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Tropical forest fragmentation and isolation: Is community decay a random process?

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ABSTRACT

Habitat destruction and degradation are the leading causes of species declines and extinctions in the world. Human altered landscapes often leave fragments of previously continuous habitat, which may be of significant conservation value. We assessed the effects of habitat fragmentation on the taxonomic diversity, community composition, and nestedness of avian communities before and after fragment isolation at the Biological Dynamics of Forest Fragments Project research site in the Amazon rainforest. Species loss in 10ha and 100ha fragments was significantly different from random taxonomic loss. In addition, after fragment isolation, but not prior to fragmentation, the species in the 10ha fragments were a nested subset of the species in the 100ha fragments. Finally, within the fragments two distinct communities formed, those on the edge of the fragments and those at the interior of the fragments, indicating that edge species did not penetrate the interior portion of the fragments. The controlled isolation of fragments from continuous forest resulted in rapid changes in the taxonomic diversity and species composition where fragment size served as a driver of species assemblages across the landscape. We suggest that future research continue to assess community level adjustments to habitat fragmentation and investigate the drivers behind the non-random loss of taxonomic groups and the nested structure of species composition of smaller fragments into larger ones after habitat fragmentation.

1. Introduction

Fragmentation of continuous habitat through anthropogenic disturbance is happening at unprecedented scales and affecting species and habitats in ecosystems around the world (Betts et al., 2017; Haddad et al., 2015; Hansen et al., 2013). In fact, many habitats have been divided into smaller fragmented pieces to the point at which the fragments face biodiversity

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loss, potential trophic collapse (Terborgh et al., 2001), and the loss of ecosystem services (Dobson et al., 2006; Layman et al., 2007).

Habitat destruction and degradation are also the leading causes of current species extinctions (Brooks et al., 2002; Pimm et al., 2014). Habitat destruction generally leads to habitat fragmentation in which isolated fragments of formerly continuous habitat remain in place of continuous habitat. Despite extensive research on the subject of fragmentation (reviewed in Haddad et al., 2015; Turner and Corlett, 1996), there is still active debate regarding the effects of fragmentation and the importance of the size of fragments that should be conserved in order to maintain biodiversity (see Fahrig et al., 2019; Fletcher et al., 2018; Miller-Rushing et al., 2019).

The most common metric used to infer the effects of fragmentation on community structure, relative to continuous habitat, are species richness or species diversity. However, species richness and diversity metrics do not assess the potential ecological interactions among species, the role species play in their habitat, or the taxonomic diversity within a community. For example, species richness is simply a count of the number of species at a location, yet says nothing about the range, rarity, prevalence, endangerment, ecological function, or taxonomic distinctness of the species that are being counted. For conservation purposes using metrics such as species richness alone and counting all species equally might not be enough to effectively prioritize the conservation value of different sites. However, including additional metrics such as community composition, lifecycle phenology, functional significance, and taxonomic distinctiveness can better inform conservation decisions (Fleishman et al., 2006; Mace et al., 2012; Wolfe et al., 2019).

Studies of community composition in fragmented habitats could reveal not just how many species or which species are lost when a forest is fragmented but could also illuminate behaviors and dietary patterns associated with a species' extirpation. For example, studies of avian feeding guilds at multiple locations in Amazonian tropical rainforests have observed that terrestrial insectivores and those in mixed species flocks, are more likely to decline after fragmentation than nectarivorous or frugivorous species (Gray et al., 2007; Lees and Peres, 2008; Stouffer and Bierregaard, 1995).

