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ORIGINAL PAPER

Temporal bird community dynamics are strongly affected by landscape fragmentation in a Central American tropical forest region

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Abstract Habitat loss and fragmentation are considered the main causes of species extinctions, particularly in tropical ecosystems. The objective of this work was to evaluate the temporal dynamics of tropical bird communities in landscapes with different levels of fragmentation in eastern Guatemala. We evaluated five bird community dynamic parameters for forest specialists and generalists: (1) species extinction, (2) species turnover, (3) number of colonizing species, (4) relative species richness, and (5) a homogeneity index. For each of 24 landscapes, community dynamic parameters were estimated from bird point count data, for the 1998–1999 and 2008–2009 periods, accounting for species' detection probability. Forest specialists had higher extinction rates and a smaller number of colonizing species in landscapes with higher fragmentation, thus having lower species richness in both time periods. Alternatively, forest generalists elicited a completely different pattern, showing a curvilinear association to forest fragmentation for most parameters. Thus, greater community dynamism for forest generalists was shown in landscapes with intermediate levels of fragmentation. Our study supports general theory regarding the expected negative effects of habitat loss and fragmentation on the temporal dynamics of biotic communities, particularly for forest specialists, providing strong evidence from understudied tropical bird communities.

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Introduction

The modification of natural systems by humans and associated habitat loss for biodiversity are considered the main causes of species extinctions (Wilson and Peter 1988; Lindenmayer and Fischer 2006), particularly in tropical ecosystems (Pimm and Raven 2000; Millennium Ecosystem Assessment 2005). Habitat modification at the landscape scale affects the distribution and abundance of organisms (Lindenmayer and Fischer 2006; Turner et al. 2001), and for habitat specialists, habitat reduction and fragmentation can cause disruptions in key biological processes such as reproduction, dispersion and resource acquisition (Saunders et al. 1991; Harrison and Bruna 1999; Lindenmayer and Fischer 2006).

In landscapes with greater habitat fragmentation, the theories of island biogeography (MacArthur and Wilson 1967; Simberloff 1974; Lomolino 2000) and metapopulations (Hanski and Gilpin 1991; Hanski 1998; Hanski and Ovaskainen 2002) predict greater extinction rates. Both theories predict that a population in a small, isolated habitat fragment, or a metapopulation consisting of small, isolated fragments is necessarily more threatened by extinction than a population in a large, well connected patch, or a metapopulation consisting of large, well connected fragments, mainly due to a smaller population size and lower colonization rates.

At the community level, higher extinction and lower colonization rates of habitat specialists should translate into lower species richness. Alternatively, dynamic ecological systems offer unsaturated habitats, providing colonization opportunities for generalist species (Boulinier et al. 2001). For a community in a dynamic state of equilibrium, island biogeography theory predicts that the expected number of local extinctions should be equal to the expected number of colonizations (MacArthur and Wilson 1967; Simberloff 1974). If the community is not in equilibrium, then species richness should be increasing or decreasing in time. Thus, the degree of community equilibrium can be evaluated by examining the estimated rates of change in species richness (or relative species richness) and the number of colonizing species (Boulinier et al. 2001).

Island-biogeography theory (IBT) has been criticized for its extreme simplification of extinction-colonization dynamics in terrestrial forest ecosystems (Laurance 2008), because what is considered "the inhospitable matrix", or the collection of modified vegetation types in the landscape matrix, in fact provides differential suitabilities for species survival, while IBT assumes it is homogeneous (Brown and Lomolino 2008). For species with a greater habitat breadth, their ability to exploit a wider range of secondary habitats in the landscape matrix probably enhances their ability to traverse suboptimal habitat in order the reach primary habitat patches, and the opposite would be expected for habitat specialists (Cerezo et al. 2010). Consequently, the landscape matrix is affecting the degree of connectivity of habitat patches for species with differential dispersal abilities, directly affecting extinction-colonization dynamics. Both island-biogeography and metapopulation theories hold the degree of connectivity as one of the two central aspects governing extinction-colonization dynamics in fragmented landscapes (the other being habitat amount or fragment size). Nevertheless, IBT oversimplifies natural systems by assuming that there are no differences in specieś abilities to disperse between habitat patches (Brown and Lomolino 2008). In our study, we build upon island-biogeography and metapopulation theories, especially on the importance they both attribute to the temporal, dynamic nature of communities in fragmented landscapes, but incorporate the advances made through tropical bird life-history ecology and countryside biogeography (Daily et al. 2001; Wolfe et al. 2015), specifically, the importance of the landscape matrix for extinction-immigration dynamics in fragmented landscapes, in our analytical approach or discussion.

Other changes in community composition in time, not necessarily involving species extinction or colonization, can be associated with an increase in habitat fragmentation. Human alteration is recognized as a principal force in the homogenization of natural communities (Lockwood et al. 2000; Olden et al. 2004; Olden 2006). Because habitat specialists are considered more vulnerable to the effect of habitat modification than generalist species (Henle et al. 2004), the current trend is for generalist species to dominate modified natural communities, which should lead to taxonomic and functional homogenization (Olden 2006; Devictor et al. 2008a).

Albeit the importance of these time-dependent effects of habitat loss and fragmentation on biotic communities, most fragmentation studies are carried out in a discrete moment in time, and are therefore not capable of registering important community dynamics that potentially operate in the medium and long term in modified landscapes (Ewers and Didham 2005). This work evaluated the temporal dynamics of bird communities in landscapes with different levels of tropical forest fragmentation in eastern Guatemala, by comparing bird community dynamics in fragmented landscapes between 1998–1999 and 2008–2009. We adopt the definition of fragmentation as "the process by which habitat loss leads to a greater number of smaller patches of lower total area, isolated from each other by a matrix of dissimilar habitats" (Wilcove et al. 1986, Fahrig 2003; Didham et al. 2012). Although it has been argued that it is important to evaluate the effects of fragmentation on biotic communities that are independent of forest cover (Andrén 1994; Fahrig 1998; Villard et al. 1999; Trzcinski et al. 1999; Fahrig 2003), fragmentation is often strongly and negatively correlated with forest cover in true landscapes (i.e., fragmentation increases with habitat loss; Gustafson and Parker 1992; Fahrig 2003; Lindenmayer and Fischer 2006; Fischer and Lindemayer 2007). Consequently, the adopted definition of habitat fragmentation and empirical results of the relationship between habitat (e.g., forest) cover and fragmentation imply that these two processes are closely and causally related, fragmentation being necessarily a consequence of habitat loss (Didham et al. 2012).

