes onto our simulated bee communities, and only retaining bees that remained in forest habitat (Section 2.4). We assessed the effects of fragmentation by comparing the remaining bee communities among habitats with different levels of fragmentation for a given area of forest loss, and when measured at different spatial extents (Sections 2.4 and 2.5).

2.1 | Selecting real-world forest sites

To realistically simulate forest loss, we selected 450 real-world landscapes from the northeastern USA. To test for geometric effects of fragmentation, and whether the strength of those effects depends on the intensity of forest loss, we selected landscapes that varied independently in percent forest area and fragmentation. Further, to test whether the strength of geometric effects depends on the spatial scale of study, we selected landscapes that varied in their spatial extent. In each landscape, we measured percent forest area as percentage forest cover within the landscape, and measured fragmentation as forest edge density in the landscape—that is, the length of forest edge per unit area—while controlling for percent forest area. Although edge density is typically highly correlated with percent forest area, controlling for percent forest area makes edge density an appropriate proxy for fragmentation per se (Fahrig, 2017).

To locate our landscapes and ensure they were representative of real-world fragmentation patterns, we surveyed forests across the northeastern USA. First, we used R to generate an array of 18,580 points (hereafter, *sites*) on a 5 km grid across the states of Maine, Vermont, New Hampshire, Massachusetts, Rhode Island, Connecticut, New York, Pennsylvania, New Jersey, Delaware, and Maryland. Around each site, we measured percent forest area and forest edge density within five square, concentric buffers with areas 36, 174, 302, 441, and 576 ha. Each buffer represents a landscape size, or study extent. We chose these sizes because of computational feasibility and because they are within the range of typical sizes for protected areas (e.g. 78% of all global protected areas are between 1 and 1000 ha in size; Volenec & Dobson, 2019). This yielded a total of 92,750 potential study landscapes (18,580 sites × 5 landscapes/site).

To measure the percent forest area and edge density in each of these landscapes, we used the 2016 USGS National Land Cover Database (United States Geological Survey [USGS], 2016). Landcover in this database is classified to 20 classes at 30 × 30 m resolution. For the sake of simplicity, we aggregated these data into four classes: forest, matrix, wetland, and water. The forest category included all deciduous, coniferous and mixed forest, as well as wooded wetlands; the wetland category was reserved for emergent herbaceous wetlands; water included all open water (fresh or saline); and the matrix category included everything else (mean 51.7% agriculture, 38.0% developed, and 10.3% shrub-, herbaceous- and barren-land). We then measured the percent cover of each of these classes in each of the 92,750 landscapes.

Before going further, we excluded landscapes whose measurements might not be representative of anthropogenic forest loss or fragmentation. Specifically, we removed landscapes covered by more than 5% (combined) water and wetland, because these are natural features of the landscape that can affect forest edge density measurements. We also excluded landscapes that overlapped the edge of the land cover data and thus partially lacked land cover data. To keep the sample size consistent between the five spatial scales, when we excluded a landscape at one scale, we also excluded corresponding landscapes at the other scales. After this filtering step, there were 72,405 landscapes totally, with 14,481 landscapes at each of the five spatial scales.

Finally, to select study landscapes, we measured percent forest area and edge density in each of these 72,405 landscapes. We measured percent forest area as the percentage of forested land after excluding water and wetland. We measured forest edge density as the length of forest edge that borders matrix habitat, divided by landscape area (such that edge density has units of m per ha). Across all study sites, edge density follows a quadratic relationship with percent forest area, where landscapes with 0% or 100% forest have no edge, and landscapes with 50% forest tend to have the most edge. To control for this relationship while also testing for an effect of habitat area, we filtered our pool of potential sites to only those with 10%, 30%, or 50% forest (±2.5 percentage points). Then, among landscapes within these three groups, and at each spatial scale, we selected the 15 landscapes with the highest edge density (the most fragmented) and the 15 with the lowest edge density (the least fragmented; Figures 1 and 2). Thus, in total, our analysis uses 450 landscapes fully crossed between our three treatments: spatial scale (36, 174, 302, 441, and 576 ha), percent forest area (10%, 30%, and 50% forest remaining), and fragmentation (high- vs. low-edge density), with 15 replicates per combination of treatments. Landscapes were not randomly sampled, but instead selected for being the 15 most and least fragmented within each combination of landscape size and forest area.

2.2 | Bee community data used to parameterize model

To realistically simulate the effects of forest loss on forest-specialist bees, we needed to start with a realistic forest-bee community. To do so, we based our simulations on forest-bee communities we observed at 27 sites over 2 years in temperate deciduous forests in the Piedmont eco-region of New Jersey (Smith et al., 2021). We used only records of forest-specialist bees (habitat associations defined in Smith et al., 2021)—a total of 5083 individual bees of 31 species. We then used these observations across sites to estimate relevant parameters for our simulated bee community. Admittedly, these bee communities likely differ from those in conifer forests of northern New England. Our intention, however, is to match realistic forest-bee communities with realistic forest cover patterns, not explicitly link specific bee communities with specific forests.