Species in tropical forests tend to be less closely related to each other than those in human modified landscapes, such as agricultural systems (Frishkoff et al., 2014). When tropical forests are cleared, there can be a drastic reduction in the number of species (Alroy, 2017; Wolfe et al., 2015), or the number of species can remain similar but the community composition and the degree of relatedness of those species in forest and adjacent communities can change drastically, with more closely related species in the human-modified system and greater taxonomic diversity in the forest habitat (Bregman et al., 2015; Frishkoff et al., 2014). However, less is known about the conservation of taxonomic diversity within habitat fragments after they have been isolated. If species sensitivity to fragmentation is random, one might predict that each fragment could hold a suite of taxonomically diverse species and overall taxonomic diversity might be conserved amongst multiple habitat fragments across a landscape. For example, taxonomic diversity among tropical woody tree species at several locations in the Atlantic rainforest of Brazil is not reduced in forest fragments but similar species richness is maintained (Santos et al., 2010; Arroyo-Rodríguez et al., 2012). Conversely, among bat species in a tropical fragmented landscape taxonomic diversity was significantly reduced in small fragments (1ha) but remained stable in larger fragments (10ha and 100ha) and continuous forest (Aninta et al., 2019), and in tropical bird communities in the Atlantic Rainforest overall phylogenetic diversity was not affected by fragmentation but it was reduced for species that were forest specialists (Morante-Filho et al., 2018).

Niche conservatism suggests that more closely related species are more ecologically similar than less closely related species (Losos, 2008). If species sensitivity to habitat fragmentation is not random, then a similar suite of species might be lost from all habitat fragments and overall taxonomic diversity would be reduced across the landscape (Bregman et al., 2015). For example, human modified landscapes have led to increased homogenization of taxonomic diversity in amphibian species, especially in lowland tropical habitats (Nowakowski et al., 2018). Perhaps animal species tend to have more taxonomic clustering in their responses to habitat conversion and fragmentation than woody tree species, which would lead to less random structuring of animal communities, alternatively animal communities might respond more quickly to habitat alteration and tree communities could have a longer response time (Laurance et al., 2018).

In addition to taxonomic diversity, species composition may vary between fragments in different locations and of different sizes across the landscape. For instance, species composition could be similar in all fragments across a landscape or each fragment could have a unique composition of species. In general, larger sized fragments have more species than smaller sized fragments due to species area relationships and reduced edge effects (Haddad et al., 2015). If species loss in fragments is not random, then one might predict that the species composition of smaller fragments would be a nested subset of the species composition of larger fragments in the same landscape (Bolger et al., 1991; Wright et al., 1997). However, if species loss due to fragmentation is random, then each fragment would be likely to have a distinct subset of species and each fragment might warrant conservation protection.

Edge effects take a prominent role in the context of habitat fragmentation and can shape community structure and ecological processes well beyond the border of the fragment edge (Laurance et al., 2007). Laurance et al. (2018) described edge effects in tropical forests penetrating up to 200 m into a fragment. Edges tend to have increased light, lower moisture, and relatively fast-growing vine and tree species when compared to more interior regions of habitat fragments (summarized in Laurance et al., 2018). Some species, so-called edge species, seem to prefer the altered microclimate and habitat structure near the edge; for example, many butterfly, bird, and some tree species are more likely to be found in habitat edges than the forest interior (Fowler et al., 2016; Laurance et al., 2000; Banks-Leite et al., 2010; Morante-Filho et al., 2015). While some species prefer the second growth, forest gaps, or forest edge we know less about the difference in composition between edge and interior communities, or how far edge species also penetrate into the forest interior.

The Biological Dynamics of Forest Fragments Projects (BDFFP) was designed specifically to address research questions related to the ecological effects and conservation implications of forest fragmentation in a previously continuous tropical forest habitat. Unlike the majority of habitat fragmentation studies that are based on observational methodologies and tend to lack pre-isolation data, the BDFFP is an experimentally fragmented forest landscape. The BDFFP has before and after isolation data as well as comparative understory bird species data in remaining continuous Amazonian forest. In addition, the BDFFP has replicated forest fragments of different sizes, 1ha, 10ha, and 100ha and, to date, is the longest running experiment to look at fragmentation at a landscape scale (Laurance et al., 2018). Finally, the project is ideal for asking questions about the conservation value of fragments as well as the importance of the size of fragments for conserving species.

Here we use data from the BDFFP to investigate the effects of fragmentation, not on the number of species in the landscape, but the type of species affected and the effects of fragmentation on community composition. We assess differences in species composition among fragments, before and after fragmentation occurred, in terms of their taxonomic distinctiveness and their microhabitat associations.

In this paper we test the following three research questions:

1. Are taxonomic groups reduced nonrandomly after fragment isolation?
2. Do species stratify into distinct communities near the edge compared to the interior of a fragment?
3. Are avian communities in smaller fragments a nested subset of communities in larger fragments?