Methods

Study area, bird sampling, and GIS analysis

The study was carried out in Cerro San Gil Reserve (henceforth, CSG) and its surrounding areas, in eastern tropical Guatemala (Fig. 1; 15° 40′ 32.03′′ N, 88° 45′ 34.08′′ W). The natural, predominant habitat type is Central American Atlantic Moist Forest, according to the Ecoregions classification of Olson (2001), with mean annual precipitation and temperature of 3000 mm and 26.7 °C, respectively (INSIVUMEH, 2005). Since the 1950s, approximately 65 % of its surface has been converted to cattle pastures or cropping areas, and recently, forest plantations and oil-palm (Castellanos et al. 2011, Regalado et al. 2012).

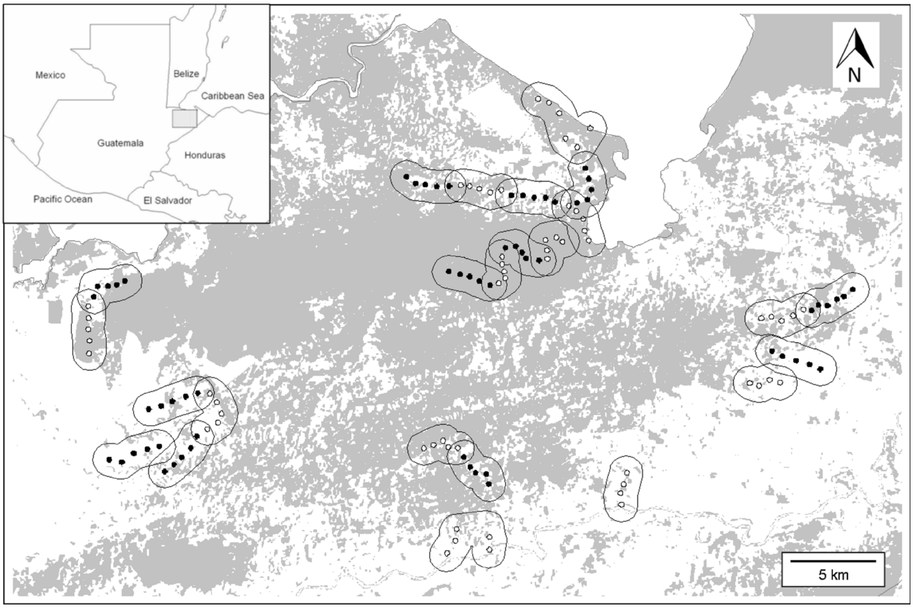


Fig. 1 Study area (*inset*) in eastern Guatemala. Tropical forest cover appears in *light gray*. Surveyed landscapes are shown. *Black* and *white circles* indicate survey points (sub-samples) corresponding to different surveyed landscapes

In 1996, a network of 210 bird monitoring point counts was established, on secondary and tertiary roads, within and around CSG (Fig. 1; the reserve consists mainly of the large forest block in the center of the image, and surrounding areas). Point count locations are separated by 500–600 m, and the network is sampled annually, between the last week of April and the first week of May. In each location, during 5 min, note is taken of all bird species and individuals seen or heard. For our evaluation of forest bird community dynamics, we used data for the 1998–1999 and 2008–2009 periods. Surveys in both time periods (1998–1999) and (2008–2009) where conducted by A. Cerezo and a second observer which differed between years. The second observer in 2008–2009 was trained by A. Cerezo (M. Ramírez) so we expected observer bias to be negligible between the two time periods.

We evaluated changes in forest fragmentation in the studied landscapes using forest cover classifications from the years 2001 and 2010, developed by a partnership between the National Forest Institute, National Council for Protected Areas, and Rafael Landívar and Del Valle universities of Guatemala (Castellanos et al. 2011, Regalado et al. 2012). Studied landscapes consisted of areas that contained a series of five point counts (with some exceptions; some landscapes contained four or six points, see Fig. 1). Landscape area was defined by a 1-km radius around a line that connected the points in each landscape, and varied between 675 and 1344 ha (mean = 867 ± 136 ha). Twenty-four (24) landscapes were included in the study (Fig. 1). The 1-km radius was used because most species responded to this radius in a previous, species-specific study in the region (Cerezo et al. 2010).

To quantify forest fragmentation, we used the landscape division index (Jaeger 2000), which has the following desirable properties: 1) low sensitivity to very small patches, as opposed to the mean patch size; 2) monotony of its reaction to different fragmentation phases (perforation, incision, dissection, dissipation, shrinkage and attrition, sensu Forman 1995; Jaeger 2000), as opposed to the number of patches, which has a non-linear response to fragmentation (Gustafson and Parker 1992; Saura and Martínez-Millán 2000; Fahrig 2003). The landscape division index (Jaeger 2000) discriminated among landscapes that where indistinguishable using forest cover, particularly at intermediate levels of forest cover (Fig. 2).

Statistical analysis

Four temporal bird community dynamic parameters were estimated for each landscape (see next paragraph for their description). Furthermore, because different ecological processes may affect species depending on their habitat dependence, habitat specialists being necessarily more threatened than generalists (Henle et al. 2004), all parameter estimations were carried out for two species groups: forest specialists, species that are completely dependent on native tropical forest, and forest generalists, species that depend on tropical forest but are frequently detected in other vegetation types. Assignment of species to these two groups was done according to Stotz et al. (1996) and Cerezo et al. (2009, 2015).

The estimated community dynamic parameters were: (1) extinction rate, $1 - \hat{\varphi}_{12}$, where $\hat{\varphi}_{12} = \frac{\hat{M}_2^{(R_1)}}{R_1}$, $\hat{M}_2^{(R_1)}$ is the number of observed species in the first time period that are estimated to be present in the second period, and R_1 is the number of observed species in the first period; (2) species turnover rate, $1 - \hat{\gamma}_{21}$, where $\hat{\gamma}_{21} = \frac{\hat{M}_1^{(R_2)}}{R_2}$, $\hat{M}_1^{(R_2)}$ is the number of observed species in the second period estimated to have been present in the first period and R_2 the number of observed species in the second period; (3) number of colonizing species, $\hat{B} = \hat{N}_2 - \left(\hat{\varphi}_{12} \times \hat{N}_1\right)$, where $\hat{N}_1$ y $\hat{N}_2$ are the estimated number of species for the first and second time periods, respectively, and; (4) relative species richness, $\hat{\lambda}12 = \hat{N}2\big/\hat{N}1$(Nichols et al. 1998); (5) species homogenization index, calculated as the change in the proportion of estimated generalist species between the two periods (DeVictor et al. 2007).