To assess geometric effects of fragmentation, the relevant community parameters were local diversity (alpha diversity), which we measured as species richness, and species turnover (beta diversity), which we measured as the Jaccard dissimilarity. Alpha diversity represents the average number of species at each site, and thus the number of species available to be saved or lost at any given site. Beta diversity represents the average proportion of species that are not shared between pairs of sites, and thus determines the number of species lost when one site in a pair is lost, in our case due to deforestation.

Because our simulation starts with bee communities in completely forested landscapes (i.e. before any deforestation occurs), we estimated alpha and beta diversity for sites in completely forested landscapes (i.e. no deforestation or fragmentation). First, to estimate the alpha diversity of the forest-specialist bee communities sampled from completely forested landscapes, we used Poisson regression to model species richness of forest-specialist bees as a function of percent forest area (at a 500-m radius; Figure S1). We used this model to estimate the mean number of forest-specialist bee species sampled in landscapes with 100% forest area because only two sites in our data had that level of forest coverage (range 13% to 100% forest cover at

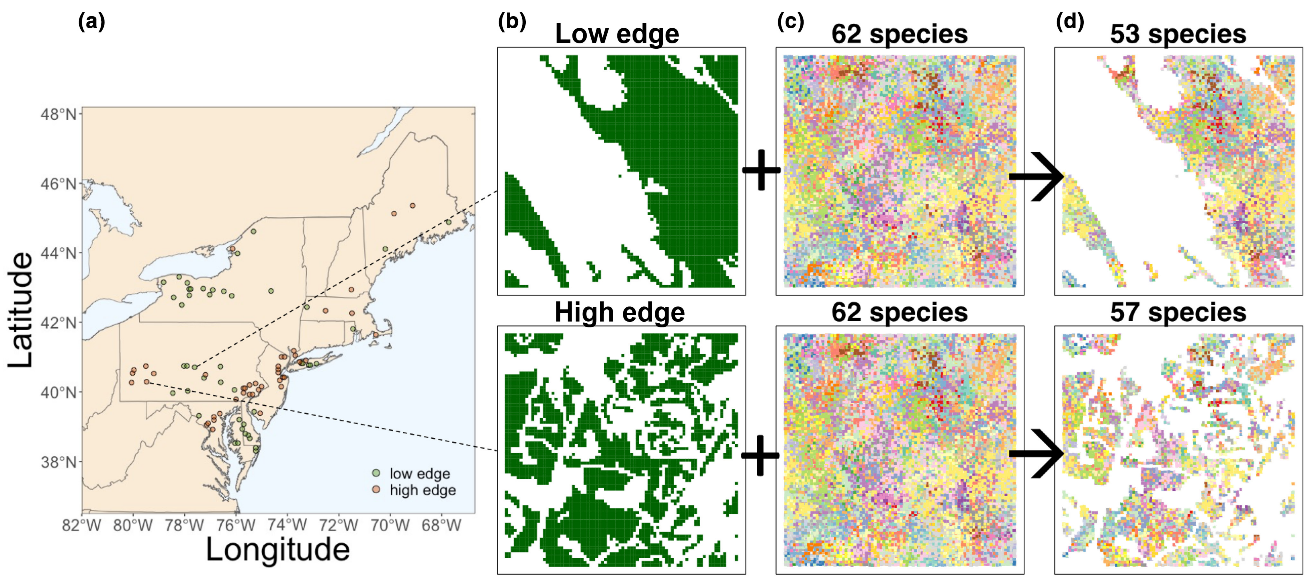

FIGURE 1 The map of the northeastern United States (a) shows the locations of the high- and low-edge forest landscapes that we used in the simulation of forest loss at the 576 ha spatial scale. The dotted lines connect two landscapes from this map to the corresponding, higher-resolution maps used in our simulations (column b), where forest habitat is represented by green and matrix habitat by white. We next simulated communities (column c) and matched them with the forest landscapes. Individuals residing in matrix habitat were removed (white spaces in the maps in column d) and the percentage of remaining species was calculated. In columns (c) and (d), the different colours represent individuals of different species and the titles of the graphs show how many species reside in the communities.