2. Methods

The BDFFP is located among continuous primary tropical rainforest approximately 80 km north of the city of Manaus in the state of Amazonas, Brazil (Laurance et al., 2018). Fragments at the BDFFP were first isolated in the early 1980s (Bierregaard and Lovejoy, 1989). Our analysis focuses on understory forest avian species captured in mistnets in each of the four 10ha and two 100ha fragments at the BDFFP. Mist net data were collected before and after isolation events. We used mist net data from locations within fragments across the three BDFFP ranches (Fig. 1). We limited our analysis to mist net data from the five years before isolation and five years after isolation which ranged from 1979 to 2001. We did not include the year of isolation as the bird communities are especially volatile in the year directly after isolation (Bierregaard and Lovejoy, 1989). Before fragments were isolated mist nets were set in lines of 8 or 16 nets in the areas that were to be fragmented into 10 and 100ha fragments. Nets had 36-mm mesh and were roughly 12 m long and 2.5 m tall with the bottom trammel of the nets set at ground level. One line of nets was open per day and nets were open from 0600 to 1400. Netting occurred at each location roughly once every two months for the duration of this study. Data were grouped into two categories, before (5-0 years before the first isolation event) and after isolation (1–5 years after the first isolation event). We accounted for sampling effort (mistnet hours at a location) to standardize efforts at different locations as well as before and after isolation. Before analysis we removed all data regarding canopy species, defined as those species that predominately occupy canopy habitat, caught in mist nets since they were not specifically targeted with mist net surveys. Data from fragments five years or more after isolation were not included in our study as previously cleared habitat began to form second growth forest in some locations around 5 years, which created connectivity between continuous mature forest and fragments and some bird species began to recolonize the fragments (Stouffer and Bierregaard, 1995; Stouffer et al., 2011).

2.1. Taxonomic groups

Understory bird species were categorized into unique groups to test for the effect of fragment isolation on taxonomic and compositional species diversity. Taxonomic groups were considered at the family and genus levels, based on SACC standards (Remsen et al., 2019). Tests for our hypothesis based on taxonomic differences included two analyses. First, we tested total species richness as a fraction of the number of genera and families present within a fragment before and after fragmentation to test how fragment isolation influences these two ratios. Second, we tested the number of genera or families present at each fragment before and after each isolation event. Non-random species loss after fragment isolation was tested for 10 and 100ha fragments. To determine if the observed loss of species within families and genera was significantly different from random species loss (RSL) we simulated random thinning that would occur if RSL was the determinant factor driving species loss. Three separate chains of 100 highly constrained random community matrices were constructed and thinned to every 100 iterations after a burning of 1000 iterations. Since these data were treated as count data, not binary data, the quantitative 'swap_count' permutation method was used to preserve row and column totals and fill across our simulated communities after isolation using the 'commsim' function in the R-package vegan version 2.5–4. The actual number of unique species lost after isolation for each family and genus was calculated using the observed data. The number of species simulated to be randomly lost was calculated by subtracting each simulated random community after isolation from our observed data before isolation, which yielded 300 random simulations of how species could be lost within families and genera while retaining species totals across fragments and family/genus. To determine if non-random loss occurred we used a simple calculation based on the definition of a p-value (i.e. the probability to obtain, under the null hypothesis, a loss of families or genera that is

