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Research article

Forest fragmentation effects on mutualistic interactions: frugivorous birds and fruiting trees

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While many effects of forest fragmentation are reasonably well understood, knowledge of interspecific interactions in fragmented ecosystems is much more limited, particularly for high diversity tropical forests. Using nearly 40 years of data from the Biological Dynamics of Forest Fragments Project in Central Amazonia, we assessed whether forest fragment area and time since isolation impact mutualistic interactions between frugivorous birds and their food resources. We used structural equation modeling to analyze the complex pathways between four main variables determining these interactions: fruiting tree abundance, frugivorous bird abundance, forest fragment area, and time since fragment isolation. Our results confirm that fragment area alters the abundance of some tree resources, with successional plant families increasing in abundance with decreasing fragment size. However, these changes do not drive alterations in the abundance of frugivorous birds. We also tested if bird species with a greater relative diet breadth are less vulnerable to forest fragmentation and found that specialist frugivores are more vulnerable to forest fragmentation immediately after isolation but are not differentially impacted within the long term. Collectively, our results demonstrate the need to further evaluate human-driven habitat change across multiple timescales to fully understand its impacts on complex species interactions.

Keywords: Amazon rainforest, conservation biology habitat disturbance, mutalism, species interaction, structural equation model

Introduction

Tropical forests are renowned for complex species interactions (Schemske et al. 2009, Escribano-Avila et al. 2018). Given that more than 70% of remaining forests now lie within 1 km of forest edge (Haddad et al. 2015), habitat fragmentation research addressing responses of single taxonomic groups leaves critical gaps in

our understanding of how fragmentation affects these interconnected communities. Studies that only report changes in species richness or abundance of individual taxa restrict our understanding of the mechanisms by which forest fragmentation reduces diversity and prevent us from accurately predicting long-term outcomes such as faunal relaxation in interaction networks (Koh et al. 2004, Morris 2010). Recent meta-analyses and multi-taxa studies that have attempted to address this gap found forest mutualisms to be more negatively impacted by forest fragmentation than antagonistic interactions (Laurance et al. 2011, Magrach et al. 2014, Marjakangas et al. 2020). Research suggests that increased specialization between mutualistic partners could explain the higher degree of population declines or species losses as the loss of one species can negatively impact other species (Bond 1994, Koh et al. 2004). Study outcomes, however, do not always find specialized interactions with a greater degree of flexibility to be as vulnerable as one-to-one interactions or for specialized interactions to be more vulnerable that generalized ones overall (Aizen et al. 2002, Vázquez and Simberloff 2002, Abramson et al. 2011), nor do all mutualistic interactions respond similarly or equally to forest fragmentation (Laurance 2005).

We might attribute these inconsistencies to additional, numerous factors beyond the degree of dependency of the individual interactors in asymmetric mutualisms (Ashworth et al. 2004), such as differences in species identity, population size (Kolb 2008), responses of interacting species to edge effects or forest fragment size (Hagen et al. 2012), and time since fragmentation (Galetti et al. 2013). For example, many ant–plant mutualisms are resilient (Passmore et al. 2012), and ants colonize some species of plants at higher rates in forest fragments than in intact forest (Bruna et al. 2005). Similarly, forest fragmentation has a neutral, or even positive, effect on interactions in some pollination systems (Dausmann et al. 2008, da Silva Elias et al. 2012). Flower visits by bird pollinators in a fragmented forest in Chile, for instance, increased for trees on the edges of smaller fragments than larger fragments (Smith-Ramirez and Armesto 2003). However, many studies that report resiliency or positive outcomes are short term and often examine interactions decades after initial fragmentation, when they may have reached new stable states.

The most well-studied mutualistic interaction in forest fragmentation research is frugivory and seed dispersal (Magrach et al. 2014). Like pollinators, seed dispersers serve a critical ecosystem function (Wunderle 1997, Link and Di Fiore 2006, Hernández-Montero et al. 2015, Donoso et al. 2020), with up to 90% of tropical woody plant species dependent on animal dispersal (Gentry 1992). Forest fragmentation frequently reduces density and recruitment of animal dispersed trees by altering abundances of frugivorous birds and primates (Cordeiro and Howe 2001, Uriarte et al. 2011, Hooper and Ashton 2020). Studies indicate a nuanced effect of forest fragmentation on seed dispersal that depends on fragment size and seed or seed disperser size, with fragment area negatively impacting the seed removal of small-seeded species at edges, but not altering the removal of large-seeded species (Chen et al. 2017). These studies provide evidence that species identity or specific species traits (e.g. body size, bill size – Galetti et al. 2013, Bovo et al. 2018) may influence the outcome of fragmentation on extinction (Galetti et al. 2013), interaction integrity, and long-term changes in community structure (Hagen et al. 2012). Although short term multispecies network studies (Vidal et al. 2014) and reviews (Marjakangas et al. 2020) help elucidate important species traits that contribute to outcomes, studies that track individual species for longer time periods will provide mechanistic information to help predict interaction outcomes.