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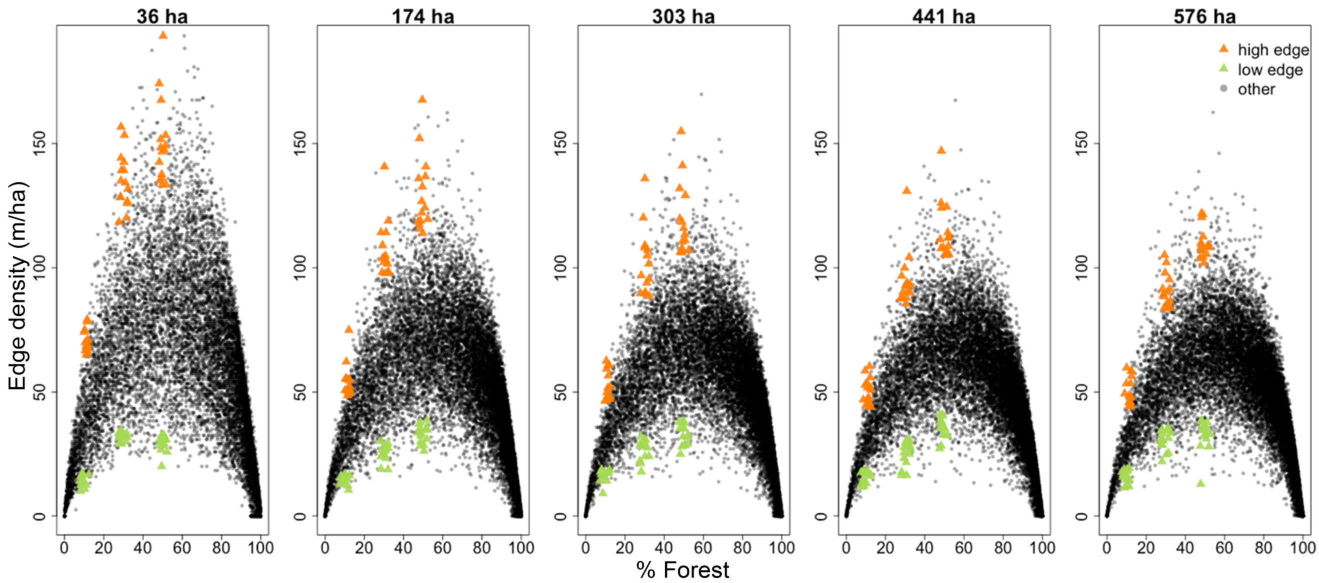

FIGURE 2 The relationship between the percentage of a landscape covered by forest and the density of forest edge habitat in that landscape, for $n = 14,481$ landscapes in the northeastern USA at five different spatial scales. On the figure, the green and orange triangles represent the high- and low-edge landscapes that we used in the simulation. All other landscapes are represented by black circles.

a 500-m radius). We measured variation around this prediction using Wald confidence intervals on the fitted function based on standard errors of the model coefficients. Next, to estimate beta diversity of forest-bee communities in completely forested landscapes, we measured pairwise Jaccard distance between communities of forest bees sampled from our most heavily forested sites (at least 80% forest area at a 500-m radius; $n = 13$ sites), then calculated the mean Jaccard distance across all pairs of sites. To measure variation around this value, we used the 10th and 90th quantiles of the distribution of pairwise Jaccard distance. We use mean pairwise Jaccard distance, rather than a measure accounting for geographic distance (e.g. the slope of the distance-decay curve) because the data showed a weak relationship with geographic distance (slope of distance-decay line on log–log scale = 0.02; adjusted $R^2 = 0.003$; Figure S2). The steps above provided us with estimates for the mean and variation of alpha and beta diversity, for forest-specialist bees inhabiting continuously forested landscapes. Additionally, we estimated our bee sample density at our study sites (i.e. bees caught per unit area; see Supporting Information) as a basis for our simulated communities (see Section 2.3 below).

2.3 | Simulating bee communities with a neutral model

Based on our empirically estimated parameters, we simulated bee communities inhabiting contiguous landscapes. To do so, we used a spatially explicit neutral model. In the model, individuals probabilistically survive and propagate, and diversity is generated and maintained through occasional (random) speciation. This type of simple model has a proven track record of recreating patterns of diversity observed in nature (Chave et al., 2002; Condit et al., 2002; Rosindell & Cornell, 2009).

Our simulated communities were spatially analogous to our real-world forested landscapes (Section 2.1). They occupied an 80 × 80 grid, with each grid cell defined as 30 m × 30 m (0.09 ha), to match the pixel size of our landcover data and the extent of our largest landscape (576 ha). To match our observed bee sample density, we fixed bee density to two individuals per grid cell (or 22 bees/ha; see Section 2.2 and Supporting Methods). Individuals on the edge of the grid were treated as if they were adjacent to individuals on the other side of the grid (i.e. periodic boundaries). For the smaller landscape sizes, we generated the community using the full 80 × 80 grid, then 'cut out' the smaller community from the centre (to reduce boundary effects).