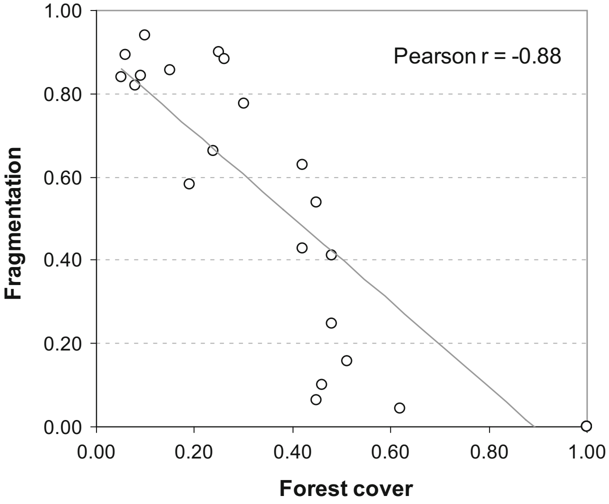


Fig. 2 Relationship between the landscape division index, used for quantifying forest fragmentation, and forest cover. The index distinguished landscapes with varying fragmentation at intermediate levels of forest cover

Estimation of parameters associated with community dynamics where carried out with COMDYN software, which produces estimates (and their variances) that take into account heterogeneity in species detection probability within a period and among periods (Hines et al. 1999; Nichols et al. 1998). The basic estimator for species richness that underlies these statistical procedures is the Jackknife estimator proposed by Burnham and Overton (1979) for mark-recapture data. The different points within each landscape were used as subsamples, which are necessary for the Jackknife estimation process (Boulinier et al. 2001; Burnham and Overton 1979).

The relationship between the estimated bird community parameters and tropical-forest fragmentation was evaluated with generalized linear models (Zuur et al. 2009). Predictive variables in linear models were forest fragmentation in 2001 (“fragmentation” in Table 2) and its squared polynomial (“fragmentation^2”), and change in forest fragmentation (“frag. change”) and forest cover (“cover change”) between the two time periods (2001 and 2010; see Table 2). Because of the spatial nature of our experimental units (landscapes), errors were modeled with an exponential spatial autocorrelation structure (Pinheiro and Bates 2000). These models with spatially-correlated errors where compared with models without spatially-correlated errors (assuming independence between experimental units) using the Akaike information criterion (AIC, Burnham and Anderson, 1998). For all community parameters, the models with greatest support (i.e., smallest AIC value) were those without spatially-correlated errors (i.e., lower AIC values, Table 1). Although some differences in AIC values might indicate relative support for models with a spatial autocorrelation error structure (ΔAIC < 2), this small difference basically indicates that there is no substantial gain in model specification and fit by adding a spatial error structure. In these cases, it is recommended to retain the model with the simplest structure (Zuur et al. 2009).

All response variables were modeled assuming normally-distributed errors, and when variables did not meet model assumptions (normality and homogeneity of variances), these where transformed using a logit transformation for extinction and turnover rates, and a log

Table 1 AIC values for full models with and without spatial autocorrelation in errors

	Models with spatial autocorrelation	Models without spatial autocorrelation
Interior-forest species		
Species richness 98–99	29.29	28.53
Species richness 08–09	20.01	18.86
Extinction rate	44.81	43.10
Turnover rate	39.92	37.97
Relative species richness	25.63	23.79
Number of colonizing species	41.59	39.62
Homogeneity index	−3.63	−4.22
Edge-generalist species		
Species richness 98–99	38.65	38.3
Species richness 08–09	22.79	20.79
Extinction rate	47.26	47.00
Turnover rate	60.14	58.15
Relative species richness	36.84	37.08
Number of colonizing species	−10.68	−11.61

transformation for species richness variables (including relative species richness and the number of colonizing species) (Zuur et al. 2009). Linear models of the homogeneity index met statistical assumptions. The significance level (α) for all statistical tests was 0.05. Linear model analyses were carried out with Infostat (Di Rienzo et al. 2008) and R (nlme package, function “gls”, Pinheiro et al. 2013) softwares.

Results

Estimated species richness for forest specialists decreased significantly in both periods (1998-1999 and 2008-2009) with fragmentation in 2001, but estimated species richness for 2008-2009 was not associated with changes in forest fragmentation or cover between periods (Fig. 3a, b; Table 2). The estimated extinction rate was significantly associated with forest fragmentation in 2001, increasing with fragmentation (Fig. 3c). The species turnover rate (Fig. 3d) and relative species richness for forest specialists (Fig. 3e) were not significantly associated to forest fragmentation in 2001 (Table 2). The number of colonizing species was significantly associated with forest fragmentation in 2001, decreasing with fragmentation (Fig. 3f). None of the estimated parameters for forest specialists were significantly associated to change between periods in forest cover or fragmentation (Table 2).

For forest generalists, species richness for both time periods elicited a significant curvilinear relationship with fragmentation in 2001 (Figs. 4a, b), but were not significantly associated with change in fragmentation or cover between periods (Table 2). Species turnover rate was positively associated to fragmentation in 2001 (Fig. 4d), and negatively associated to change in fragmentation between periods, but these relationships were marginally significant ($p = 0.08$ and 0.09, respectively, Table 2). Turnover rate was not associated to change in forest cover between periods (Table 2). Extinction rate and relative species richness for this group were neither significantly associated to fragmentation in 2001 (Fig. 4c and e, respectively) nor to change in fragmentation or cover between periods (Table 2). The number of colonizing species, as was the case for estimated species richness for both periods, elicited a significant curvilinear relationship with fragmentation in 2001 (Fig. 4f). Finally, the homogenization index (i.e., the change in the proportion of generalist species between periods) was not significantly associated with fragmentation in 2001 or to fragmentation and cover changes between periods (Fig. 5, Table 2).