We used long-term datasets on fruiting trees and frugivorous birds from an experimentally fragmented site, the Biological Dynamics of Forest Fragments Project (BDFFP), to assess the temporal effects of forest fragmentation on bird dispersal mutualisms in the Brazilian Amazon. We assessed if population trends in fruiting tree abundance and frugivorous bird abundance in forest fragments differed from those in nearby, continuous forest. Additionally, as the effects for forest fragmentation can take years to manifest, a phenomenon known as 'extinction debt' (Tilman et al. 1994), we assessed changes to the relationship of fruiting trees and their avian dispersers using data spanning almost 40 years. More specifically, we asked the following questions: 1) are mutualistic interactions between understory and midstory frugivorous birds and their resource trees impacted by tropical forest fragmentation? And 2) do frugivorous bird species with wider relative diet breadths increase in abundance after forest fragment isolation relative to species with narrower relative diet breadths?

Material and methods

For this study we utilized data previously collected from the Biological Dynamics of Forest Fragments Project (BDFFP). The BDFFP is located 80 km north of Manaus in the state of Amazonas, Brazil, and was founded in 1979 to study the impacts of forest fragmentation on biodiversity. Initially, most of the experimental fragmentation of forests at the site occurred at the beginning of 1980 through slashing and burning to create cattle pastures between fragments and continuous forests. The BDFFP isolated 11 forest fragments in all, including 5 of 1 ha, 4 of 10 ha, and 2 of 100 ha (Bierregaard et al. 1992). In the late 1980s to 1990s cattle were removed and secondary forests developed in the matrix, reconnecting the forest fragments with the continuous forest. The forest fragments were re-isolated in 2013 and 2014 by re-clearing a 100 m buffer around nine of the original 11 forest fragments (Laurance et al. 2018), around which the forest was allowed to regrow in the buffer area over time. The project currently contains secondary regrowth of varying ages alongside the forest fragments and continuous forest (Fig. 1). For the duration of this study we focus on the nine long-term forest fragments originally isolated and later reisolated. This includes 3 of 1 ha, 4 of 10 ha, and 2 of 100 ha fragments.
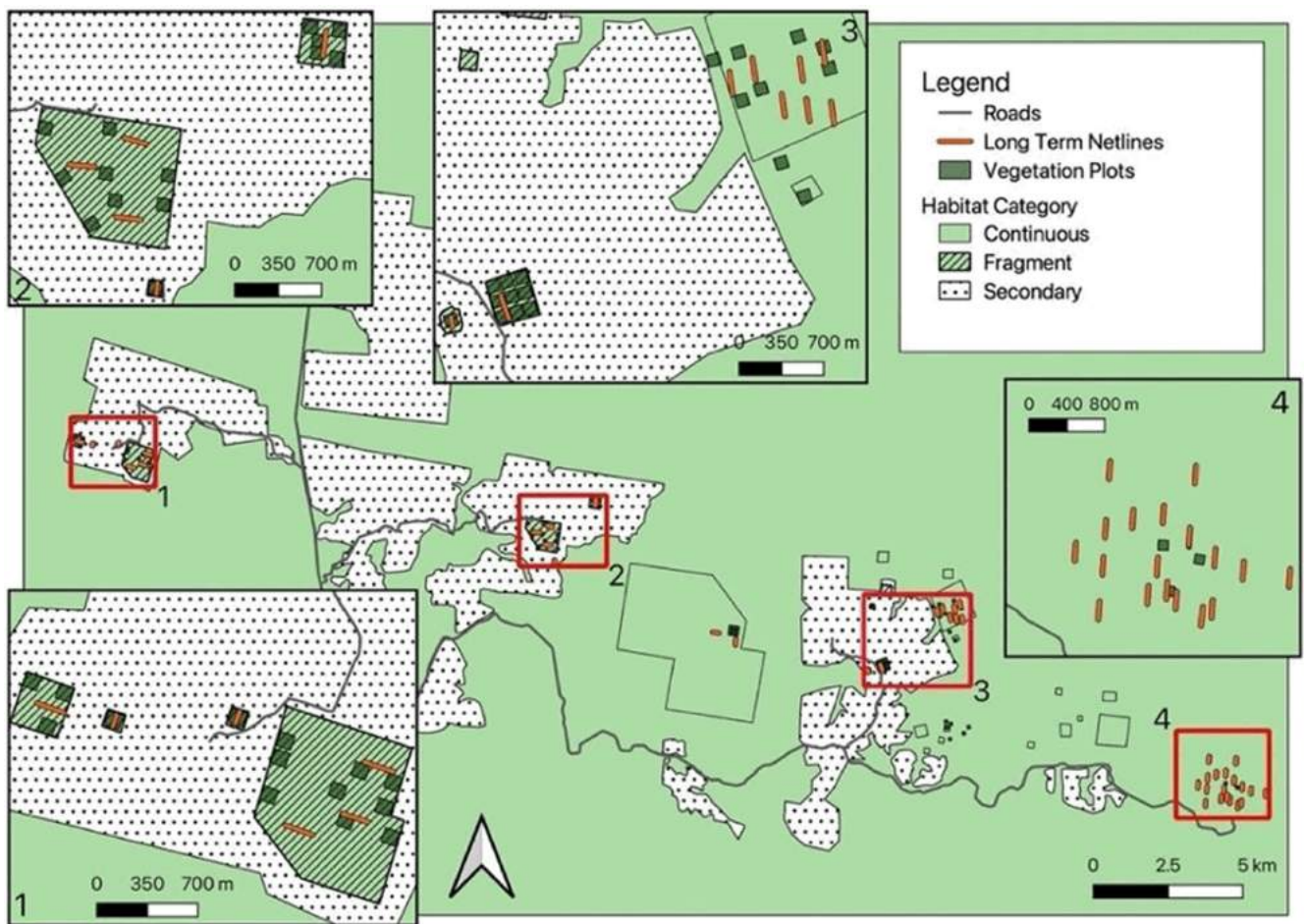
Figure 1. Map of the Biological Dynamics of Forest Fragments Project in central Amazonia, showing the location of the forest fragments, continuous forest, secondary regrowth, long-term forest dynamics plots, and long-term mist net lines.