The neutral model simulation proceeds as follows: to start, the grid is occupied entirely by individuals of one species. With each timestep, all individuals in the community die and are replaced by one of two options: (1) a new species enters the community (i.e. speciation occurs) with probability *v*; or (2) the individual is replaced by propagation and dispersal. This propagule, or offspring can arrive via long-range dispersal, by being drawn at random from anywhere within the community, with probability (1-*v*) • *l*, or via short-range dispersal, by being drawn at random from within the focal cell or its eight nearest neighbours, with probability (1-*v*) • (1-*l*). The speciation rate, *v*, determines the equilibrium species richness of a simulated community (Rosindell et al., 2011). The long-range dispersal rate, *l*, governs species turnover because, when individuals are more likely to disperse locally, populations remain more aggregated. We ran each simulation for 100,000 timesteps, which was enough time to reach an equilibrium with respect to species richness and turnover (Figures S3 and S4).

To determine the appropriate range of speciation and long-distance dispersal rates, we explored the parameter space of the neutral model and picked the range of values that recreated patterns of alpha diversity and species turnover in the observed data. To do so, we first used a trial-and-error approach to find a range of parameter values where diversity matched between the simulated communities and the observed bee data. We then systematically varied the model parameters within this range to find a more precise range of values. Specifically, we varied the long-range dispersal rate between the values of 1×10^{-3} and 1.0 on a log scale in increments of 0.2, while keeping the value of the speciation rate constant ($v = 0.00032$). We also varied the speciation rate between the values of 4.65×10^{-5} and 7.67×10^{-4}, in increments of 1.8×10^{-3}, while keeping the long-range dispersal rate constant ($l = 1 \times 10^{-2.2}$).

To compare the simulated communities with our empirical bee data, we sampled our simulated communities in a way that mimicked our empirical dataset. We determined the sample size (as number of individual bees) by drawing randomly from a truncated-normal distribution fit to the empirical bee data, using the R package *truncnorm* (Mersmann et al., 2018). Rather than sample the whole community grid at random, we sampled 'sites' within the grid in the same way the real-world data sampled sites across a region. We thus drew random samples from within the smallest square whose size was greater than the number of individuals being sampled. For example, if the number of individuals being sampled was 20, we randomly drew from a 5×5 square of 25 cells (vs. a 4×4 square, which is <20). To estimate alpha diversity, we drew one sample from the centre of each grid and counted the number of species. To estimate beta diversity, we drew four samples from the centres of the four quadrants of each grid, then calculated mean pairwise Jaccard distance of these samples. We calculated the median richness and Jaccard distance of each parameter combination (with $n = 500$ replicates per parameter combination). We then estimated the relationship between the parameters and the diversity metrics by fitting best-fit lines to the subset of the data for which the modelled diversity estimates fell within the range of our empirical data. As expected, speciation was positively correlated with alpha diversity (sample species richness), and long-range dispersal was negatively correlated with beta diversity (Jaccard distance; Figure S5).

To pick the range of parameter values to use in our simulations, we solved for the parameter values for which the diversity measures were consistent with our bee data. That is, where the best-fit lines crossed the upper and lower intervals of the observed bee data. For each parameter, we then had two ranges of parameter values—one range for richness and one for Jaccard. We drew from the intersection of these two ranges in the final simulation: the speciation rates we used for the final simulations were drawn from a uniform distribution between 0.00028 and 0.00043 and the long-range dispersal rates used for the final simulations were drawn from a uniform distribution between $10^{-1.55}$ and $10^{-2.43}$.

2.4 | Simulation of forest loss

To simulate the effect of forest loss on bee communities, we first randomly matched each of the 450 forest landscapes selected from the northeastern USA (Section 2.1), with 100 simulated communities. We assumed that all the landscapes were originally completely forested unless there was a body of water or wetland in the landscape, in which case we left these natural features intact and assumed bees were absent in these areas because they are unsuitable for bee nesting. To simulate forest loss, we superimposed each forest landscape over the corresponding simulated community, and removed all individuals located within matrix habitat (Figure 1). Because we specifically modelled forest specialists (see Section 2.2 and Smith et al., 2021), we assumed that no individuals could reside in deforested, matrix habitats. Following this removal step, we counted the number of species remaining in the landscape. To assess the geometric effects of fragmentation, we compared the percent of remaining species between high- and low-edge forest landscapes for each level of percent forest area and each spatial scale.

2.5 | Measuring geometric effects of fragmentation and its interaction with spatial extent

We measured the geometric effect of fragmentation in two ways. First is the per-unit effect of fragmentation—that is, the unit change in biodiversity per unit change in fragmentation. In our analysis, we measure this as the slope of the relationship between edge density and percent species remaining after forest loss (assuming this relationship is approximately linear). A positive slope implies fewer species are lost in more fragmented landscapes. The second measure is the total realized effect of fragmentation. We measured this as the percentage point difference in species remaining between the highest and lowest edge landscapes. This outcome depends on both the per-unit effect, described above, and the range of variation in edge density between the most and least fragmented landscapes. It is important to consider both of these measures because they could yield different answers: if there is little variation in fragmentation of real-world landscapes, even a large per-unit effect could translate into a small realized effect. Conversely, if variation in fragmentation is large, then even a weak-per unit effect could have a large realized effect.