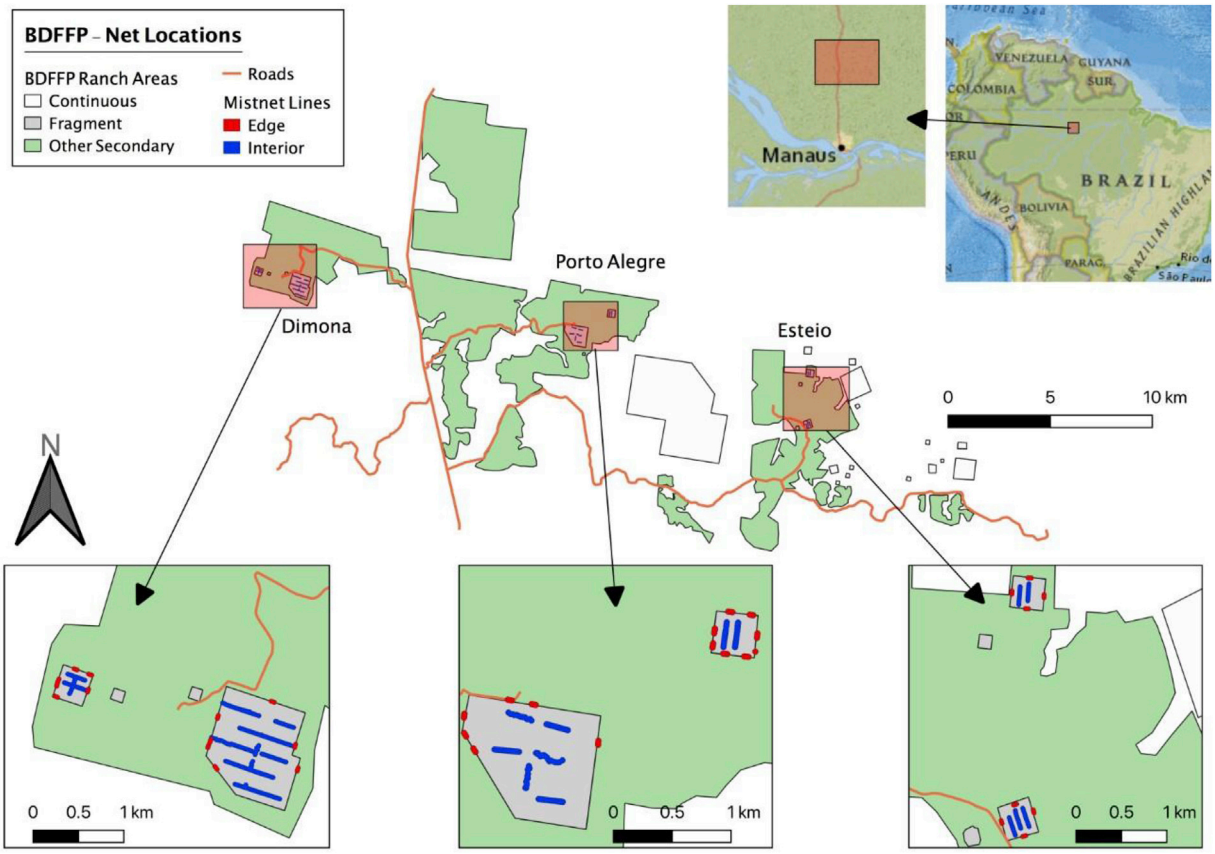

Fig. 1. Map of the study site and the ranches with forest fragments. The map indicates the locations of the mistnet lines, blue are interior fragment nets and red are fragment edge nets, within the fragments. The white regions indicate continuous forest, green represents the forest that was cleared and gray represents the fragments of forest that remained after the forest was cleared. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

greater than or equal to the observed value of species lost for any given family/genus across sites), which was calculated for each of the 300 total simulated communities and then averaged for a final p-value.

Non-random loss of families and genera in different fragment sizes was assessed using a simulated bootstrap method. Simulated random loss of families and genera were generated by repeatedly sampling from the community pre-isolation 100,000 iterations. The number of families or genera randomly sampled was equivalent to the number of families or genera that remained in fragments post-isolation. The number of times the observed families or genera occurred after isolation was compared to those selected from the random distribution. We considered a significant difference from random loss if the families or genera that existed at each fragment post-isolation were selected less than 5% (0.05) in the random distribution, which was averaged for the 10 and 100ha fragment sizes.