Botanical dataset

A unique aspect of the BDFFP is that the site's biodiversity was censused before and after fragment isolation, as well as in nearby continuous forest. Long-term data have been collected on trees and birds over the past 40 years (summarized by Laurance et al. 2018). The BDFFP has 96 permanent plots of 1 ha known as 'forest-dynamics plots' where trees were inventoried and monitored regularly. One ha fragments have 1 plot, 10 ha fragments have 3 to 4 plots, 100 ha fragments have 9 plots and continuous forest sites have 3 plots. The plots are currently tracking information on more than 62 000 trees > 10 cm in diameter at breast height (DBH). When the plots were first established, the trees within them were mapped, measured, and tagged with unique identifiers. Voucher material was collected for almost all present individuals and stored at the National Institute for Amazonian Research (INPA) (Rankin-de-Merona et al. 1990, 1992, Laurance 2001). Individual trees were identified to the species level (Laurance et al. 2010), and subsequent individuals were added during surveys if they were also > 10 cm DBH. Data were collected at regular intervals, roughly every five years, from 1979 through 2016. We grouped tree species according to plant family to make them comparable to the information available in the literature on avian diets as many studies only report diet to the plant family level.

In order to model changes in plant abundance across sites, the total abundance for each family was standardized to be the average number of individuals across all plots within each fragment or permanent site (for plots within the continuous forest). The proportion of trees was relativized by forest fragment as the number of individuals within each family out of the total number of individuals of interest in each fragment. Plant families that are included in our study as food resources were determined through a detailed literature search of the diets of understory and midstory frugivorous bird species at the BDFFP.

Bird dataset and frugivore classification

Researchers at the BDFFP conducted mist net surveys on birds from 1979 through 2016. Mist nets (36 mm mesh, 12 × 2 m, with the bottom trammel on the ground) were used to assess bird diversity along established trails within each forest fragment and in the continuous forest. Eight nets in a single line were used in the 1 ha fragments, 16 nets in the

10 ha fragments and two net-lines of 16 nets were used in the 100 ha fragments and in the continuous forest. Each line was netted for one day and remained open from 06:00 to 14:00 h. Each fragment was sampled multiple times within a netting year, usually at one-month intervals between samples (Stouffer et al. 2009, 2011). All individual birds, except hummingbirds, were banded and those that were recaptured on the same day were excluded from this study.

To determine which birds captured in mist nets at the BDFFP were frugivores, we used the EltonTraits Bird Guilds (Wilman et al. 2016) to assess the proportion of fruit consumed by each species present at the BDFFP. Birds were classified as frugivores if their diet was ≥ 50% fruit. Based on this criterion, 18 species were considered frugivorous. However, upon closer review, seven of these species were nectivores and removed from our analysis, leaving 11 frugivore species captured in mist nets from the BDFFP. Information on the species-specific avian diet of these 11 species was compiled from the literature by reviewing published works through Google Scholar. We searched each of the 11 species' scientific names plus the keyword 'diet' for all papers published before June 2021. In total, we reviewed 2900 publications. Information was only used if the publication stated the consumption of fruit by one of our 11 selected species. General interactions with plants were not included to avoid confounding other interactions with plants, such as nest locations. Papers that studied fruit consumption *ex situ* were excluded. Due to inconsistencies with the level of resource identification, diet was recorded at the family level to incorporate all the available information. In all, censuses at the BDFFP encountered 69 plant families, but in this study we restricted our models to 14 plant families that were both documented within the fragments and recorded as food sources in the literature for the birds encountered in mist nets. We defined relative diet breadth as the total number of taxonomic plant families upon which a species is known to feed. These data were cross-referenced with the diet information available on Cornell Lab of Ornithology's 'Birds of the World' webpage (https://birdsoftheworld.org/). Once the total diet information was collected for each species, we further removed species from our study if ≥ 50% of the plant families from which they fed were not found at the BDFFP. This ensured that we assessed species whose primary known diets were resources available at the BDFFP. Based on these criteria an additional four species were removed, which left us with seven frugivorous birds: the white-throated manakin *Corapipo gutturalis*, screaming piha *Lipaugus vociferans*, golden-headed manakin *Ceratopipra erythrocephala*, white-crowned manakin *Pseudopipra pipra*, white-fronted manakin *Lepidothrix serena*, brown-winged schiffornis *Schiffornis olivacea* and fulvous-crested tanager *Tachyphonus surinamus*. However, due to low counts of *L. vociferans* in the mist net capture data it was not possible to include this species in our study. Thus, we had a total of six frugivorous bird species that were known to feed from at least 14 plant families at the BDFFP (Supporting information).

