

Island vs. countryside biogeography: an examination of how Amazonian birds respond to forest clearing and fragmentation

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Abstract. Avian diversity in fragmented Amazonian landscapes depends on a balance between extinction and colonization in cleared and disturbed areas. Regenerating forest facilitates bird dispersal within degraded Amazonian landscapes and may tip the balance in favor of persistence in habitat patches. Determining the response of Amazonian birds to fragmentation may be hindered because many species use adjacent second growth matrices thereby limiting the applicability of island biogeography to predict species loss; alternatively, a countryside biogeographic framework to evaluate the value of regenerating forest may be more appropriate. Here, we used point-count and capture data to compare Amazonian bird communities among continuous forest, 100 ha forest fragments with adjacent second growth, young and older second growth plots, and 100 ha forested islands bounded by water, to test the applicability of island biogeography on the mainland and to assess the ecological value of a regenerating matrix. Among foraging guilds, understory insectivores and flocking species were nearly absent on true islands. Fragments surrounded by young second growth were species rich, suggesting that a developing matrix may mitigate extinction associated with fragmentation. Our findings reinforce that true islands are often extinction-driven systems with distinct, depauperate communities. In contrast, succession of bird communities in second growth facilitates recolonization of forest fragments, permitting fragments as small as 100 ha to support bird communities similar to continuous forest.

Key words: Balbina; central Amazon; continuous forest; countryside biogeography; forest fragment; island biogeography; second growth matrix; species richness; tropical bird.

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INTRODUCTION

The utility of island biogeography to predict species loss within mainland habitat patches has frequently been questioned (Mendenhall et al. 2012, 2014, Fahrig 2013). Criticism towards

applying the theory of island biogeography ('island model' hereafter) on the mainland stem from variation in the hostility of the matrix, where the surrounding landscape interspersed between habitat patches are often more salubrious than water surrounding true islands (Men-

denhall et al. 2014). Differences in matrix hostility, such as water (hostile) versus regenerating forest, determines how animals use and disperse through the landscape, thereby resulting in divergent biogeographic processes and different rates of species loss in habitat patches. In fact, the matrix surrounding remnant habitat patches may even provide some ecological value to wildlife which led Daily (1997) to suggest a new theoretical framework, called ‘countryside biogeography’, to study the diversity, abundance, conservation and restoration of species in human-dominated landscapes. More specifically, countryside biogeography recognizes that many human-dominated landscapes are not analogous to inhospitable bodies of open water interspersed between islands of habitat—a necessary assumption of the island model.

Countryside biogeography is particularly relevant to tropical forest-dwelling birds that may be dispersal limited and reliant upon human-dominated matrices to maintain metapopulation connectivity in heterogeneous landscapes (Seker-cioglu et al. 2002). For example, Stouffer et al. (2011) demonstrated that Amazonian forest birds were able to disperse from source populations in pristine habitat through a regenerating pastoral matrix to recolonize previously depauperate forest fragments, suggesting that species are lost following isolation, but the trajectory of loss does not continue downward when coupled with matrix recovery (Marsden et al. 2003, Ferraz et al. 2007, Laurance 2008, Stouffer et al. 2011). Not only does an adjacent matrix facilitate fragment recolonization, but it may also dampen predicted area effects associated with the island model (Zimmerman and Bierregaard 1986) as demonstrated in the central Amazon where fragments of different sizes yielded similar estimates of species richness as the adjacent matrix matured (Stouffer et al. 2006). Additionally, many species recolonize Amazonian forest fragments, even if they do not persist (Stouffer et al. 2011) demonstrating that presence or absence of a matrix will result in the disproportionate influence of either extinction or colonization on Amazonian bird assemblages in forest fragments and islands bounded by water, respectively (Terborgh et al. 2001).

Conversely, forest patch size within a regenerating matrix in Costa Rica yielded a strong

influence on hummingbird abundance and the subsequent seed set of native plants species they pollinate (Hadley et al. 2014). These results suggest that habitat patches in Costa Rica may act more like true islands where some hummingbirds may respond to the regenerating matrix as extremely hostile and are, therefore, subject to area effects as predicted by the island model. Although the response of birds to fragmentation appear contradictory in the aforementioned studies from the Amazon and Costa Rica, the ecological value of landscape matrices from both study sites was measured within fragments, rather than within the matrix itself. Clearly, measuring birds within the matrix to quantify the ecological value of a regenerating tropical forest represents a critical step towards predicting species loss in the Neotropical countryside (Gardner et al. 2007).

To date, research that has sampled birds within the matrix to assess its ecological value mostly relied on examining species richness between regenerating and pristine forest; these studies have produced largely contradictory and region-dependent results. For example, Barlow et al. (2007) found fewer species in regenerating matrix relative to primary forest in Brazil, while Blake and Loiselle (2001) documented more species within young matrix relative to primary forest in Costa Rica. The influence of region on patterns of species richness within the matrix was exemplified by Martin and Blackburn (2014) where endemic species in Honduras were found to be less common in the matrix relative to primary forest, when compared with bird communities in similar aged forests in Sulawesi. Dissimilar responses of matrix bird communities probably reflect four differences among the aforementioned studies: (1) differences in avifauna and their respective ability to exploit resources; (2) differences in successional pathways; (3) differences in distance to source populations; and (4) differences in matrix age. Regional dissimilarities are potentially further complicated by the asymmetric response of foraging guilds to the age of regenerating matrix. In general, frugivorous and nectivorous birds, which are relatively more common in Neotropical forests, often fare better when subjected to clearing and subsequent forest regeneration (although see Hadley et al. 2014) relative to their insectivorous counterparts (Karr

et al. 1990, Sekercioglu et al. 2002).