We estimated each of these effects and tested whether they varied under different contexts. Specifically, we estimated both per-unit and realized effects for each level of forest loss and landscape size, then assessed whether they changed with landscape size for a given forest amount.

2.6 | Software used

The neutral model simulation was written and run in Python (www.python.org). All other code was written and run in R (R Core Team, 2022). We used the package *landscapemetrics* (Hesselbarth et al., 2019) to measure forest edge density, and the packages *sf* (Pebesma, 2018) and *stars* (Pebesma, 2021) for other land cover measurements and GIS operations.

3 | RESULTS

To predict how habitat fragmentation affects forest bee diversity, we first characterized the patterns of forest fragmentation found in real-world landscapes. As expected (Gardner et al., 1987), the relationship between forest edge density and forest cover was approximately quadratic; across the 72,405 landscapes, we sampled in the northeastern USA, forest edge density varied between a minimum of 0 m/ha in completely forested and deforested landscapes to a maximum of 193.3 m/ha in landscapes with intermediate forest cover (Figure 2).

The range of forest fragmentation observed was also affected by spatial extent. Specifically, smaller landscapes varied more in forest edge density than larger ones (Figure 2). For example, in landscapes with 10% (±2.5%) forest habitat, forest edge density varied by a factor of 8 at the smallest extent (36 ha), but only varied by a factor of 5 at the largest extent (576 ha). We expect that this is a form of sampling effect, wherein larger samples (landscapes) are more similar and smaller samples (landscapes) are more likely to have extreme values.

3.1 | Expected geometric effects of forest fragmentation on forest bee diversity

For all three categories of forest cover (10%, 30%, and 50%), the percentage of species remaining after forest loss increased with forest edge density (Figure 3). However, while there was a significant per-unit effect of fragmentation (slopes in Figure 3), the realized effect of fragmentation was relatively weak. Specifically, the realized effect of fragmentation was that high-edge landscapes harboured between 3.4% and 7.3% more species than low-edge landscapes with a similar percentage of forest habitat (comparing start- and end-points of lines in Figure 3).

These positive geometric effects were strongest for landscapes with little (10% ± 2.5%) remaining forest (yellow lines and circles in Figures 3 and 4). High-edge landscapes in this category harboured, on average, 6.8% more species than low-edge landscapes following forest loss (Figure 3). These realized effects of fragmentation decreased with increasing forest cover: when approximately 30% of forest habitat remained, high-edge landscapes harboured 5.1% more species than low-edge ones; when approximately 50% of the forest habitat remained, they harboured only 3.8% more species than low-edge ones (Figure 3). Similarly, the per-unit effects of fragmentation also decreased with increasing forest cover (compare slopes of yellow vs. blue vs. green best-fit lines in Figure 3).

3.2 | Changes of geometric effects of fragmentation with spatial extent

For a given amount of forest cover, fragmentation had similar effects on biodiversity across landscape sizes. We did observe a small increase in the per-unit effect of fragmentation with landscape size, from an average of 0.07–0.11% of species saved per m/ha increase in edge (mean of slopes in Figure 3, represented in Figure 4, left panel). But these did not amount to changes in the realized effect of fragmentation as landscape size increased (right panel in Figure 4). At the smallest landscape size (36 ha), high-edge landscapes harboured an average of 5.1% more species than low-edge landscapes (averaged