Based on the long-term research at this site each of these six species is known to persist in continuous forest, forest fragments and secondary forest at our study site (Stouffer et al. 2021). However, they are most frequently captured in mature continuous forest, and less often captured in forest fragments, and then secondary forest (Rutt et al. 2021). In addition, they have been observed moving between secondary forest and forest fragments, but only after five years of secondary forest regrowth since fragment isolation.

Establishing time since isolation and temporal variation

We assessed both the abundance of each bird species and the corresponding plant families at three separate time points: one to two years before the BDFFP's initial forest fragmentation event (time point = 0), up to four years after the initial fragment isolation (time point = 1), and the most recent data point in the 2010s, with 2016 as the most recent year of sampling in this study (time point = 2). In the rare instances that data were not available on plant abundance in the same year as the birds, we used the next available year. Time since isolation was then applied as a variable in our models to assess changes to both bird and plant abundance in each fragment or the continuous forest across the three established time points.

Statistical analyses

We applied structural equation modeling (SEM) to determine the relationships between frugivorous bird abundance, tree abundance, time since forest fragment isolation, and forest fragment area. Specifically, we modeled if the abundance of frugivorous birds and the abundance of corresponding plant families were impacted directly and indirectly by time since isolation and forest fragment area. We created a separate model for each avian species. Each model hypothesized direct relationships of forest fragment area and time since isolation on avian abundance, and then indirectly through changes to the abundance of each plant family. Since mist netting effort differed between sites, the effort was also included as an exogenous variable exclusively influencing changes to avian abundance. In total, the variables for hypothesized models included: time since isolation, forest fragment area, avian abundance, tree abundance (for each separate plant family; two to 10 in total depending on the species), and mist-netting effort. We ran each model using the R package *lavaan* (ver. 0.6–11, www.r-project.org) with the built-in maximum-likelihood estimation. Previous assessment for normality of data for birds and trees determined that our data were non-normal. As a result, we included bootstrapping in our final model to account for this. Model fit was defined by the standards set by Bentler's comparative fit index (CFI). Models with a 'good' fit had a CFI ≥ 0.95 and models with a 'satisfactory' fit had a CFI ≥ 0.90. Any models with a 'poor' fit, CFI ≤ 0.90, were not included in the study.

We used linear mixed-effect models to assess the impact of relative diet breadth and forest fragment area on the mist net effort corrected avian abundance over time. For the linear

mixed-effect models, we were able to assess the six birds originally identified as frugivorous. Analyzing all six species was possible for the linear mixed-effect models and not for the SEMs because of SEM parameters. For our analyses using SEMs, two species have such large relative diet breadths their individual models were unidentified with too many unknown variables. However, for the linear-mixed effect models their relative diet breadth is evaluated as a single number of total plant families, allowing for their inclusion in the analysis. Relative diet breadth was defined as the total number of plant families at the BDFFP that each bird is known to consume. These birds have relative diet breadths of two to 10 known tree families at the BDFFP (Supporting information). To assess change over time, we first had to account for different sampling efforts between our individual forest fragments (known as 'mist net effort'). We standardized bird counts by dividing the total abundance of each species (number of individuals per species) by the total number of mist net hours at each of the three evaluated time points (timepoints 0–2). Mist net hours were calculated by multiplying the number of hours a mistnet was open by the total number of sampling days. We then calculated the Euclidean distance between time point = 0 (1 to 2 years before fragmentation) and time point = 1 (up to 4 years after fragment isolation) to assess the short-term impacts of forest fragmentation on avian abundance for each species. We also calculated the Euclidian distance between time point = 0 and time point = 2 (most recent data collection year) to assess the long-term change in avian abundance for each species. Changes in short term and long-term avian abundance were evaluated as a response to relative diet breadth and forest fragment area, with species included as a random effect. We also evaluated the interactive effects between relative diet breadth and forest fragment area to determine if there was a relationship between these variables in the short-term and long-term. The two linear mixed-effect models were run using R ver. 2022.02.3 and the 'lme4' package ver. 1.1–27.1 (www.r-project.org). p-values and predictive plots were generated using the 'lmerTest' ver. 3.1–3, , 'jtools' ver. 2.2.0, 'sjPlot' ver. 2.8.10, and 'sjmisc' er. 2.8.9 packages.