Stouffer et al. (2006) and Powell et al. (2013) demonstrated that the presence of insectivorous birds on the periphery of Amazonian forest fragments was positively correlated with age of the surrounding matrix, with fewer birds captured in fragments bordered by young forest. In particular, forest-obligate guilds such as terrestrial insectivores, ant-followers, flock obligates and arboreal insectivores were found to be most sensitive to surrounding matrix age, possibly reflecting an inability of certain foraging guilds to disperse through young second growth to recolonize isolated forest fragments (Stouffer et al. 2006). Antithetically, hummingbirds, gap specialists and some frugivores exhibited increased abundances within fragments surrounded by a young matrix (Stouffer et al. 2006). Clearly, the age of regenerating Amazonian forest fields influence over how bird species perceive and use the matrix.

A better understanding of how a range of matrix conditions (i.e., water, young and mature second growth) affect bird communities within isolates as well as within the matrix would have significant theoretical and conservation implications. The complex nature of historic and continued degradation within the Amazon basin provides a unique opportunity to conduct such a study. Habitat loss in the Amazon basin is dynamic due to ecological and economic forces, as reflected by hydroelectric development, large-scale pasture abandonment and subsequent forest regeneration (Neeff et al. 2006). In this study we worked within the heterogeneous central Amazonian landscape, using multiple methods to describe bird communities on true islands bounded by water, in fragments within a matrix, in second growth of two ages, and in continuous forest. In general, our study focused on determining the applicability of island or countryside biogeographic frameworks to study birds in degraded and heterogeneous forests in the Amazon.

More specifically, our study aimed to test the following hypothesis: if birds can disperse through young and mature second growth, presumably at different rates, but rarely over water, then forest fragments within a regenerating matrix will be subject to more colonization and islands bounded by water to more extinc-

tion. To test this central hypothesis, we measured four predictions: (1) birds can disperse through a regenerating matrix to recolonize forest fragments but will be less able to disperse over water, thus, true islands will be less species rich when compared to similarly-sized forest fragments embedded within a regenerating matrix; (2) because birds are more prone to disperse through mature second growth (25 years old) relative to young second growth (15 years old), young second growth will be significantly less species rich than mature second growth; (3) forest-obligate birds (terrestrial insectivores, ant-followers, flock obligates and arboreal insectivores) are dispersal limited, therefore true islands will have different community structure driven by the lack of forest-obligate birds compared to similarly-sized forest fragments; and (4) forest-obligate birds (terrestrial insectivores, ant-followers, flock obligates and arboreal insectivores) are more prone to disperse through mature second growth (25 years old) relative to young second growth (15 years old), therefore young second growth will have a significantly different community structure driven by the lack of forest-obligate birds compared to mature second growth.

METHODS

The study was conducted in terra firme forest at the Biological Dynamics of Forest Fragments Project (BDFFP), about 80 km north of Manaus, Brazil and on two islands, each about 100 ha in size (Sapopara and Relógio), in the Balbina reservoir, approximately 150 km north of Manaus. Balbina dam construction was completed in 1989; Sapopara and Relógio have been isolated since then. Forest fragments at BDFFP, including two 100-ha fragments, were isolated from 1980 through 1990. We also worked in 15- and 25-year-old second growth and continuous primary forest at the BDFFP (Fig. 1). For more information about the study site see Stouffer et al. (2006).

To test the four aforementioned predictions we employed both understory mist-netting and point counts to account for birds in each stratum of forest. Point counts can detect species that are vocal, conspicuous, or occupy the canopy and mid-story. Conversely, mist-netting is useful for detecting quiet or skulking understory species (Ralph et al. 1995). Mist netting and point counts