Discussion

In an 8-year period, the studied landscapes showed a relatively high degree of dynamism in several estimated community parameters. Greater extinction rates for forest specialists were found in landscapes with increasing fragmentation in 2001 (but not to change in fragmentation between periods), as predicted by island biogeography (MacArthur and Wilson 1967) and metapopulation theories (Hanski and Gilpin 1991; Hanski 1998). Other studies have found similar results at the landscape scale in temperate regions (Boulinier et al. 2001), and at the patch scale in tropical regions (Stratford and Stouffer 1999; Şekercioğlu et al. 2002; Ferraz et al. 2003; Borgella and Gavin 2005; Sigel et al. 2006; Stouffer et al. 2009; Laurance et al. 2011). A negative relationship between species richness for both periods and the number of colonizing species and fragmentation also

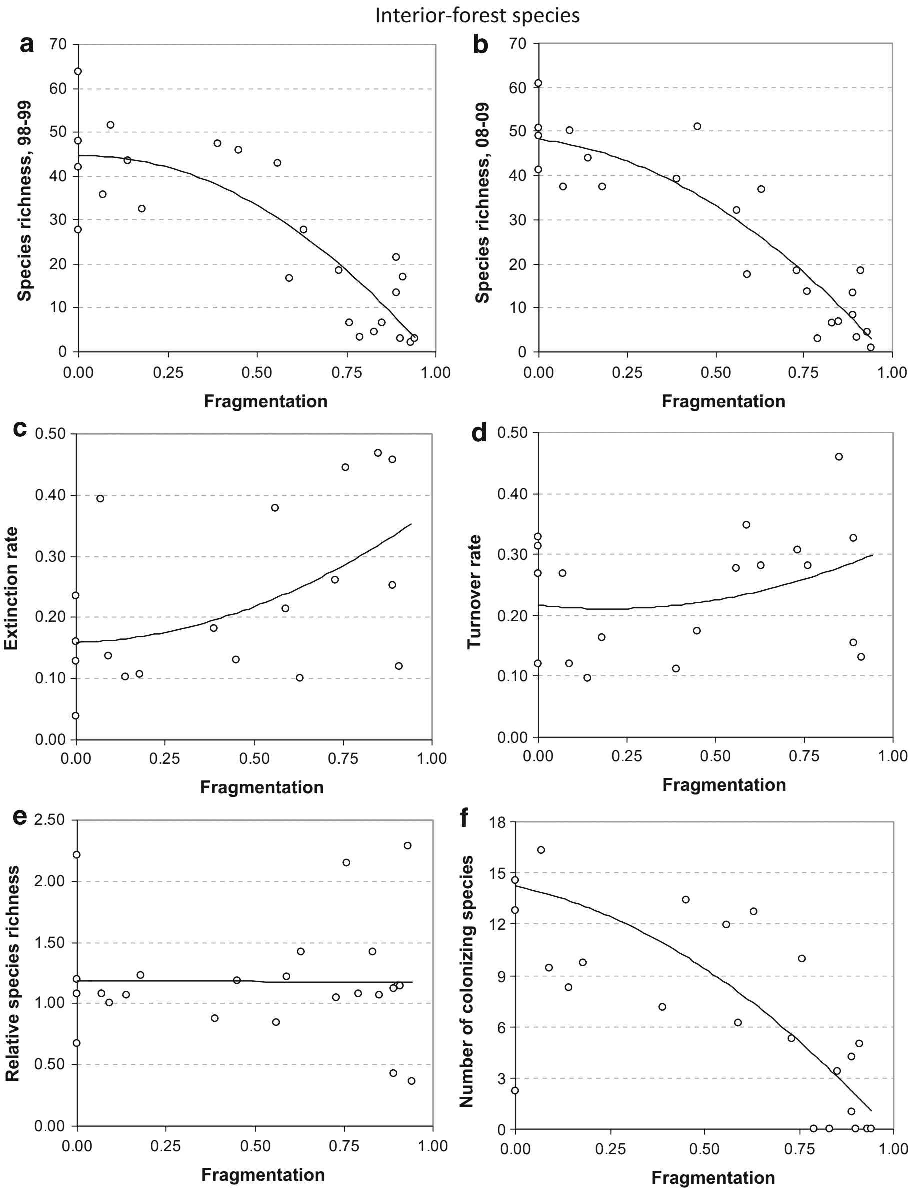


Fig. 3 Relationship between estimated community dynamic parameters and forest fragmentation in 2001 for forest specialists. *Fitted lines* are shown for illustrative purposes only. Significant coefficients in models ($p < 0.05$) can be seen in Table 2

agrees with theory: because forest specialist species richness is negatively related to fragmentation, a lower number of colonizing species is expected in highly-fragmented landscapes.

In contrast, community dynamic parameters for forest generalists showed strikingly different patterns. Most parameters showed a curvilinear relationship with fragmentation,

Table 2 Generalized linear model results

Community parameter	Landscape variable	β	Interior-forest species			Edge-generalist species	
			S.E.	*p* value	β	S.E.	p value
Species richness in 98–99	Fragmentation	−1.51	0.33	*0.00*	−0.17	0.28	0.55
	Fragmentation^2	−2.02	1.53	0.21	−3.49	1.42	*0.02*
Species richness in 08–09	Fragmentation	−1.75	0.23	*≤0.001*	0.03	0.18	0.87
	Fragmentation^2	−2.55	1.09	*0.03*	−4.53	0.89	*≤0.001*
	Frag. change	0.23	0.52	0.66	0.58	0.48	0.24
	Cover change	−1.71	1.24	0.19	−1.57	1.01	0.14
Extinction rate	Fragmentation	1.25	0.55	*0.04*	−0.57	0.36	0.13
	Fragmentation^2	0.68	2.58	0.83	−2.84	1.78	0.13
	Frag. change	1.19	1.23	0.35	−0.68	0.95	0.49
	Cover change	1.29	2.95	0.67	−2.72	1.35	0.19
Turnover rate	Fragmentation	0.46	0.46	0.34	−0.89	0.48	0.08
	Fragmentation^2	0.83	2.15	0.70	−3.68	2.39	0.14
	Frag. change	−0.14	1.03	0.89	−2.26	1.77	0.09
	Cover change	−0.35	2.45	0.89	0.77	2.7	0.78
Number of colonizing species	Fragmentation	−1.45	0.49	*0.01*	0.20	0.56	0.73
	Fragmentation^2	−3.68	2.28	0.13	−8.43	2.80	*0.007*
	Frag. change	0.74	1.09	0.51	−0.21	1.50	0.89
	Cover change	−2.84	2.60	0.29	−1.22	3.16	0.71
Relative species richness	Fragmentation	−0.19	0.28	0.51	0.15	0.27	0.59
	Fragmentation^2	−0.69	1.30	0.60	−1.15	1.37	0.41
	Frag. change	−0.01	0.62	0.98	−0.55	0.73	0.46
	Cover change	−1.14	1.48	0.45	0.88	1.55	0.58
Homogeneization index	Fragmentation	0.13	0.10	0.23			
	Fragmentation^2	−0.28	0.48	0.56			
	Frag. change	−0.14	0.23	0.54			
	Cover change	0.34	0.54	0.54			

Estimated coefficients and their standard errors and corresponding p values are shown

Italicized values are statistically significant ($\alpha = 0.05$)

showing peaks in species richness (for both periods) and the number of colonizing species richness in intermediate levels of fragmentation. Also, a shift in this pattern along the fragmentation gradient was observed between periods for generalist species richness: highest values in 1998–1999 were found nearest the lower end of fragmentation (below 0.5), and nearer the higher end of fragmentation in 2008–2009 (above 0.5), which coincided with a peak in the number of colonizing species at these levels of fragmentation. Although species turnover rate was not significantly associated with fragmentation, turnover rates in landscapes with higher fragmentation had much higher values (on average) than less fragmented landscapes. Apparently, community dynamism especially in more fragmented landscapes is driven by forest generalists.