2.2. Edge and interior species

Differences in community composition at different distances from the edge within a fragment was quantified using the Jaccard index of dissimilarity between the species present at the interior and those at the edge of a fragment, defined as 1 − Jaccard's similarity index value (i.e. if dissimilarity is zero, then species present at the edge are the same species present in the middle of the fragment). Mist netting at fragment edges only began in 1991, thus we did not use data from the 1980s for this analysis. Edge and interior nets collected data from 1991 to 1993 and again during 2000 and 2001. For these specific years we compared the similarity of species present at the interior and the edge of each 10ha and 100ha fragment. Some fragments were re-isolated in 1994 and all fragments in this study were re-isolated in 2001, and we used mist net data within 5 years after the re-isolation event to assess differences in species composition between the edge and interior of forest fragments (Fig. 1). The similarity index was calculated and averaged for communities in each 10ha and 100ha fragment. The similarity for each fragment size was averaged to assess the similarity in the species across the 10ha and 100ha fragments.

2.3. Species nestedness

We tested for nestedness patterns within different sizes of fragments for all three ranches and for paired fragment sizes within ranches. Nestedness was defined as a community of species occurring in fragments with low species richness that are a subset of the community in a different fragment with higher species richness (Atmar and Patterson, 1993; Patterson and Atmar 1986). To quantify nestedness we used the matrix temperature metric, which is commonly used as a robust method to test for nestedness (Atmar and Patterson, 1993; Rodríguez-Gironés and Santamaría, 2006) and has shown comparable results as other nestedness measures when using highly constrained null models (Joppa et al., 2010). Temperature scores can range from 0 (perfectly nested) to 100 (no nestedness). To determine if the observed temperature score was significantly different from the expected score of a randomly selected community, we constructed a series of random community matrices using the 'tswap' permutation method (preserving both row and column totals) (Miklós and Podani, 2004). We repeated the generation of random community matrices with three independent chains of 100 highly constrained null matrices, thinned to every 100 iterations after burning 1000 iterations. The significance of the observed temperature pattern and the temperature pattern across community matrices was calculated by using the 'oecosimu' function with 'nestedtemp' method from the R-package vegan version 2.5–4 (Oksanen et al., 2019).

3. Results

3.1. Taxonomic groups

Observed species loss within any given family and genera ranged from 0 to 13 and 0 to 4, respectively across all fragments. Randomly simulated communities resulted in similar values of species loss, ranging from 0 to 19 for families and 0 to 5 for genera across all fragments. In all cases, the observed loss of species within each family and genera was not significantly different from simulated random communities (p-values reported in Table 1).

Within the 100ha fragments both families (0.03) and genera (<0.001) loss was significantly different from random loss after isolation. Within 10ha fragments, there was a significant difference from random loss related to genera (<0.001), but there was no significant difference from random loss for families (0.27) after isolation.

3.2. Edge and interior species

There was substantial dissimilarity between the communities at the edge and the interior of the fragments with the Jaccard index ranging from 0.52 to 0.83. The average dissimilarity between the avian communities at the edge and interior of the four 10ha fragments was 0.73 (±0.04), which is equivalent to 73% of the species differing between the edge and interior in 10ha fragments. The average dissimilarity in 100ha fragments was 0.63 (±0.07), which is a 63% difference in species composition near the edge compared to the interior of 100ha fragments.

3.3. Species nestedness

Before fragment isolation, areas that would become 10ha fragments were not significantly nested subsets of the 100ha fragments (Table 2). However, after isolation species in the newly established 10ha fragments were considered significantly nested subsets of the species found in the 100ha fragments. The result is a hierarchy of species richness and species in 10ha fragments being a subset of the species in the 100ha fragments (temperature = 21.27, p = 0.03).

4. Discussion

Habitat isolation resulting from forest fragmentation led to substantial alterations in bird community richness and composition with taxonomic loss at the family and genera levels being significantly different from random loss. Species also segregated themselves into distinct communities within the fragments such that distinct edge and interior communities were formed. In addition, smaller fragments were a nested subset of the species in larger fragments.

Table 1
Non-random species loss (RSL) within family and genera across different fragment sizes. The minimum and maximum number of species lost within any one family or genera are reported for both observed and simulated datasets. Significant differences from RSL are indicated with p-values. Results indicate that species loss within families and genera are not different from random null simulations.

Fragment size	Taxonomic grouping	Min observed loss	Max observed loss	Min simulated loss	Max simulated loss	p-value
100ha	Family	0	6	0	19	0.85
	Geunus	0	2	0	5	0.92
10ha	Family	0	13	0	18	0.83
	Genus	0	3	0	5	0.91

Signif. codes: '***' = 0, '**' = 0.001, '*' = 0.01, '.' = 0.05.