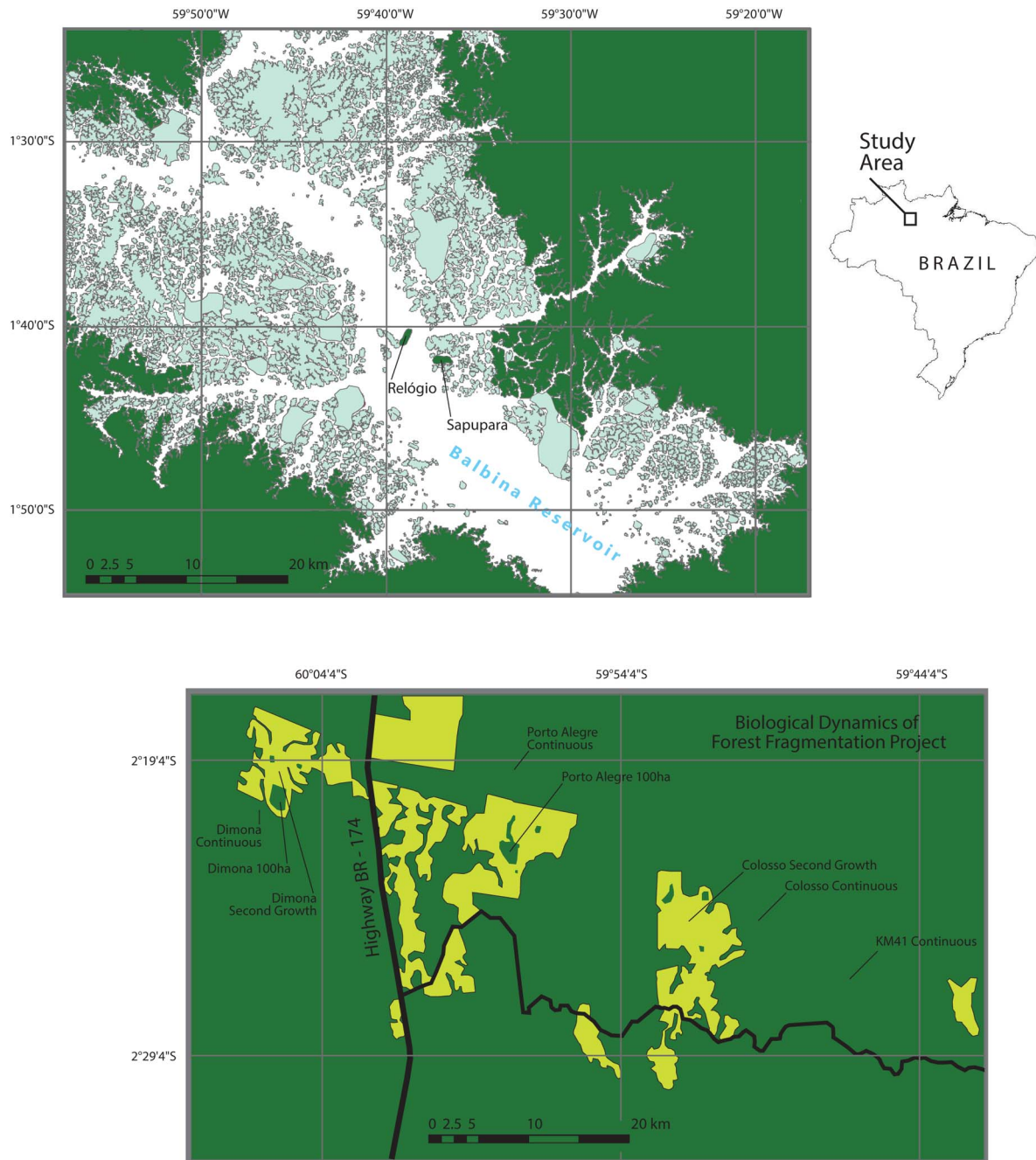


Fig. 1. Map of study regions at the Balbina reservoir and Biological Dynamics of Forest Fragments Project 80 km and 150 km north of Manaus, Brazil, respectively.

were conducted in five treatments: 100-ha forest fragment (surrounded by a 50-m buffer of 15-year-old second growth followed by a secondary 50-m buffer of 25-year-old second growth adjacent to continuous forest), 100-ha island (sur-

rounded by at least 300 m of open water within a landscape of larger islands and continuous forest), older second growth forest (25 years old adjacent to continuous forest), young second growth forest (15 years old adjacent to continu-

ous forest) and continuous forest. Treatments were aggregated into five regions: Dimona (two transects within a 100-ha forest fragment, two transects within older second growth and two transects within continuous forest), Porto Alegre (two transects within a 100-ha forest fragment and two transects within continuous forest), Colosso (two transects within older second growth forest, two transects within young second growth forest and two transects within continuous forest), KM41 (two transects within continuous forest), and Balbina (one transect on each of two 100-ha islands). Each BDFFP region was up to 50 km apart, and Balbina was 70 km to the north of the nearest BDFFP region (Fig. 1). Despite a distance of 70 km between Balbina and the other regions, each region is characterized by terre firme forest occurring on ancient soils within the Guinean Shield, resulting in comparable bird communities. Our assumption of similar bird communities across the study area is verified by earlier work that documented remarkably similar bird communities throughout the Guinean shield, from Manaus through French Guiana (Willis and Oniki 1988, Johnson et al. 2011). Furthermore, we only captured one resident species (in addition to a single migrant) at Balbina that we didn't capture at BDFFP further emphasizing the similarity of these communities.

Each transect was 200 m in length, at least 200 m apart from any neighboring transect, and hosted three point count locations at 0 m, 100 m and 200 m along the transect. Twenty minute point counts were conducted in 2012 during our study area's prolonged dry season, June through November; each point count occurred between 05:55 and 07:20 am. Given the diversity of bird species in the central Amazon, we used 20 minutes (as opposed to five or 10 minutes) to maximize the number of species encountered at each transect. For each point count, the number of individuals per species was conservatively estimated using song, call and visual documentation within a 50 m radius; flyovers were not included in the analysis. Each point-count station was visited twice by J. D. Wolfe on different days, yielding 12 20-minute point counts per treatment in each area. Each transect also hosted a line of 16 mist-nets (NEBBA-type ATX, 36 mm mesh, 12 × 2 m), with nets set with the bottom at ground level

and opened from 0600 to 1400 for a single day of sampling. All captured birds were banded with uniquely numbered aluminum bands. We mist-netted between June and November in 2010–2013, where we collected 4 days of capture data at 100-ha island transects, 4 days of capture data at young second growth transects, and 6 days of capture at 100-ha forest fragment transects, continuous forest transects and older second growth transects.

To measure differences in species richness between forest fragments, islands, regenerating matrix and continuous forest (see predictions 1 and 2), point count and capture data were organized by number of individuals per species by treatment. For capture data, the number of species captured at each transect was divided by associated effort (mist net hours) then multiplied by 100 to yield a standard number of species captured per 100 mist net hours across each transect irrespective of differences in sampling effort. We used program EstimateS (Colwell 2005) to produce Chao1 abundance-based estimates of species diversity and Chao-Jaccard abundance-based similarity indices to compare treatments. The Chao1 diversity index uses the ratio of 'singletons' and 'doubletons' (species detected only once or twice, respectively) to generate predicted estimates of species richness. Significance between Chao1 estimates are based on non-overlapping 95% confidence intervals generated through a bootstrapping routine in EstimateS. The formula used for Chao1 estimates are based on Chao (1987) where S_{obs} refers to total number of species observed in all samples pooled and F_1 and F_2 refer to singletons and doubletons (species detected only once or twice), respectively:

$$\hat{S}_{\text{chao1}} = S_{\text{obs}} + \frac{F_1^2}{F_2}$$

To measure overall community similarity between forest fragments, islands, regenerating matrix and continuous forest (see predictions 3 and 4) we used Chao's abundance-based Jaccard community similarity indices. According to Colwell (2005), Chao's abundance-based Jaccard community similarity indices are based on the probability that two randomly chosen individuals, one from each of the two samples, both belong to species shared by both samples (but

not necessarily to the same shared species; Chao et al. 2005, Colwell 2005). This approach has been shown to substantially reduce the negative bias that undermines the usefulness of traditional similarity indexes, especially with incomplete sampling of rich communities (Chao et al. 2005, Colwell 2005). The formula used for Chao-Jaccard abundance-based similarity indices are based on Chao et al. (2005), and described by Colwell (2005) where Q_1 is the frequency of uniques, Q_2 the frequency of duplicates

$$\text{var}(\hat{S}_{\text{chao2}}) = Q_2 + \left[\frac{1}{2} \left(\frac{Q_1}{Q_2} \right)^2 + \left(\frac{Q_1}{Q_2} \right)^3 + \frac{1}{4} \left(\frac{Q_1}{Q_2} \right)^4 \right]$$

and

$$\hat{S}_{\text{chao2}} = S_{\text{obs}} + \frac{Q_1^2}{Q_2}.$$

To measure community similarity between forest fragments, islands, regenerating matrix and continuous forest with respect to foraging guild (see predictions 3 and 4), we separately categorized mist-netting and point count data by foraging guild and species (following Stouffer et al. 2006; Appendix: Tables A1 and A2). We used package *Vegan* in Program R (Dixon 2003, R Development CoreTeam 2010) to separately ordinate capture and point count data, categorized by foraging guild and species within treatment, via a Detrended Correspondence Analysis (DCA). We statistically examined differences among bird communities within each treatment, by foraging guild and species, via a permutation test using 1000 iterations in package *Vegan*. In addition to estimating diversity, community similarity and ordinations, we used package *Car* (Fox et al. 2012) in program R to employ a two-way ANOVA using type III sum of squares to test guild and treatment effects on species abundance for both point count and capture data. We choose type III sum of squares ANOVA because it relies on unweighted means that account for correlations between independent variables due to unequal sample sizes.

Because our chosen diversity estimator (Chao1), community similarity metric (Chao-Jaccard abundance-based similarity index) and ordination methodology (DCA) may be sensitive to variation in effort and sample size, we also conducted a sensitivity test to ensure our results

are robust. We accounted for unequal effort among transects and treatments using the sensitivity test by randomly selecting four capture and four point count occasions per treatment (continuous, 100-ha fragment, 100-ha island, young and mature second growth) thereby creating complete equal effort among the subset of data, then repeated a portion of the above analysis on the subset of data. More specifically, we generated Chao1 diversity estimates, compared communities using the Chao-Jaccard abundance-based similarity index, and finally used package *Vegan* in Program R to ordinate and compare communities categorized by species for each treatment.

RESULTS

We recorded 3,339 individual birds representing 180 species during point counts (Appendix: Table A1). We banded 3,916 individual birds representing 121 species (Appendix: Table A2). Our first prediction, that islands are less species rich than fragments, was supported by point count data where we found significantly fewer bird species on true islands compared to fragments and all other treatments except young second growth (Fig. 2). Although not significant, capture data also yielded the lowest number of species on true islands relative to fragments and all other treatments (Fig. 2). Similarly, point count and capture data supported our second prediction that young second growth would host fewer species than mature second growth; young second growth was the most species depauperate compared to all other non-island treatments (Fig. 2). Our third prediction, that island and fragment bird communities would be significantly different, was supported by both point count and capture data. For example, the Chao-Jaccard abundance-based similarity index at the treatment scale suggested that islands and fragments were the third and second most dissimilar bird community using capture and point count data, respectively, when ranked against all other possible treatment comparisons (Fig. 3). Similarly, at the region scale, island bird communities were the most dissimilar when compared to all other regions (Appendix: Fig. A1). Supporting the assertion that island communities are the most dissimilar, Detrended Correspondence