Results

Structural equation modeling for species interactions

Models for five of the six frugivorous birds converged. *P. pipra* was the only species whose model did not converge, due to issues with model identification. Of the remaining five models, four resulted in a 'good' or 'satisfactory' model fit (Table 1; CFI ≥ 0.90). These four frugivorous species consumed fruit from five different plant families. Thus, in total, our SEMs were able to assess the pathways between four frugivorous birds and five plant families.

Forest fragment area had a direct and significant impact on multiple plant families but did not have a direct impact on any of the avian species in this study. Forest fragment

Table 1. Model fit for structural equation modeling by avian species. Of the six models tested, only five successfully converged. Pseudopipra pipra was the only model that did not converge. Models with a 'good' fit had a CFI ≥ 0.95, models with a 'satisfactory' fit had a CFI ≥ 0.90, and models with a CFI < 0.90 were considered a 'poor' fit.

Species	CFI	Model fit
C. gutturalis	0.977	good
C. erythrocephala	0.983	good
L. serena	0.939	satisfactory
S. olivacea	0.792	poor
T. surinamus	0.984	good

area had a positive, significant impact on the plant family Moraceae (standardized path coefficient = 0.72) and a negative impact on Melastomataceae (standardized path coefficient = −0.38) and Euphorbiaceae (standardized path coefficient = −0.68). The abundance of species in the remaining plant families, Rubiaceae and Clusiaceae, were not significantly altered by forest fragment area. Similarly, time since isolation did not directly impact the abundance of any of the plant families included in our models. Time since isolation also did not have a direct, significant impact on the abundance of any avian species analyzed. Based on the standardized path coefficients, mist net effort heavily influenced the models for *C. gutturalis* (standardized path coefficient = 0.85), *L. serena* (standardized path coefficient = 0.78), *C. erythrocephala* (standardized path coefficient = 0.54), and *T. surinamus* (standardized path coefficient = 0.83) (Fig. 2).

We only identified one statistically significant, indirect pathway, which was in the *C. erythrocephala* model. Forest fragment area was positively correlated with Moraceae abundance (standardized path coefficient = 0.72) and Moraceae abundance was then negatively correlated with *C. erythrocephala* abundance (standardized path coefficient = −0.52). Within this significant pathway, 55% of variance in Moraceae abundance ($R^2 = 0.55$) and 52% of the variance in *C. erythrocephala* abundance can be explained by the predictors within the model ($R^2 = 0.52$) (Fig. 2).

Linear mixed-effect model for relative diet breadth

While relative diet breadth and forest fragment area did not directly impact the abundance of the bird species in this study, the interactive effects between relative diet breadth and fragment do have a significant impact in the short-term when comparing before isolation abundance and abundance immediately after isolation (Table 2, Fig. 3). Results from immediately before (time = 0) and after fragment isolation (time = 1) show that bird abundance increases in 10 ha and 100 ha forest fragments but not 1 ha fragments for species with larger relative diet breadth relative to those with narrower relative diet breadth. Nonetheless, in the long term, relative diet breadth did not significantly impact avian abundance, which remains true for the effect of forest fragment area as well. The interactive effects between relative diet breadth and forest fragment
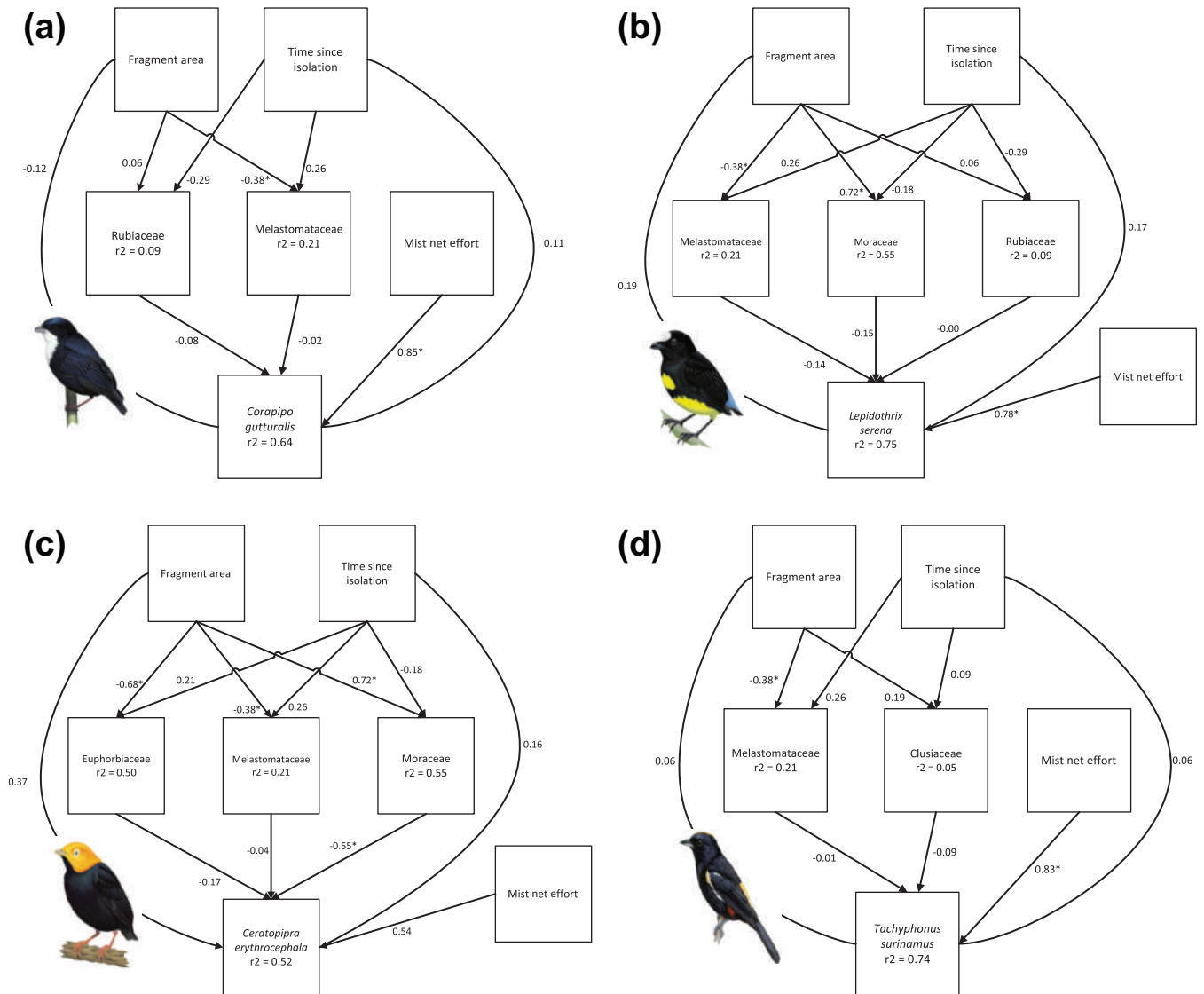
Figure 2. Path diagrams showing the results from structural equation modeling for the four avian species that converged with a satisfactory or good model fit (CFI > 0.90), the other two frugivore species did not have models that converged. (a) *Ceratopipra erythracephala,* (b) *Lepidothrix serena,* (c) *Corapipo gutturalis* and (d) *Tachyphonus surinamus.* Arrows represent the directional structure of exogenous and endogenous variables. The annotations indicate the standardized path coefficients (used to indicate each predictor's relative effect size in the model). Asterisks (*) highlight significant pathways within the models. Images from Handbook of the Birds of the World.