Mean relative species richness values (the ratio between the estimated species richnesses for 2008–2009 and 1998–1999) for forest specialists where approximately 1 (with

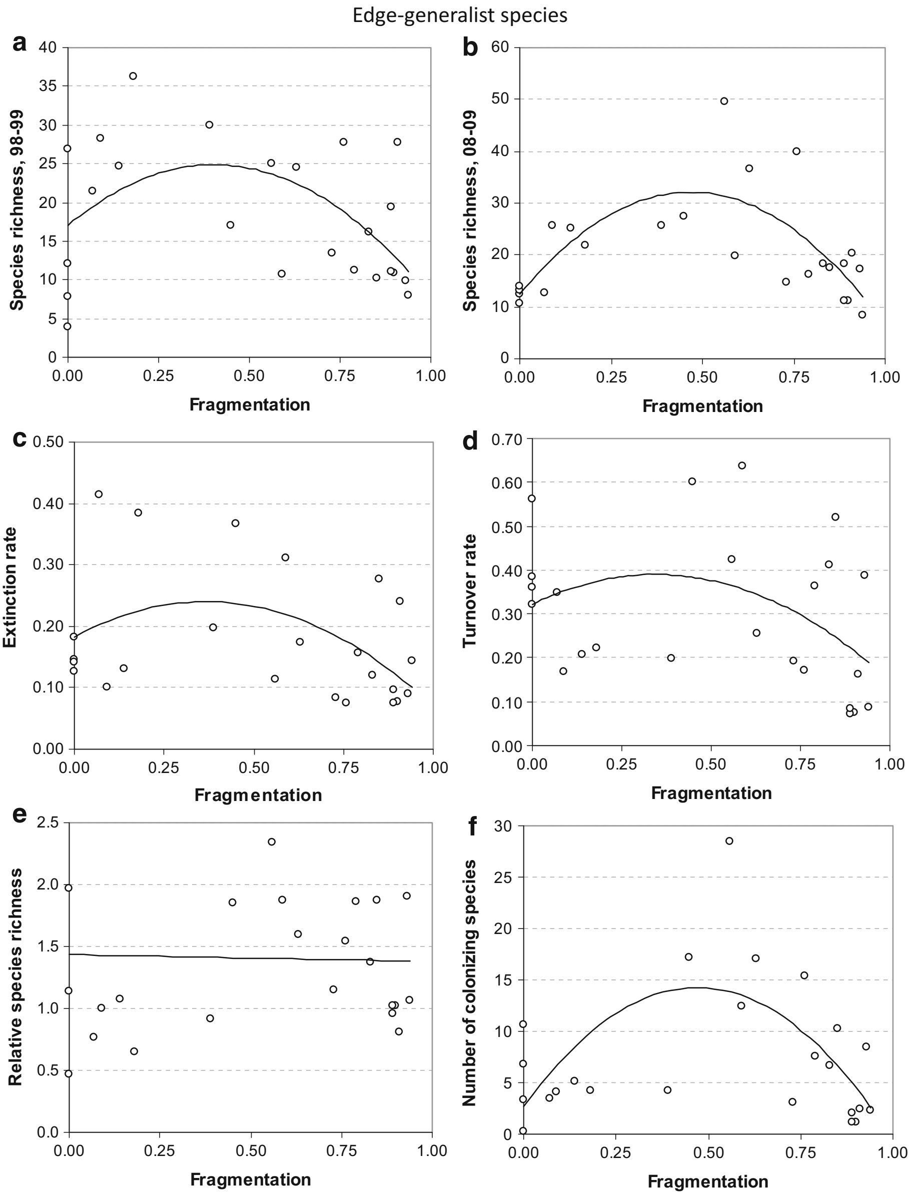
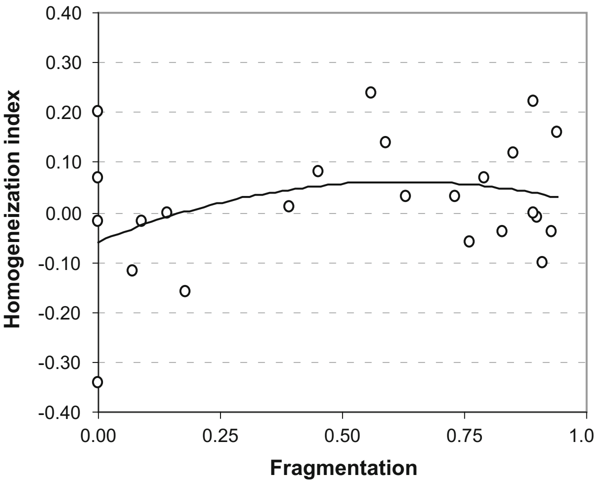


Fig. 4 Relationship between estimated community dynamic parameters and forest fragmentation in 2001 for forest generalists. *Fitted lines* are shown for illustrative purposes only. Significant coefficients in models ($p < 0.05$) can be seen in Table 2 (note that some landscapes with values = 0 are depicted along the axes)

one exception, a landscape with a value of approximately 2 at a fragmentation level of 0), at lower and intermediate fragmentation levels, perhaps indicating that for this species group, the studied landscapes have reached the "dynamic equilibrium" described by island biogeography theory, where equivalent extinction and colonization rates translate into constant species richness (Simberloff 1974). In contrast, relative species richness for forest

Fig. 5 Relationship between forest fragmentation in 2001 and the homogeneity index. The *fitted line* is only for illustrative purposes, the relationship was not significant (see Table 2; note that some landscapes with values = 0 are depicted along the axes)



generalists was approximately 1 at lower fragmentation levels, but much larger values where observed at intermediate and higher levels of fragmentation, possibly indicating non-equilibrium and highly dynamic conditions for generalists in these landscapes.