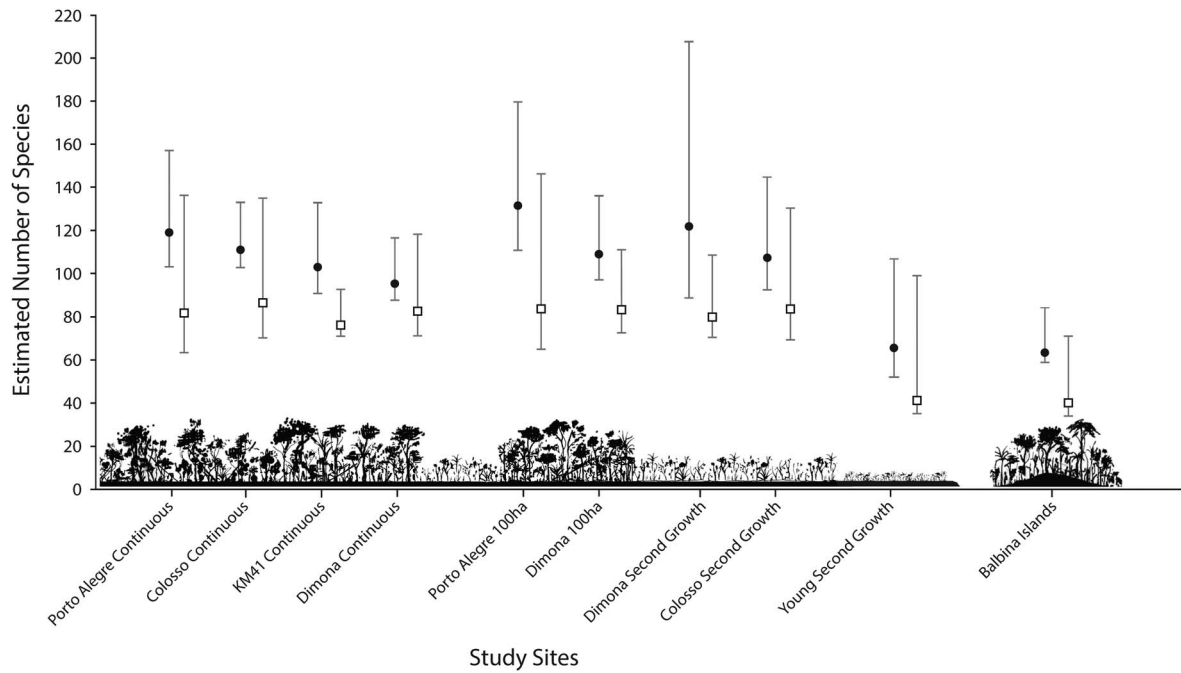


Fig. 2. Chao's estimated number of species by treatment (10-ha forest fragment, 100-ha island, continuous, older second growth forest, and young second growth forest) and region. Filled circles represent point count and open boxes represent capture data. All values are shown with 95% confidence intervals.

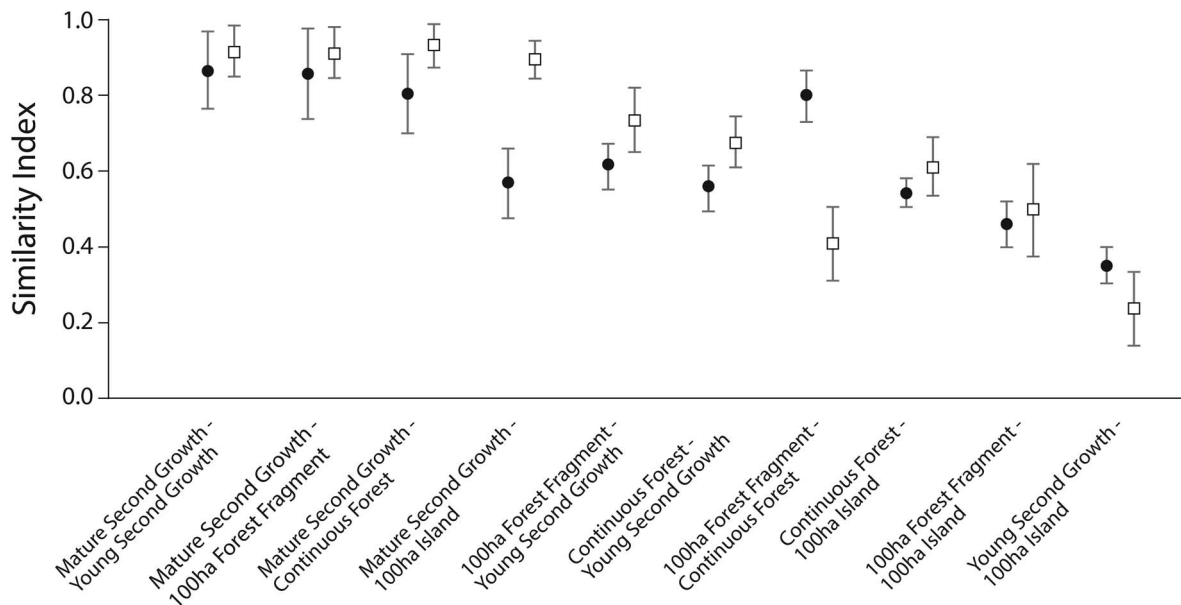


Fig. 3. Chao's abundance-based Jaccard community similarity indices based on point count data by treatment shown with standard error bars. Filled circles represent point count and open boxes represent capture data. Comparisons are ranked from most to least similar.