Table 2
Nested temperature (T) for each ranch and across all ranches. The evaluation of the nestedness "temperature" statistics using the 'tswap' permutation method is indicated in the table with the associated p-value. Results indicate that communities of birds in 10ha fragments are a nested subset of birds in 100ha communities across all 3 ranches but not within any of the ranches.

Ranch	Isolation	T	p-value
Dimona	Before	15.28	1.00
	After	16.54	1.00
Porto Alegre	Before	11.91	1.00
	After	16.00	1.00
Esteio	Before	2.16	1.00
	After	33.43	1.00
All	Before	15.03	0.37
(3 Ranches)	After	21.27	0.03 *

Signif. codes: '***' = 0, '**' = 0.001, '*' = 0.01, '.' = 0.05.

4.1. Taxonomic groups

Families and genera lost due to fragment isolation were not random. The non-random loss of genera and families implies that certain taxonomic groups of species are much more susceptible to forest fragmentation than others and has important implications for the conservation of Amazonian avian species (Barlow et al., 2006; Bregman et al., 2015; Lees and Peres, 2010; Sekercioglu, 2007, also reviewed in Laurance et al., 2018). Ferraz et al. (2003) modeled the rate of avian species loss in 100ha fragments and predicted a loss of half of the species in the 100ha fragments in less than a 15-year period, if there is no recolonization from exterior populations. The non-random loss of certain avian families and genera in the fragments could be partially explained by the incredible diversity of species at the study site (Cohn-Haft et al., 1997; Rutt et al., 2017), the fact that many families and genera in the Amazon basin are only represented by one or two species in a given community (Terborgh et al., 1990) and most species in Amazonia occur at low densities (Stouffer, 2007). If certain genera or families have only one or two species represented at a site that becomes fragmented, and those species required larger territories or specific niches that were no longer accommodated by the newly fragmented habitat, the whole genera or family could be lost from that fragment.

While the specific families and genera lost after fragmentation were different from random loss, the number of species lost after fragment isolation within certain genera and families was not different from random, these results are supported by Bregman et al. (2015) who also found that more closely related species are likely to be lost from relatively small fragments. The random loss of species within genera and families could result from species within the same taxonomic groups having similar functional groups (Bregman et al., 2015). Similarly, in the Atlantic Rainforest, taxonomic diversity of forest dependent species is reduced in heavily fragmented landscapes (Morante-Filho et al., 2018). Such findings make sense in the context of niche theory, where habitats fragmented into relatively small patches have less area and might contain fewer resources (food, water, etc.) per species, and or those resources may become more unstable in fragments than in equivalent sized areas in continuous forest. In such circumstances, niche theory predicts that species might need to broaden their niche leading to increased resource overlap and competition among closely related species. An increase in resource overlap is expected to contribute to the rate of extirpation of a closely related species if the niche is too similar (Macarthur and Levins, 1967; Cavender-Bares et al., 2006). Certain species that specialize on a particular food resource could be vulnerable to unstable food resources after fragmentation, resulting in niche collapse (Layman et al., 2007) and extirpation. However, testing whether changes in niche structure and resource competition contribute to the species loss would need experimental manipulation of food resources, which to our knowledge has not been done at the BDFFP or elsewhere as an explicit test of niche structure.

4.2. Edge and interior species

After fragment isolation, distinct communities emerged near the fragment edge compared to the interior of both 10ha and 100ha forest fragments. These results give insight as to how species and communities reorganize within fragments after isolation, which results in distinct species assemblages near the edge and in the interior of fragments, as was found by Banks-Leite et al. (2010) in bird communities in the Atlantic Rainforest of Brazil. Our findings illustrate that edge species are not penetrating the interior of fragments and interior species do not commonly approach the edges (Banks-Leite et al., 2010; Powell et al., 2015), which potentially explains why certain guilds and species have more negative responses in smaller fragments with greater edge-to-habitat ratios (Laurance et al., 2011) as edge effects reduce the suitable habitat area for forest interior species. Edge effects can be severe and include increased desiccation stress and wind turbulence (Laurance, 1996; Ewers and Banks-Leite, 2013). The effects of desiccation can reach nearly 200 m into the forest from the forest edge (Malcolm, 1998), which can increase tree mortality (Laurance, 1996) and alter the forest structure near the fragment edge (Laurance et al., 2000, 2006). Many animal groups, such as some bees, wasps, flies (Fowler et al., 1993), beetles (Didham et al., 1998a, 1998b), ants (Carvalho and Vasconcelos, 1999), butterflies (Brown and Hutchings, 1997), and understory birds (Laurance, 2004; Banks-Leite et al., 2010), decline in abundance near fragment edges. On the other hand, some species remain stable or even increase in abundance near habitat edges. In particular, some species even favor edge habitat, such as forest gap-

