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Tolerance of frugivorous birds to habitat disturbance in a tropical cloud forest

Laurens G.L. Gomes^{a,1}, Vicencio Oostra^{a,1}, Vincent Nijman^b,
Antoine M. Cleef^a, Maarten Kappelle^{c,d,*}

^aInstitute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, P.O. Box 94062, 1098 SM Amsterdam, The Netherlands

^bOxford Brookes University, School of Social Sciences and Law, Department of Anthropology and Geography, OX3 0BP Oxford, UK

^cThe Nature Conservancy, Mesoamerican and Caribbean Science Program, Apartado 230-1225, Plaza Mayor, San José, Costa Rica

^dDepartment of Geography, 304 Burchfiel Geography Building, University of Tennessee, Knoxville, TN 37996-0925, USA

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ABSTRACT

In view of the continued decline in tropical forest cover around the globe, forest restoration has become a key tool in tropical rainforest conservation. One of the main – and least expensive – restoration strategies is natural forest regeneration. By aiding forest seed influx both into disturbed and undisturbed habitats, frugivorous birds facilitate forest regeneration. This study focuses on the tolerance of a frugivorous bird community to anthropogenic habitat disturbance within the broader context of natural forest regeneration with conservation purposes. It was carried out in the tropical cloud forest of Costa Rica's Talamanca Mountains. Bird community response and tolerance to habitat disturbance was assessed by comparing bird presence and densities along a disturbance gradient, ranging from open pastures to closed mature forests. Birds were censused along nine transects applying the variable width line transect procedure. Forty relevant frugivorous bird species were observed during 102 h of survey time. Densities were calculated for 33 species; nine species responded negatively to increasing level of disturbance and nine others positively. Results indicate that large frugivores are generally moderately tolerant to intermediate, but intolerant to severe habitat disturbance, and that tolerance is often higher for medium and small frugivores. It appears that moderately disturbed habitats in tropical cloud forests are highly suitable for restoration through natural regeneration aided by frugivorous birds. Due to a lack of large forest seed dispersers, severely disturbed habitats appear less suitable.

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1. Introduction

Deforestation and habitat degradation continue to form a major threat to Neotropical montane cloud forests (Kappelle and Brown, 2001). In Latin America, forest clearing has primarily been taking place for the purpose of cattle-ranching (Holl et al., 2000; Harvey et al., 2005). Short-term economic

use of cleared lands is often followed by abandonment (Aide and Grau, 2004). This eventually gives rise to a patchy landscape mosaic of grasslands, successional forests in different stages of recovery, and croplands (e.g., Buschbacher, 1986; Uhl et al., 1988; Aide et al., 1995; Kappelle and Juárez, 1994, 2006). In an effort to understand and facilitate reforestation processes, restoration ecology has increasingly received

* Corresponding author. Tel.: +506 220 2552x104; fax: +506 220 2551.

E-mail addresses: lgomes@science.uva.nl (L.G.L. Gomes), v.oostra@biology.leidenuniv.nl (V. Oostra), vnijman@brookes.ac.uk (V. Nijman), cleef@science.uva.nl (A.M. Cleef), mkappelle@tnc.org (M. Kappelle).

¹ These two authors contributed equally to this work.

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attention during the last two decades (e.g., Young, 2000; Meli, 2003). Previous studies have shown local forest seed availability to be one of the limiting factors to secondary succession in abandoned pastures, and thus natural forest regeneration (Nepstad et al., 1991; Aide and Cavelier, 1994; Martínez-Garza and Howe, 2003). Total seed rain and proportion of animal-dispersed (zoochorous) seeds to wind-dispersed seeds is much lower in pastures than in forest interiors away from forest edges (Holl et al., 2000; Wijdeven and Kuzee, 2000; Wilms and Kappelle, 2006). Similarly, it appears that during regeneration trees and shrubs dispersed by abiotic agents (wind, water) are replaced by woody species dispersed by animals (Tabarelli and Peres, 2002). Compared to temperate forests, a high proportion of tropical forest seeds is animal-dispersed (Howe and Smallwood, 1982; Wunderle, 1997; Tabarelli and Peres, 2002). Therefore, frugivorous birds as well as mammals are considered important dispersal agents of seeds in Neotropical forests. Whether these frugivores act as dispersers of forest seeds, from intact forests to disturbed habitats, thus enhancing forest regeneration and restoration, strongly depends on their tolerance to disturbance, as demonstrated by their presence and densities in and use of disturbed habitats (Schupp, 1993).