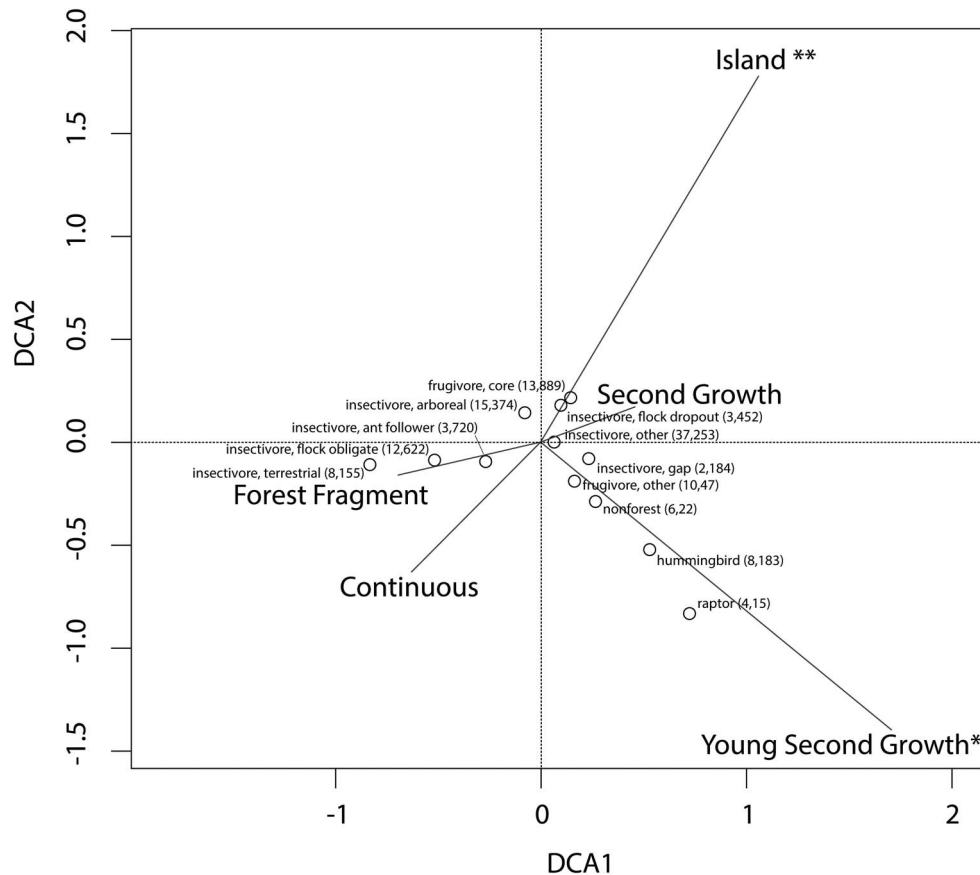


Fig. 4. Detrended correspondence analysis (DCA) ordination of capture data, classified by foraging guild and treatment. Asterisks represent significance levels where * and ** represent $p < 0.1$ and $p < 0.05$, respectively. Numbers in parentheses represent number of species within foraging guild and total number of individuals captured within each foraging guild.

Analysis (DCA) results suggested that, based on mist-net data, true islands represented significantly different communities ($p < 0.05$) when classified by foraging guild and species (Figs. 4 and 5). Guild ordinations based on point count data also suggested that true islands approached significance ($p < 0.1$). Support for our fourth prediction, that young and mature second growth bird communities would be significantly different, was not supported by the Chao-Jaccard abundance-based similarity index at the treatment scale based on species captured (Fig. 3). However, when grouped by guild, the DCA ordination based on capture data yielded a significant difference between young second growth and mature second growth thereby supporting our fourth prediction (Fig. 4). These

differences were driven by the abundance of non-forest and hummingbird foraging guilds associated with young second growth (Appendix: Table A1).

In general, continuous, forest fragment and older second growth bird communities were most similar irrespective of method (mist-netting or point count). Estimated diversity and community similarity analyses showed that bird communities on true islands and in young second growth forest were most depauperate and dissimilar from communities in continuous forest. Interestingly, when classified by species, forest fragment, older second growth, young second growth and true islands all yielded significantly different bird communities ($p < 0.05$; Figs. 6 and 7). Our two-way ANOVA using

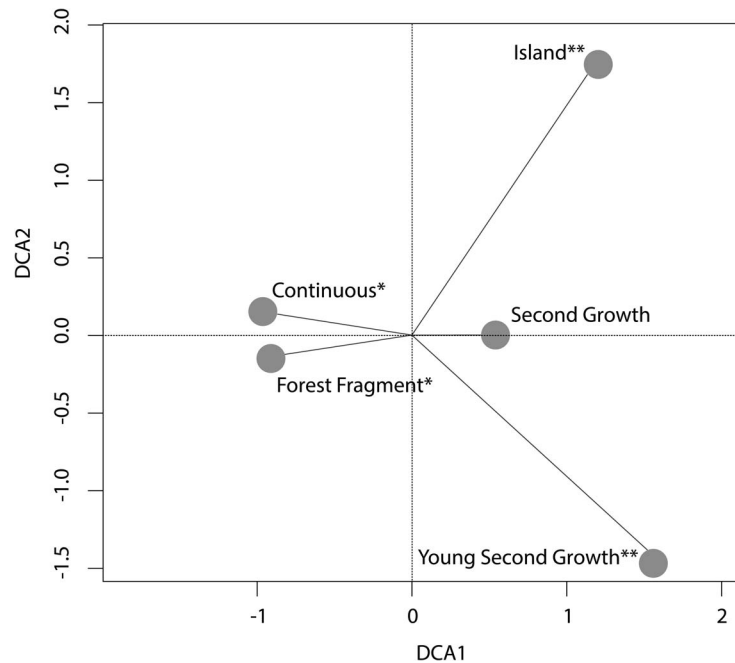


Fig. 5. Detrended correspondence analysis (DCA) ordination of capture data, classified by foraging guild and treatment. Asterisks represent significance levels where * and ** represent $p < 0.1$ and $p < 0.05$, respectively.

type III Sum of Squares based on foraging guild classification, for point count ($df = 48$, $f\text{-stat} = 10.04$, $p < 0.001$) and mist-net data ($df = 44$, $f\text{-stat} = 6.57$, $p < 0.001$) yielded highly significant differences among treatments and guilds. Differences were driven by high number of core frugivores in older second growth, and the absence of flock obligates, flock dropouts and terrestrial insectivores on true islands and in young second growth (Appendix: Figs. A2 and A3). Finally, our sensitivity test, where we generated the same statistics using a subset of data with equal effort, clearly demonstrated that differences in sampling effort did not bias our results where islands yielded half the number of estimated species than forest fragments (Appendix: Tables A3 and A4). Additionally, the DCA ordination based on equal capture and point count effort suggested that islands represented significantly different bird communities (Appendix: Figs. A4 and A5).

Several species intolerant to second growth (e.g., documented in continuous forest but never in regenerating forest) were found on true islands: *Piaya melanogaster*, *Celeus undatus*, *Tyrannetes virescens*, and *Ramphotrigon ruficauda*.