Table 2. Results from linear mixed-effect model assessing the short-term effects of forest fragmentation on avian abundance, relative to their diet breadth. Listed are the structural parameters and their effect on changes to the standardized avian abundance at the Biological Dynamics of Forest Fragments Project (BDFFP) within four years of fragment isolation. Relative diet breadth is the total number of plant families serving as food resources for frugivorous birds. The remaining terms indicate the area of the fragment. Colons indicated interactive effects. Asterisks (*) indicate a significance level < 0.05.

| LMM model	Structural parameters	Estimate	SE	t value	Pr (>|t|)
Change in abundance	relative diet breadth	−0.0001735	0.0002395	−0.724	0.4731
	1 ha fragment	−0.0027128	0.0016931	−1.602	0.1446
	10 ha fragment	−0.0035434	0.0018982	−1.867	0.0879
	100 ha fragment	−0.0035230	0.0024938	−1.413	0.1693
	relative diet breadth:10 ha fragment	0.0005770	0.0002756	2.094	0.0434*
	relative diet breadth:100 ha fragment	0.0009081	0.0003982	2.281	0.0287*
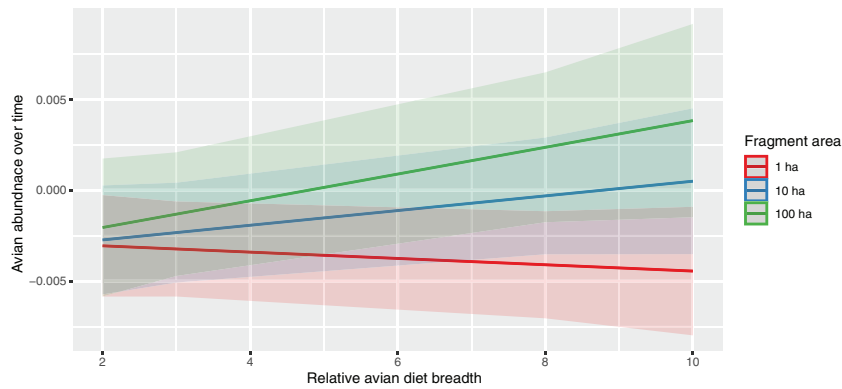
Figure 3. Short-term changes in the abundance of frugivorous birds, based on changes that occurred immediately after fragment isolation. The figure shows how species responses are mediated by relative diet breadth, the total number of plant families each species consumes, within each fragment area.

area also did not significantly impact changes to avian abundance over the long term (Table 3).