Several studies of bird community dynamics in tropical forests have found that species richness increased in modified landscapes (Gascon et al. 1999; Ferraz et al. 2003; Stouffer et al. 2009), and these increases are attributed to re-colonizations habilitated by secondary vegetation growth around studied fragments. Also, Boulinier et al. (2001) found that landscapes in one of three studied states in the U.S.A. (Pennsylvania) registered increases in species richness in time, and suggested that these changes were due to observed changes in vegetation in the landscape matrix. In the study region, re-colonization opportunities could have increased recently, due to arboreal vegetation recuperation and forest plantation establishments in the landscape matrix (unpublished data, also shown by land-cover classifications, Castellanos et al. 2011, Regalado et al. 2012). Relative species richness for forest generalists effectively showed increases in landscapes with intermediate fragmentation (with values between 0.5 and 0.8), so arboreal vegetation increases in the landscape matrix may be particularly beneficial for this species group. Although there was no association between the homogeneity index and fragmentation, landscapes with intermediate and high fragmentation levels (>0.5) evidently have a greater homogeneity index than landscapes with lower fragmentation and continuous forest. In conclusion, landscapes with medium or low fragmentation were much more dynamic and showed a much stronger tendency towards forest bird community homogenization, dominated by habitat generalists, a process that has been described in the literature as one of “ecosystem decay” (Lovejoy et al. 1984; Laurance et al. 2002).

Additionally, the distinction between forest specialists and generalists was important in determining completely different community dynamics for the two groups. Forest specialists elicited the community dynamics predicted by island biogeography and metapolulation theories, with increases in extinction rate and decreases in number of colonizing species with increasing fragmentation. For forest generalists more dynamic communities where found at intermediate levels of fragmentation, where species richness for the second period (2008–2009) for this group peaked, due to high estimated numbers of colonizing species. Without this distinction, important extinction dynamics for forest specialists, especially at higher levels of fragmentation, might have been masked by different dynamics shown by forest generalists. This distinction has proven useful in several fragmentation studies in determining different species response patterns to fragmentation dynamics (Bender et al. 1998; Boulinier et al. 2001; Robinson 2001; Steffan-Dewenter 2001; Krauss et al. 2003; DeVictor et al. 2007, 2008b). Furthermore, recent studies indicate than in the Tropics, and in particular the Neotropics, those species more vulnerable to habitat loss, fragmentation and degradation are understory insectivores (Bregman et al. 2014; Powell et al. 2015; Visco et al. 2015). Our data indicates that a higher proportion of insectivores found in lower strata (terrestrial, understory and mid-level, see appendix) are interior-forest specialists (26 % of interior-forest specialists are insectivores, compared to 19 % of edge-generalists), and in these strata, all bark or leaf-litter insectivores are classified as interior-forest specialists (12 % of all interior-forest specialists). Mounting evidence indicates that understory birds might be severely dispersal-limited in fragmented landscapes, are highly specialized in their feeding habits (such as bark and leaf-litter insectivores), and/or suffer greater nest predation rates, making them more vulnerable to habitat loss, fragmentation and degradation processes in modified landscapes (Visco et al. 2015).

Finally, as expressed by Boulinier et al. (2001), any study that involves measurements at the landscape scale to infer ecologic processes has the negative aspect of being observational, and/or of being poorly replicated. Consequently, these studies possibly provide weak inferential evidence, with respect to experimental studies, at the landscape scale (Wiens et al. 1993; Turner et al. 2001). On the other hand, manipulative experiments that evaluate habitat modification effects are generally conducted at much smaller scales and with communities of organisms that are usually not threatened, and their results are difficult (or impossible) to extrapolate to larger scales and other organisms (Turner et al. 2001; Lindenmayer and Fischer 2006). In this sense, we rescue the value of mensurative fragmentation studies, which are executed at the adequate scales to the phenomenon of interest, the landscape scale, and generally with the organisms that are the focus of conservation concern. More importantly, our study supports general theory regarding the expected negative effects of habitat loss and fragmentation on the temporal dynamics of biotic communities, particularly for forest specialists, providing strong evidence from understudied tropical bird communities.

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Appendix

Species list with landscape and life-history information. Proportion of landscapes (Prop. lands.) occupied in each period; mean fragmentation (Mean frag.) of occupied landscapes in each period; Main habitat; Foraging stratus: *T* terrestrial, *U* understory; *M* midlevel, *C* canopy, *A* aerial; Feeding guild: *G* granivore, *F* frugivore, *I. A* aerial insectivore, *I.B.I.* interior bark insectivore, *I.B.S* surface bark insectivore, *I.Gl* gleaning insectivore, *I.L* leaf-litter insectivore, *I.S* sallying insectivore, *N* nectarivore, *O* omnivore, *R* raptor; nest type and height. Taxonomic order is according to the North American Ornithologistś Union Checklist of North and Middle American Birds (7th edition). Life-history information from Stotz et al. (1996), Skutch (1954, 1960, 1969) Stiles and Skutch (1989), and Terborgh et al. (1990).

Scientific name	Prop. lands. 98–99	Prop. lands. 08–09	Mean frag. 98–99	Mean frag. 08–09	Main habitat	Foraging stratus	Feeding Guild	Nest type	Nest height (m)
Tinamus major	0.38	0.33	0.17	0.12	Interior	T	G	Ground	0.0
Crypturellus soui	0.25	0.38	0.40	0.50	Edge-generalist	T	G	Ground	0.0
Crypturellus boucardi	0.33	0.42	0.18	0.26	interior	T	G	Ground	0.0
Ortalis vetula	0.46	0.33	0.71	0.61	Edge-generalist	T/C	F	Platform	5.0
Penelope purpurascens	0.04	0.00	0.00	–	Interior	U/C	F	Open cup	4.0
Rupornis magnirostris	0.08	0.13	0.78	0.38	Edge-generalist	C	R	Platform	15.0
Pseudastur albicollis	0.00	0.04	–	0.24	Interior	C	R	Platform	15.0
Spizaetus tyrannus	0.04	0.08	0.45	0.21	Interior	C/A	R	Platform	16.8
Spizastur melanoleucus	0.04	0.00	0.45	–	Interior	C	R	Undescribed	–
Patagioenas nigrirostris	0.46	0.42	0.29	0.31	Interior	C	F	Platform	17.5
Claravis pretiosa	0.21	0.13	0.26	0.49	Edge-generalist	T/M	F	Platform	6.0
Geotrygon montana	0.08	0.29	0.00	0.23	Interior	T	F	Platform	1.5
Leptotila cassinii	0.25	0.25	0.15	0.23	Edge-generalist	T	F	Platform	3.0
Piaya cayana	0.42	0.38	0.25	0.28	Interior	C	I.Gl	Open cup	6.0
Streptoprocne zonaris	0.42	0.25	0.42	0.42	Interior	A	I.A	Platform	20.0
Chaetura vauxi	0.71	0.29	0.42	0.69	Interior	A	I.A	Open cup	10.0
Florisuga mellivora	0.13	0.00	0.30	–	Interior	M/C	N	Open cup	2.0
Phaethornis longirostris	0.17	0.33	0.04	0.21	Interior	U	N	Open cup	3.0
Phaethornis striigularis	0.13	0.42	0.18	0.32	Interior	U	N	Open cup	2.0
Thalurania colombica	0.04	0.13	0.00	0.00	Interior	U/M	N	Open cup	3.0
Amazilia candida	0.29	0.58	0.11	0.41	Interior	U/C	N	Open cup	2.0
Amazilia tzacatl	0.17	0.58	0.45	0.45	Edge-generalist	U/C	N	Open cup	3.5
Trogon massena	0.38	0.33	0.20	0.30	Interior	M/C	O	Cavity	9.0
Trogon melanocephalus	0.71	0.63	0.58	0.60	Interior	M/C	O	Cavity	4.5
Trogon caligatus	0.46	0.38	0.29	0.26	Interior	C	O	Cavity	5.0