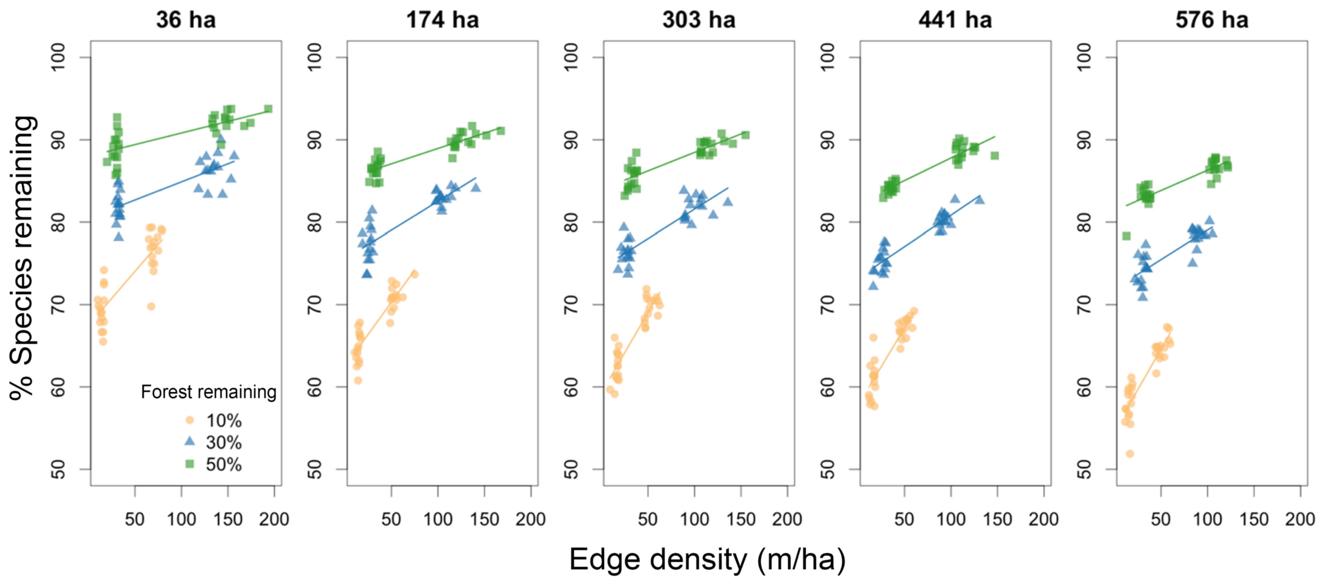

FIGURE 3 As the density of forest edge in a landscape increases, so does the median percentage of species that remain in that landscape immediately after forest loss. For a given level of forest loss, the per-unit effect of fragmentation was slightly greater in larger landscapes (slopes slightly increase from left to right, where panels show results for landscapes of increasing size). The absolute effect of edge density, however, remains similar across scales. This is because the range of observed edge densities decreases with landscape size (such that the lines become steeper but shorter, and as a result the vertical increase does not change).

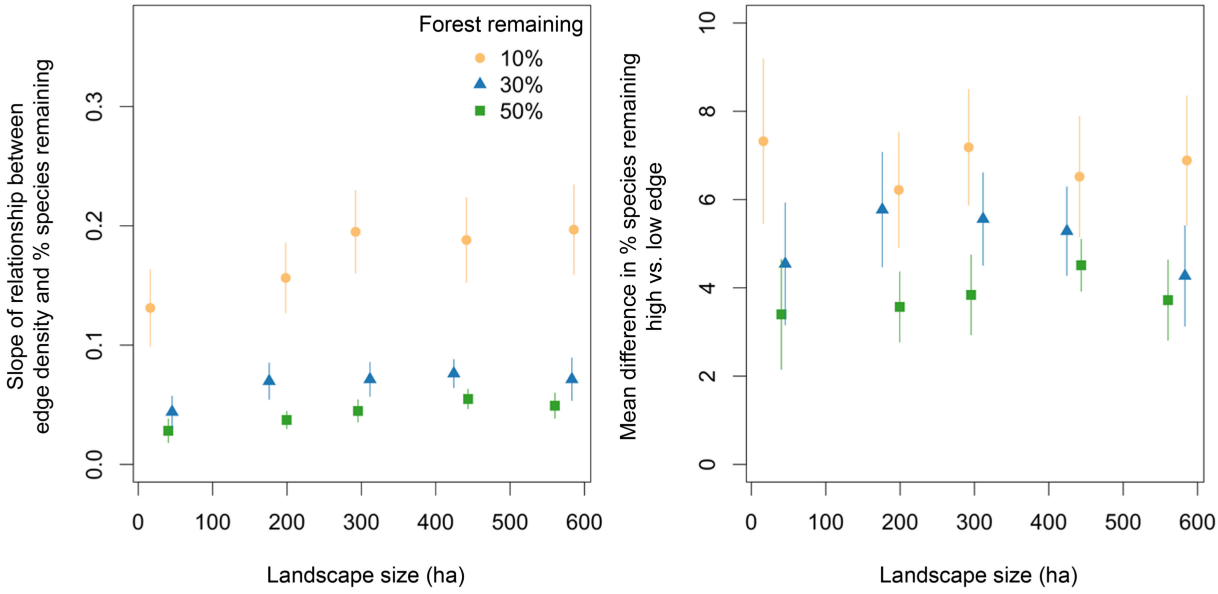

FIGURE 4 The relationship between landscape size and the strength of the effect of edge density on biodiversity. The effect of edge density is defined two ways: first as the slope of the relationship between edge density and the percentage of species remaining, for a given category of percent forest (left graph; corresponds to the slopes of the lines in Figure 3); and second as the mean difference between high and low-edge landscape categories in the percentage of species remaining after forest loss (right graph; corresponds to the vertical increase of the lines in Figure 3). This second measure depends, in part, on the empirical range of variation remaining in the real-world landscapes used in our analysis, and thus provides stronger scope of inference for how geometric effects might operate in the real world. The lines show the confidence intervals around the estimates, and a random jitter was added to the x-axis to allow overlapping points and lines to be seen.

across percent forest cover categories). Similarly, at the largest landscape size (576 ha), high-edge landscapes harboured an average of 5.0% more species.