Discussion

The relative diet breadth of frugivorous birds had a significant, interactive effect with forest fragment area, such that bird abundance increased in 10 ha and 100 ha forest fragments as relative diet breadth increased, indicating broader diets could play an important role in their responses to habitat disturbance. However, these relationships were only strong in the years immediately after fragment isolation and the relationship disappeared decades later once the matrix became secondary forest. Therefore, these changes may be the result of regrowth around the forest fragments that is old enough to facilitate movement of understory birds and reconnect the fragments to continuous forest. Researchers hypothesize that a wider diet breadth may increase the persistence of species in disturbed landscapes (Laurance 1991, Gehring and Swihart 2003, Banks-Leite et al. 2014, Zungu et al. 2018). While studies are limited, research on butterflies in Finland showed that species with specialist larvae are more likely to be listed as threatened because of restricted food resources compared to species with generalist larvae (Kotiaho et al. 2005). Our data are limited by both the number of forest fragments available for analyses and the history of the BDFFP. As the landscape at the BDFFP has partially recovered due to secondary forest replacing the cattle pastures created in the 1980s the

availability of food should increase over time, allowing species to recuperate to pre-isolation levels. Our sample size for constructing interactive models was particularly small for 100 ha fragments, which only have two replicates at the BDFFP. As a result, future efforts should work to increase this sample size to better evaluate the effects in 100 ha fragments.

For the mutualistic interactions, changes to tree abundance did not alter frugivorous bird abundance – except for one indirect pathway (Fig. 1c). Stouffer et al. (2021) previously hypothesized that understory tropical frugivorous birds are unlikely to respond negatively to changes in food availability and our results support this hypothesis as we did not detect abundance level changes in frugivorous birds in direct response to alterations in their tree food resources, potentially because there are many other fruiting tree species available. In fragmented landscapes with regenerating secondary forest, bat- and bird-dispersed plants can increase (Laurance et al. 2006) due to the tendency of many dispersers to forage using the secondary forest surrounding fragments (Tewksbury et al. 2002, Stouffer et al. 2011). At the BDFFP, the matrix surrounding fragments is now dominated by 25- to 35-year-old secondary growth (the forest fragments were last isolated in 2013–2014, but only by a 100 m-wide strip of cleared forest around each fragment; Laurance et al. 2018). The high degree of connectivity between forest fragments and nearby intact forests would explain why these mutualisms appear unaffected, as frugivores traverse the matrix to find food in different patches (Mueller et al. 2014) and the matrix itself (Prevedello and Vieira 2010). Increased food availability

Table 3. Results of the linear mixed-effect model assessing the long-term effects of forest fragmentation on avian abundance, relative to their diet breadth. Listed are the structural parameters and their effect on changes to the standardized avian abundance at the Biological Dynamics of Forest Fragments Project (BDFFP) since fragment isolation. Relative diet breadth is the total number of plant families serving as food resources for frugivorous birds. The remaining terms indicate the area of the fragment. Colons indicated interactive effects.

LMM model	Structural parameters	Estimate	SE	t value	Pr (>|t|)
Change in abundance	relative diet breadth	0.0004039	0.0005078	0.795	0.4312
	1 ha fragment	−0.0009576	0.0034176	−0.280	0.7834
	10 ha fragment	−0.0040950	0.0038670	−1.059	0.3044
	100 ha fragment	0.0015362	0.0052248	0.294	0.7706
	relative diet breadth:10 ha fragment	0.0010472	0.0005975	1.752	0.0877
	relative diet breadth:100 ha fragment	0.0005514	0.0008642	0.638	0.5273

in the matrix (Levey 1988) may also provide refuge and resources (Driscoll et al. 2013) for mobile species to maintain their seed-dispersal mutualisms (Lehouck et al. 2009), although the impacts on movement are sometimes mixed in fragmented forests (Laurance et al. 2004a, b).

We identified one significant, indirect pathway in which *C. erythrocephala* abundance was negatively correlated with Moraceae abundance and forest fragment area. Research in other forested ecosystems indicates that Moraceae are more abundant in larger forested areas (Olotu et al. 2011, Benítez-Malvido et al. 2022). At the BDFFP, as the forest fragment area increased, so did the abundance of Moraceae. However, an increase in the abundance of Moraceae was correlated with a decrease in *C. erythrocephala*. We hypothesize that this relationship is due to an unidentified confounding variable. More research is needed on these interacting species.

Of the four frugivorous birds analyzed using SEM, three are midstory frugivores (*C. gutturalis, C. erythrocephala,* and *T. surinamus*) and one is an understory frugivore (*L. serena*) (Stouffer et al. 2021). Consistent with other research from the same site, populations of midstory- and understory-frugivore foraging guilds have been sampled via mistnets consistently for over 40 years yet have not changed significantly in that time (Stouffer et al. 2021). The lack of change is likely due to the guild's ability to use the surrounding matrix (Luck and Daily 2003, Laurance et al. 2004a, b) and move between forest fragments (Neuschulz et al. 2013, Vélez et al. 2015), which would explain why forest fragments, at the BDFFP and more generally, are more species rich when surrounded by secondary growth forest (Wolfe et al. 2015, Reider et al. 2018). Capture rates of birds, both understory and mid-story, show an increase with the age of secondary forest for all guilds other than non-forest species (Stouffer and Bierregaard Jr. 2007, Powell et al. 2013). For the species in our models, the abundance of *C. erythrocephala, T. surinamus,* and *L. serena* have significantly increased while *C. gutturalis* has slightly decreased in disturbed habitat (Stouffer et al. 2021). The spatial distribution of mating leks of *C. gutturalis* at the BDFFP, and the number of individuals attending those leks, varies based on the percentage of forest cover and proximity to edge habitat. Adult males are less numerous at leks with greater forest cover, which might explain why they are not as abundant in primary forest or 100 ha fragments, compared to secondary forest and smaller fragments (Tolentino and Anciães 2020).