continued

Scientific name	Prop. lands. 98–99	Prop. lands. 08–09	Mean frag. 98–99	Mean frag. 08–09	Main habitat	Foraging stratus	Feeding Guild	Nest type	Nest height (m)
Trogon collaris	0.17	0.08	0.13	0.00	Interior	M/C	O	Cavity	3.0
Momotus momota	0.50	0.75	0.34	0.41	Interior	U/M	I.S	Cavity	0.0
Electron carinatum	0.08	0.13	0.00	0.14	Interior	M	I.S	Cavity	3.0
Malacoptila panamensis	0.04	0.04	0.63	0.18	Interior	M/C	I.S	Cavity	1.0
Galbula ruficauda	0.04	0.04	0.18	0.24	Edge-generalist	M	I.S	Cavity	0.0
Pteroglossus torquatus	0.29	0.33	0.11	0.22	Interior	C	F	Cavity	18.0
Ramphastos sulphuratus	0.50	0.54	0.45	0.42	Interior	C	F	Cavity	15.0
Melanerpes pucherani	0.29	0.13	0.22	0.00	Interior	C	I.B.I	Cavity	18.0
Picoides fumigatus	0.00	0.13	–	0.41	Interior	M/C	I.B.I	Cavity	5.0
Colaptes rubiginosus	0.13	0.08	0.42	0.09	Interior	C	I.B.I	Cavity	10.0
Celeus castaneus	0.08	0.29	0.05	0.17	Interior	M/C	I.B.I	Cavity	12.5
Campephilus guatemalensis	0.25	0.25	0.18	0.20	Edge-generalist	C	I.B.I	Cavity	10.0
Herpetotheres cachinanns	0.13	0.13	0.44	0.33	Edge-generalist	C	R	Cavity	12.0
Micrastur semitorquatus	0.08	0.00	0.65	–	Interior	M/C	R	Cavity	5.0
Falco rufigularis	0.08	0.29	0.32	0.28	Edge-generalist	C/A	R	Cavity	15.0
Eupsittula nana	0.63	0.63	0.56	0.51	Edge-generalist	C	G	Cavity	7.0
Pyrilia haematotis	0.25	0.38	0.20	0.25	Interior	C	G	Cavity	10.0
Pionus senilis	0.50	0.50	0.40	0.50	Interior	C	G	Cavity	10.0
Amazona autumnalis	0.50	0.58	0.65	0.66	Edge-generalist	C	G	Cavity	10.0
Amazona farinosa	0.08	0.13	0.00	0.04	Interior	C	G	Cavity	10.0
Dysithamnus mentalis	0.04	0.04	0.00	0.00	Interior	U/M	I.Gl	Open cup	2.0
Microrhopias quixensis	0.00	0.04	–	0.13	Interior	M	I.Gl	Open cup	6.5
Cercromacra tyraninna	0.08	0.08	0.37	0.19	Edge-generalist	U	I.Gl	Hanging pouch	3.3
Formicarius analis	0.29	0.29	0.08	0.19	Interior	T	I.L	platform	2.0

continued

Scientific name	Prop. lands. 98–99	Prop. lands. 08–09	Mean frag. 98–99	Mean frag. 08–09	Main habitat	Foraging stratus	Feeding Guild	Nest type	Nest height (m)
Sclerurus mexicanus	0.00	0.04	–	0.00	Interior	T	I.L	Cavity	1.0
Sclerurus guatemalensis	0.04	0.04	0.00	0.00	Interior	T	I.L	Open cup	0.0
Dendrocincla anabatina	0.17	0.08	0.17	0.00	Interior	U	I.B.S	Cavity	4.0
Glyphorynchus spirurus	0.13	0.08	0.02	0.00	Interior	U/M	I.B.S	Cavity	3.0
Dendrocolaptes sanctithomae	0.00	0.04	–	0.00	Interior	U/M	I.B.S	Cavity	4.0
Xiphorhynchus flavigaster	0.42	0.46	0.32	0.28	Interior	U/M	I.B.S	Cavity	3.0
Xiphorhynchus erythropygius	0.04	0.08	0.45	0.00	Interior	M	I.B.S	Cavity	5.5
Xenops minutus	0.04	0.04	0.09	0.18	Interior	U/M	I.Gl	Cavity	5.0
Automolus ochroloaemus	0.00	0.08	–	0.00	Interior	M	I.Gl	Cavity	1.0
Ornithion semiflavum	0.00	0.25	–	0.35	Edge-generalist	C	I.S	Undescribed	–
Mionectes oleagineus	0.13	0.17	0.07	0.03	Interior	U/C	O	Hanging pouch	2.0
Oncostoma cinereigulare	0.46	0.46	0.27	0.27	Edge-generalist	U/M	I.S	Hanging pouch	0.5
Todirostrum cinereum	0.04	0.08	0.76	0.88	Edge-generalist	U/C	I.Gl	Hanging pouch	8.0
Tolmomyias sulphurescens	0.21	0.38	0.34	0.34	Interior	C	I.S	Hanging pouch	12.0
Onychorynchus coronatus	0.00	0.08	–	0.00	Interior	M	I.S	Hanging pouch	4.0
Attila spadiceus	0.33	0.50	0.17	0.40	Interior	M/C	I.S	Open cup	3.4
Rhytipterna holerythra	0.13	0.13	0.00	0.08	Interior	M/C	I.S	Open cup	10.0
Myiarchus tuberculifer	0.42	0.38	0.64	0.61	Interior	M/C	I.S	Cavity	8.0
Megarhynchus pitangua	0.17	0.42	0.39	0.56	Edge-generalist	C	I.S	Open cup	10.0
Myozetetes similis	0.75	0.79	0.61	0.60	Edge-generalist	M/C	I.S	Globular structure	8.5
Myiodynastes maculatus	0.13	0.00	0.33	–	Edge-generalist	M/C	I.S	Cavity	13.5
Schiffornis veraepacis	0.04	0.04	0.00	0.42	Interior	U	F	Open cup	1.0
Tityra semifasciata	0.63	0.67	0.42	0.57	Interior	C	O	Cavity	21.0
Pachyramphus cinnamomeus	0.00	0.04	–	0.13	Edge-generalist	C	I.S	Globular structure	19.0