favoring species and nectarivorous bird species such as some species of hummingbirds (Stouffer and Bierregaard, 1995), light-loving butterflies (Leidner et al., 2010) and some frog species (Gascon, 1993). Thus, divergent preferences for and against edge habitat appear to segregate species into distinct assemblages near the interior and closer to the habitat edge of isolated forest fragments.

4.3. Species nestedness

Species assemblages in 10ha fragments were a nested subset of assemblages in 100ha fragments, which provides strong evidence for preserving fragments of larger sizes compared to smaller sizes. Prior to forest fragment isolation species in the locations of the 10ha fragments contained distinct assemblages that were not nested subsets of the soon to be isolated 100ha fragments, but once the forest patches were isolated the species in the 10ha quickly (within 5 years) became a complete nested subset of the species in 100ha fragments, such that the species in 10ha fragments contained no species that were not also in the 100ha fragments. However, for 10ha fragments relatively far from one another, post fragmentation communities diverged shortly after isolation (Stouffer and Bierregaard, 1995). Over longer timescales, such as decades, the communities in 10ha fragments tended to have compositional changes as a result of the forest between fragments re-growing and new colonization events occurring in the fragments (Stouffer et al., 2011). Our finding that species composition in 10ha fragments are a nested subset of the species in 100ha fragments align with studies that have found forest fragments to be nested subsets of nearby pristine forest (Fleishman et al., 2002; Driscoll, 2008), however we are unaware of any other studies that find relatively smaller fragments to have nested subsets of species in larger fragments. On the other hand others have found that fragments are not nested subsets of more pristine forest (Banks-Leite et al., 2012), potentially the conflicting findings are a result of relatively high species turnover as compared to species loss in certain fragments or systems. In our study the larger fragments retained a broader diversity of species than smaller fragments. Species-area curves cannot explain the nested subset aspect of our results, focus on the species composition in the 10ha and 100ha fragments not the number of species in each size of fragment. Our results indicate non-random processes that select for which species, with a non-random loss of genera and families in both 10 h and 100ha fragments, not just how many species are lost, in relatively small sized fragments.

Our results are based upon mist net data which indicates species presence and is not a true reflection of survival, abundance, or reproductive effort, all of which are important for populations to sustain themselves in habitat fragments. Ferraz et al. (2003) predicted that in 100ha fragments there would be a 50% loss of forest interior bird species in less than 15 years, however the models did not account for recolonization of species into the fragments from the nearby continuous forest. Such a finding indicates that a species presence after fragmentation is not enough to sustain populations within fragments. In fact, many other metrics such as abundance, survival, dispersal ability and reproductive success are important for understanding which species can persist in forest fragments in the long term (Lees and Peres, 2009; Stouffer et al., 2006). Thus, repeated assessments, and multiple metrics, are critical for understanding how habitat fragmentation affects community dynamics in the short and long term.

5. Conclusions

The null model simulations that observed the non-random structure of genera and families that remain in fragments and the nested structure of the 10ha fragment communities within the 100ha fragments communities illustrates the importance of preserving larger fragments. Such results also highlight the importance of preventing fragmentation in the first place if we are to retain vulnerable species that are non-randomly lost when fragmentation occurs. Future efforts should continue to assess community processes, such as changes to how resource competition and facilitation are affected by habitat alteration. This insight will provide a deeper understanding of the long-term effects of habitat fragmentation on the structure and function of communities (Gonzalez et al., 2011).

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