Of the plant families we followed during the 40 years of this study, Euphorbiaceae and Melastomataceae decreased in abundance in larger fragments. Many of the trees in these families are early successional species, which increase with disturbance and amounts of forest edge (Laurance 2001, Laurance et al. 2004a, b, Allenspach and Dias 2012, Jesus et al. 2012, Sousa et al. 2017). Additional light infiltration from the edge enhances growth for successional species compared to their growth in primary forests, which have less light available in the understory (Kapos 1989, Delgado et al. 2007). Based on the estimates by Gascon et al. (2000), 1 and 10 ha forest fragments at the BDFFP would lack the core habitat needed to buffer against edge effects and, in combination

with the higher frequency of gap formation, create the ideal conditions for successional species to proliferate.

For trees, it is also possible that the impacts of forest fragment isolation have not fully manifested as they have for birds due to generation time. The estimated average longevity for trees > 10 cm DBH at the BDFFP is 330 years, although some are more than 1000 years old (Laurance et al. 2004a, b). While individuals may persist for long periods of time, previous BDFFP work found that the density of dispersed tree seeds is six times lower in smaller fragments compared to nearby intact forest (Hooper and Ashton 2020). Therefore, many trees may remain in forest fragments when their dispersers and pollinators are no longer present (Janzen 2001). Such species can face an 'extinction debt' in fragmented forests given additional time (Tilman et al. 1994). More likely, however, is that the BDFFP is a recuperating landscape. Many pollinators and seed dispersers initially impacted by forest fragmentation may return due to the permeability of regrowth in the matrix (Ewers and Didham 2005). As the ecosystem recovers, the matrix becomes more hospitable, and populations in fragments may be 'rescued' by immigrants from intact forest (Brown and Kodric-Brown 1977), helping maintain tree diversity and important mutualistic interactions.

In this study we only assess dietary resources at the family level for plants at the BDFFP because species-level diet information for the birds we evaluated is lacking in the literature. This limits our ability to extensively analyze diet breadth as food items are grouped into less granular categories and birds who have < 50% of their diet as fruit were removed. Research that can target species-specific interactions may be more nuanced and provide a clearer understanding of how mutualisms fare in fragmented landscapes. They may also be able to provide a truer picture of the total diet breadth for each species. This includes future research that works to better understand the avian effects on plant communities. Data from the botanical plots is also limited to trees > 10 cm DBH and does not assess other fruiting resources. Other work analyzes direct relationships, assessing birds like *P. erythrocephala* or *C. gutturalis* as primary dispersers of *Heliconia*, an understory plant not included in the botanical dataset (Uriarte et al. 2011). However, these direct datasets currently only provide information over shorter time periods, whereas our study provides one of the first looks at how mutualisms fare across longer timescales. Finally, there is evidence that frugivorous understory birds consume fruit from individuals of Melastomataceae and Rubiaceae that are smaller than 10 cm DBH (Hasui et al. 2007). Future data sampling that includes smaller sized food resources may be helpful in fully understanding potential impacts on fruit–frugivore interactions.

Mutualistic interactions are considerably complex, driven by factors such as specificity, resilience, adaptation and time. Our research provides some of the first, long-term empirical data showing that, when looking at changes to abundance in a fragmented landscape, mutualistic interactions between frugivorous birds and their fruiting-tree resources are not altered by forest fragment area or the time since fragment isolation. For the frugivores in this study, we found almost no evidence

that their mutualistic interactions were impeded by fragment isolation, outside of a single indirect pathway between Moraceae and *C. erythrocephala*. Furthermore, predictions that species with a wider relative diet breadth would fare better in the context of disturbance held true, but only in the first several years following the fragmentation process. To fully understand the impacts of forest fragmentation on ecosystems like the Amazon rainforest, future studies must consider the complexities of species interactions over long periods of time.

Author contributions

Tovah Siegel: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Writing – original draft (lead); Writing – review and editing (supporting). **William Cooper**: Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Writing – review and editing (equal). **Rebecca Forkner**: Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Writing – review and editing (equal). **William Laurance**: Data curation (equal); Investigation (supporting); Methodology (supporting); Resources (equal); Writing – review and editing (equal). **Jose Camargo**: Data curation (equal); Investigation (supporting); Methodology (supporting); Project administration (supporting); Writing – review and editing (equal). **David Luther**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (lead).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.hdr7sqvrz (Luther. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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