continued

Scientific name	Prop. lands. 98–99	Prop. lands. 08–09	Mean frag. 98–99	Mean frag. 08–09	Main habitat	Foraging stratus	Feeding Guild	Nest type	Nest height (m)
Lipaugus unirufus	0.08	0.08	0.04	0.00	Interior	M/C	F	Platform	7.5
Manacus candei	0.17	0.17	0.30	0.37	Edge-generalist	U	F	Open cup	2.5
Ceratopipra mentalis	0.08	0.13	0.07	0.00	Interior	U/M	F	Open cup	6.0
Hylophilus ochraceiceps	0.13	0.17	0.19	0.05	Interior	U/M	I.Gl	Open cup	3.5
Hylophilus decurtatus	0.33	0.58	0.15	0.29	Interior	M/C	I.Gl	Open cup	12.0
Vireolanius pulchellus	0.04	0.00	0.00	–	Interior	C	I.Gl	Open cup	14.0
Cyanocorax yncas	0.21	0.08	0.01	0.12	Interior	C	O	Open cup	10.0
Tachycineta albilinea	0.04	0.00	0.83	–	Interior	A	I.A	Open cup	2.0
Microcerculus philomela	0.04	0.08	0.00	0.00	Interior	T/U	I.L	Undescribed	–
Pheugopedius maculipectus	0.67	0.71	0.40	0.44	Edge-generalist	U/M	I.Gl	Globular structure	3.5
Henicorhina leucostica	0.42	0.33	0.17	0.23	Interior	U	I.Gl	Globular structure	0.3
Henicorhina leucophrys	0.04	0.00	0.00	–	Interior	U	I.Gl	Globular structure	1.0
Ramphocaenus melanurus	0.25	0.29	0.18	0.13	Edge-generalist	U/M	I.Gl	Open cup	0.2
Myadestes unicolor	0.04	0.04	0.00	0.00	Interior	M/C	F	Open cup	3.0
Turdus grayi	0.79	0.75	0.61	0.67	Edge-generalist	T/M	O	Open cup	15.5
Turdus assimilis	0.13	0.00	0.05	–	Interior	U/M	O	Open cup	4.5
Basileuterus culicivorus	0.04	0.13	0.00	0.00	Interior	M	I.Gl	Globular structure	0.0
Thraupis episcopus	0.58	0.63	0.66	0.73	Edge-generalist	C	F	Open cup	15.0
Thraupis abbas	0.46	0.71	0.75	0.64	Edge-generalist	M/C	F	Open cup	3.0
Tangara larvata	0.08	0.08	0.26	0.89	Edge-generalist	M/C	F	Open cup	14.8
Chlorophanes spiza	0.08	0.00	0.00	–	Interior	C	O	Open cup	7.0
Ramphocelus sanguinolentus	0.08	0.00	0.65	–	Edge-generalist	U/M	F	Open cup	4.0
Ramphocelus passerinii	0.08	0.08	0.64	0.57	Edge-generalist	U/C	F	Open cup	3.0
Cyanerpes cyaneus	0.08	0.00	0.74	–	Interior	C	O	Open cup	8.5

continued

Scientific name	Prop. lands. 98–99	Prop. lands. 08–09	Mean frag. 98–99	Mean frag. 08–09	Main habitat	Foraging stratus	Feeding Guild	Nest type	Nest height (m)
Coereba flaveola	0.08	0.04	0.00	0.00	Interior	M/C	N	Globular structure	3.0
Saltator maximus	0.04	0.33	0.56	0.66	Edge-generalist	M/C	O	Open cup	1.1
Saltator atriceps	0.54	0.63	0.60	0.67	Edge-generalist	M/C	O	Open cup	2.3
Arremonops chloronotus	0.04	0.29	0.45	0.73	Edge-generalist	T/U	O	Open cup	0.0
Chlorospingus ophtalmicus	0.00	0.04	–	0.00	Interior	U/M	O	Open cup	7.5
Piranga leucoptera	0.00	0.04	–	0.92	Interior	C	I.Gl	Open cup	14.0
Habia rubica	0.08	0.13	0.00	0.00	Interior	U/M	I.Gl	Open cup	3.9
Habia fuscicauda	0.08	0.04	0.07	0.00	Edge-generalist	U	I.Gl	Open cup	2.0
Caryothraustes poliogaster	0.13	0.13	0.00	0.14	Interior	M/C	F	Open cup	4.5
Cyanocompsa cyanoides	0.29	0.21	0.30	0.17	Interior	M/C	G	Open cup	2.5
Dives dives	0.83	0.83	0.62	0.63	Edge-generalist	T/C	O	Open cup	4.5
Molothrus oryzoborus	0.04	0.04	0.56	0.76	Edge-generalist	U/M	O	Globular structure	20.0
Icterus prosthemelas	0.13	0.00	0.74	–	Edge-generalist	C	O	Hanging pouch	6.5
Amblycercus holosericeus	0.00	0.17	–	0.60	Edge-generalist	U	O	Open cup	2.0
Psarocolius wagleri	0.13	0.46	0.00	0.40	Interior	C	O	Hanging pouch	10.0
Psarocolius montezuma	0.54	0.50	0.51	0.48	Interior	C	O	Hanging pouch	10.0
Euphonia hirundinacea	0.13	0.33	0.38	0.65	Edge-generalist	C	F	Globular structure	8.0
Euphonia gouldi	0.25	0.17	0.17	0.00	Interior	U/C	F	Globular structure	8.5

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