Additionally, two species particularly common in second growth samples were also found on true islands: *Myiarchus ferox* and *Notharchus macrorhynchus* (although, *N. macrorhynchus* more associated with older forest at BDFFP; Cohn-Haft et al. 1997). In general, woodpeckers (Picidae) and toucans (Ramphastidae) were well represented on true islands while terrestrial insectivores (e.g., *Formicarius colma*, *Corythopsis torquatus* and *Sclerurus ruficularis*) and obligate flocking species (e.g., *Thamnomanes caesius* and *T. ardesiacus*) were absent from true islands (Appendix: Tables A1 and A2).

DISCUSSION

The succession of bird communities in second growth facilitated the recolonization of forest fragments, permitting fragments as small as 100 ha to support bird communities similar to continuous forest. Clearly, a regenerating forest matrix is not as hostile as open-water, thereby demonstrating that island biogeography is not an appropriate model to predict species loss in forest fragments at our study site in the central Amazon. We suggest future site studies use a

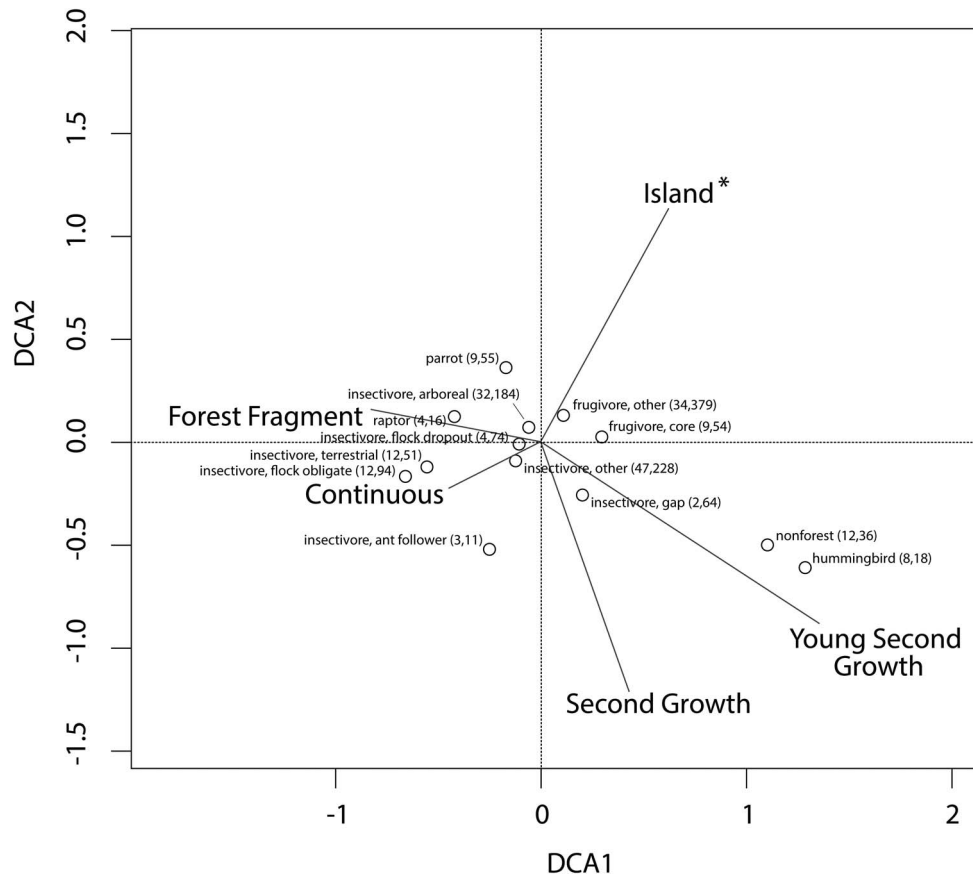


Fig. 6. Detrended correspondence analysis (DCA) ordination of capture data, classified by foraging guild and treatment. Asterisks represent significance levels where * represents $p < 0.1$. Numbers in parentheses represent number of species within foraging guild and total number of individuals captured within each foraging guild.

countryside biogeographic framework to examine how diverse Amazonian bird communities perceive and use regenerating forest matrices. In general, we found support for each of our four predictions used to examine the processes responsible for differences in bird species richness and community assemblages between islands and forest fragments, and young and mature second growth, respectively. With regard to differences in diversity and community assemblages between islands and fragments (predictions 1 and 3), our study demonstrated that species richness in forest fragments within a regenerating matrix is not driven by extinction dynamics as predicted by the island model. Instead, species richness appears to be dependent on the permeability of the surrounding matrix, which allows recovery of bird communities in

formerly isolated fragments. In contrast, for true islands, small area coupled with the complete absence of an adjacent second growth matrix subjected each island to severe and irreconcilable local extinction events despite the presence of primary forest at our study site.

With regard to differences in diversity and community assemblages between young and mature regenerating forest (predictions 2 and 4), we found that bird communities varied significantly, when separated by guild, between young (15 year) and older (25 year) second growth; such differences appear to have been driven by the absence of terrestrial insectivores and flocking species, and the abundance of nonforest species, gap-specialists and hummingbirds in young second growth. Our study clearly demonstrated that foraging guilds closely asso-