Because geometric effects depend on community evenness (Deane et al., 2022), we conducted a post-hoc test to ask how the evenness of the simulated communities varied with spatial extent. We measured evenness using Pielou's J, which measures a community's evenness relative to the range of possible evenness values for a given number of species (Jost, 2010). Our communities were less even (i.e. more skewed) at large spatial extents (Figure S6), which may partially explain the greater per-unit effect of fragmentation observed at larger extents (Deane et al., 2022).

4 | DISCUSSION

Here we show that in realistic landscapes and communities, fragmentation can mitigate the biodiversity loss that results from habitat conversion. With our data-informed simulations, we found that the most fragmented forest landscapes in the northeastern USA could harbour 3.4%–7.3% more forest bee species than the least fragmented forest landscapes. This positive effect of fragmentation on remaining biodiversity occurred across multiple spatial scales and increased in magnitude as habitat loss became more severe (Figure 3). These effect sizes are also consistent with previous theoretical predictions (Deane, 2022). Thus, our results demonstrate that the geometric effects of habitat fragmentation, while modest in magnitude, are likely to be positive in real-world landscapes.

Our results build on those of two previous bodies of research that suggest the possibility of positive effects of fragmentation on biodiversity. First, modelling studies suggest that more species or individuals can be conserved after habitat loss in more fragmented landscapes, with results that depend on the pattern of fragmentation and the spatial arrangements of the individuals living in the community (Chisholm et al., 2018; Deane, 2022; Kobayashi, 1985; Lasky & Keitt, 2013; May et al., 2019). Here, we show that these positive effects of fragmentation are also seen—with similar effect sizes—when using real-world landscape patterns and model parameterizations informed by data from real-world communities of forest-specialist species. Second, studies of island biogeography and reserve design have found that several small islands or reserves tend to harbour more species than a single large one of equal area (i.e. 'SLOSS' studies; Quinn & Harrison, 1988; Simberloff & Abele, 1976, 1982). Here, we demonstrate that positive geometric effects of fragmentation can occur due solely to the aggregated arrangement of individuals within the landscape. While such an aggregated distribution can occur because of environmental heterogeneity, it can also occur through purely neutral processes (Rosindell et al., 2011). That is, geometric effects of fragmentation do not rely on habitat heterogeneity.

We found that the per-unit effect of fragmentation increased with the spatial extent of study. That is, the change in percent species remaining per unit change in edge density is greater in larger landscapes than in smaller landscapes (slopes in Figures 3 and 4 left panel). This is consistent with previous, simulation-based work showing the effect of fragmentation to increase with spatial extent from local to continental scales (Chisholm et al., 2018). Here, we confirmed this hypothesis at smaller, conservation-relevant scales and with fragmentation patterns from real-world landscapes. We expect this result is caused by greater species turnover across larger landscapes than smaller ones, and by our communities having more skewed species abundance distributions in larger landscapes (Figure S6; Deane et al., 2022).

In contrast to the per-unit effect, the realized effect of fragmentation on biodiversity was similar across landscape sizes (Figure 4, right panel). This may be because, in our data, species turnover among communities did not show a strong relationship with geographic distance (Figure S2), and an interesting avenue for future research would be to investigate whether this pattern holds in communities with higher beta diversity. Additionally, smaller landscapes showed a higher variability in edge density than larger landscapes. This is apparent in Figures 2 and 3, where the range of fragmentation values becomes smaller as landscape size increases (i.e. moving left to right across the graphs). As a result, the percentage of species remaining changes more steeply but within a shorter range of edge densities (i.e. steeper slope but shorter horizontal range) in larger landscapes. Consequently, the realized effect of fragmentation (i.e. vertical change in Figure 3) is similar across landscape sizes. The pattern that larger landscapes have a smaller range of habitat configurations would not show up in previous work that used simulated rather than empirical habitat configurations (Chisholm et al., 2018). Thus, our result suggests that while spatial extent has at least some potential to modulate the effect of fragmentation, this potential may not be realized in real-world landscapes at the spatial extents most relevant to conservation decisions. We may thus expect that the effects of fragmentation may generally be similar across large and small landscapes, at least at management-relevant scales and for real-world fragmentation patterns.