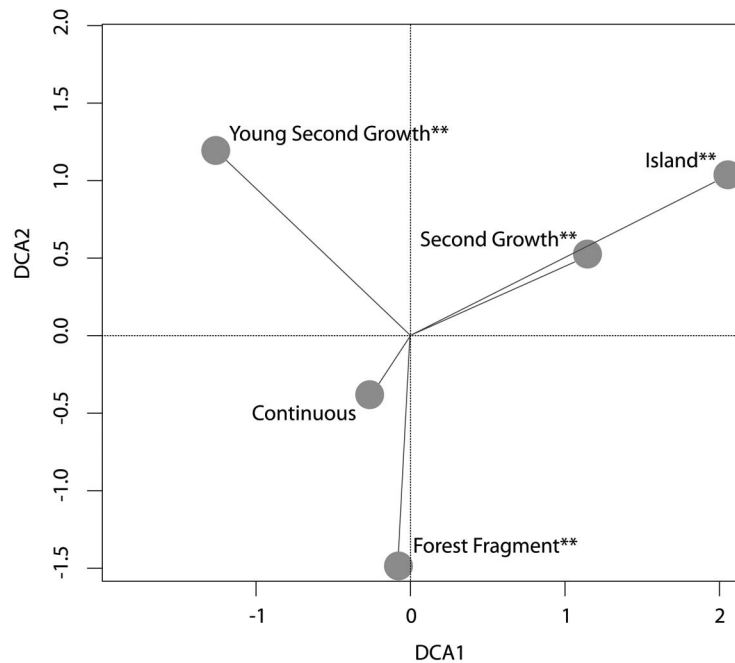


Fig. 7. Detrended correspondence analysis (DCA) ordination of capture data, classified by foraging guild and treatment. Asterisks represent significance levels where ** represents $p < 0.05$.

ciated with forest, such as terrestrial insectivores and flocking species, perceive and use young and mature second growth very differently. Within 25 years of clearing, many forest-dwelling birds are frequently encountered within second growth thereby creating a community more reflective of those found in continuous forest. Whether or not these pioneering birds form stable populations in mature second growth or persist through the addition of dispersing individuals from source populations is not known and represents an important facet of further study.

We also found that young second growth was species poor, with approximately the same number of species as true islands. Despite similar number of species, community structure at the levels of both guild and species were statistically different between true islands and young second growth. Differences in community structure coupled with low species richness suggest two divergent responses to dissimilar system perturbations: second growth bird communities reflect the successional nature of regenerating forest where gap specialists, nonforest species, and hummingbirds are replaced by flocking and insectivorous species as the forest approaches

25 years of age. Conversely, islands are characterized by species capable of major dispersal events and small remnant populations of forest-obligate species.

Although the complexity of the landscape used in this study hinders generalizing our results to other tropical systems, our results do support previous assertions that a species' capacity to disperse through matrix to recolonize tropical forest fragments ultimately determines metapopulation connectivity in degraded landscapes (Sekercioglu et al. 2002). Interestingly, several species absent from second growth at BDFFP were detected on true islands. Although we can't be sure, we believe these species are remnants from populations present at the time the reservoir was flooded. Conversely, many solitary ground-dwelling insectivores and core-flocking species that are common in continuous forest and easily detected with both sampling techniques were conspicuously absent from true islands, indicating the inability of these guilds to recolonize islands across open water. This finding is not surprising given previous studies found that these same guilds were less apt to cross open spaces and most prone to go extinct in forest

fragments immediately after isolation (Ferraz et al. 2003, Laurance et al. 2004, Stouffer et al. 2006, Stouffer et al. 2009). Although open water is not suitable for many dispersing forest-dwelling birds, the remains of dead trees above the water's surface are common throughout the reservoir and presumably facilitate the dispersal of species capable of utilizing snags (Appendix: Fig. A6). In fact, that is what we found: woodpeckers and toucans used snags on the open water and had relatively high diversity on islands (Appendix: Table A1).

Our results parallel findings from another tropical reservoir where smaller and more isolated islands (1–12 ha in size and $1 \text{ km} \leq$ from source populations) had fewer species and fewer transient individuals capable of recolonization (Terborgh et al. 1997). Although we don't know the mechanism responsible for extinction events within islands at our study sites, given similarities between our findings and Terborgh et al. (1997), we suspect that communities were altered by biological (remnant mesopredators) and stochastic (extinction) processes leading to a dynamic equilibrium. Relative to Terborgh et al. (1997), however, our island sites were larger (100 ha) and farther from source populations, thereby reducing area effects associated with small habitat patches (Terborgh et al. 1997, Stouffer et al. 2006, 2009). We believe our depauperate true island diversity estimate probably represents an ongoing extinction debt which will result in future equilibrium characterized by low species richness, including only those birds most capable of dispersing and most resilient to the effects of fragmentation (Ferraz et al. 2003). Thus, we recognize that differences in species assemblage and richness between true islands and other forest types may be dependent on how long the islands have been isolated thereby determining if an extinction debt has been paid in-full. Overall, islands are an extinction driven system, forest fragments in regenerating matrix are a recolonization driven system, and second growth is a successional driven system at our study site in the central Amazon.

In addition to informing ecological theory, our study has important conservation implications. For example, we provide evidence of a dynamic relationship between bird communities and degraded tropical landscapes, an understanding

that is important for conservation purposes for regions with unparalleled diversity, such as the Amazon basin. Over the last 20 years the Brazilian government subsidized forest clearing to enhance farming opportunities for an expanding populace resulting in the loss of 328,000 km² of Amazonian forest (INPE 2010). In addition to agricultural expansion, the Brazilian government authorized the construction of 30 additional hydroelectric dams in the Amazon basin, resulting in, on average, one new dam being constructed every four months over the next seven years (Eletrobrás 1987, Ministério de Minas e Energia 2011). The threat of massive Amazon forest loss due to hydroelectric development is considerable given that a single dam in the central Amazon, Balbina, flooded 2360 km² of tropical rainforest (Fearnside 1989). Dams lead to hilltop islands surrounded by water, a much more static landscape than when forest is removed for agriculture. Such differences mean that islands and isolated habitats behave differently and represent a larger threat to the preservation of biodiversity than habitat patches within a matrix. These ecological, economic and political realities coupled with our results suggest that many more bird communities will be subject to the deleterious effects of ecological decay associated with hydroelectric development.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

The Appendix can be found online: <http://dx.doi.org/10.1890/ES15-00322.1.sm>