In considering how the effects of fragmentation play out in real life, it is worth bearing in mind the assumptions and limitations of our approach. First, in our simulation, habitat loss is instantaneous, and it is unclear how incremental habitat loss might further mitigate or exacerbate diversity loss. Second, although our neutral model accurately recreated patterns of diversity for forest bees, it is undoubtedly imperfect. For example, the model assumes bee nests to be continuously distributed across a landscape, when in fact, they are patchily distributed (Michener et al., 1958). Third, because we only compared the most and least fragmented landscapes, we are unable to detect nonlinear effects of fragmentation on biodiversity loss. Finally, positive geometric effects could be magnified or countered over time by positive or negative demographic effects, which are not considered here. Species that were initially 'saved' by the geometry of fragmented landscapes might later go locally extinct if they are sensitive to the increase in habitat edge or isolation (Develey & Stouffer, 2001; Laurance et al., 2004; Matlack, 1994). Conversely, they may be more likely to persist if they benefit from edge habitat or from certain dynamics that are more likely to take place in more fragmented landscapes, such as increased risk-spreading, more stable predator–prey dynamics or increased colonization (Fahrig, 2017; Fahrig et al., 2022). Thus, the net effect of fragmentation on forest bee diversity should depend on the relative effect sizes of demographic and geometric effects, and on how these effects change over time. Assessing these relative effects, though, is a challenge. On the one hand, the geometric effects of fragmentation in our study appeared weak, with the most fragmented landscapes having only 3.4%–7.3% more species than the least fragmented ones after forest loss. On the other hand, a meta-analysis of long-term fragmentation experiments also found weak negative demographic effects of fragmentation on species richness within patches, having a log response ratio for more fragmented to less fragmented of just below zero (Figure 3b of Haddad et al., 2015). Complicating matters, demographic effects may also be scale dependent, with positive demographic effects like risk spreading being only being observed at the landscape scale (Fahrig et al., 2022). We are aware of only one case in which geometric and demographic effects were assessed using the same database, and this pair of studies found a net positive effect of habitat fragmentation on biodiversity (Riva & Fahrig, 2023) despite significant negative demographic effects at the patch level (Chase et al., 2020).

Ultimately, the net effects of fragmentation are likely context-dependent. The strength of geometric effects should depend on the intensity and spatial scale of fragmentation relative to the spatial turnover in the focal communities (Chisholm et al., 2018; May et al., 2019; this study). In our study, the strength of the effects we observed is specific to both the landscape structure in the northeastern USA and beta diversity of northeastern forest-specialist bee communities. Our observed effect could have been stronger or weaker if the bees were more or less aggregated (or even negative, if bees were regularly distributed), or northeastern forests were more or less fragmented. Nonetheless, the geometric effects of fragmentation should vary predictably between study regions and taxa. Broadly, positive geometric effects should be strongest for taxa and regions with high levels of species turnover and when little natural habitat remains in a landscape (Figures 3 and 4). In our study, geometric effects were stronger in cases of greater habitat loss, likely because patch size decreases as habitat amount decreases. This is consistent with predictions from theoretical models that geometric effects only occur when habitat patches fall below a certain size, relative to the spatial aggregation of individuals (Deane et al., 2022). In contrast, negative demographic effects should be strongest for species that are dispersal-limited, live at low population densities, and that are sensitive to edge habitat (Bender et al., 1998; Develey & Stouffer, 2001; Halley et al., 2014; Laurance et al., 2004; Matlack, 1994; Wiegand et al., 2005). Positive demographic effects should be strongest for species that easily disperse through the matrix (Fahrig et al., 2022). An important focus for future research, then, is to parse and quantify the importance of these traits and conditions, which would facilitate reliable predictions regarding biodiversity loss.

Untangling the effects of habitat loss and fragmentation on biodiversity has clear implications for conservation policy. Yet, despite decades of research (Chase et al., 2020; Fahrig, 2019;

Fletcher et al., 2018; Quinn & Harrison, 1988; Riva & Fahrig, 2023; Simberloff & Abele, 1976, 1982), there remains disagreement on how fragmentation per se affects biodiversity loss following habitat conversion in real-world ecosystems. Here, we show that fragmentation can, at least initially, mitigate biodiversity loss following habitat destruction due to species turnover within remaining natural habitat. These geometric effects of fragmentation are often overlooked in discussions about how fragmentation affects biodiversity (Fletcher et al., 2018; Hanski, 2015), but here we show that they can be meaningful in real-world landscapes, with consistently positive effects across a range of spatial scales. Furthermore, these geometric effects did not require that more fragmented landscapes preserve different types of habitat, which is a mechanism often posited in the SLOSS debate (Fahrig, 2020), but instead were purely the result of bee species' spatial distributions (Deane et al., 2022; Kobayashi, 1985; May et al., 2019). Given that patterns of spatial aggregation are likely to differ among taxonomic groups, the strength of these effects could differ among taxa and landscapes. Future research should investigate the importance of geometric effects relative to demographic effects, and test whether geometric effects can have meaningful contributions to biodiversity conservation in real-world landscapes.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

The data and code used in the analyses from this manuscript are available on Zenodo (https://zenodo.org/record/8327336).

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BIOSKETCH

Colleen Smith is interested in predicting and understanding biodiversity change in bees.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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