We studied the tolerance of a frugivorous bird community in response to anthropogenic habitat disturbance in a montane cloud forest in Costa Rica's high Talamanca region. While some parts of these cloud forests have been cleared for cattle-ranching, others have only been altered moderately, or remain as intact mature oak forest (Kappelle and Juárez, 1994, 2006). Tropical cloud forests are particularly vulnerable to habitat alteration due to their slow natural regeneration caused by low diurnal temperatures and to their occurrence as naturally fragmented forest 'islands' on mountain tops (Bubb et al., 2004). A previous study indicates that it takes at least 80 years for successional forest to reach a structure (maximum canopy height and basal area) that resembles the structure of a mature forest (Kappelle et al., 1996). However, it may take well over a century to recover most of the cloud forest species, including epiphytes and vertebrates. Very few studies on seed availability and forest tree dispersal syndromes are available for our study area. At a lower elevation (1500 m) in the same area Holl (1999) has found that the availability of animal-dispersed forest seeds in pastures is dramatically low. Close to the study area but at slightly higher elevation Wijtzes (unpublished data) observed that most forest tree seeds are endozoochorously dispersed. The study area has been object of study for two decades, covering research on its mature and successional forest vegetation (for an overview see Kappelle, 1996, 2006). These studies offer a good background setting for the present study. So far, only one study briefly addressed the role of frugivorous birds in forest recovery (Wilms and Kappelle, 2006) and one study addressed the effects of deforestation on the endemic avifauna (Oostra et al., 2008).

The aim of the present study was to address the tolerance of a frugivorous cloud forest bird community to anthropogenic habitat disturbance as one of the key conditions for a role of frugivorous birds in natural forest regeneration. This was done by quantifying frugivorous bird densities along a disturbance gradient and by comparing densities in undis-

turbed habitats with densities in habitats with intermediate or severe levels of disturbance.

2. Methods

2.1. Study area

The study was conducted during a dry season (December 2003–April 2004) in the north-western sector of the Talamanca Mountains in southern Costa Rica. Study sites were located between 9°32'N, 83°48'W and 9°44'N, 83°57'W, and along the Inter-American Highway between 52 and 80 km from San José, at elevations between 2200 and 2600 m along both slopes of the mountain range (Fig. 1). The climate in the study area is humid and cold with a dry season running from December to April. Annual average temperature ranges from 12 to 15 °C and the annual average precipitation is ca. 2100–3000 mm. Occurrence of mist and clouds is very frequent. The original vegetation in the area is tropical montane evergreen rain/cloud forest dominated by oak (*Quercus*) often with a dense understory dominated by *Chusquea* bamboo. It is bordered by páramo at ca. 3400 m and pre-montane forest at ca. 1500 m altitude (Kappelle et al., 1989, 1996).

Human colonization of the area has left a profound mark on the original vegetation. After the completion of the Inter-American Highway in 1943, connecting San José with Costa Rica's southern zone, commercial logging and subsequent colonization took place between 1950 and 1970, leading to the clearing of large montane forest tracts. In the following decades (1980–2000) commercial logging ended and several public protected areas were established, of which the majority nowadays is part of the Amistad Biosphere Reserve. At the borders of this Biosphere Reserve lie two forest reserves (Río Macho and Los Santos) which serve as buffer zones, while suffering from limited human activity and enjoying a certain level of legal protection. In these reserves, economic activities (tourism, agriculture and trout hatching) occur on a small and local scale. The areas outside these buffer zones contain relatively small human settlements with more diverse economic activities. Outside the main forest area, tracts of mature and moderately to strongly disturbed forests are alternated with successional forests, pasturelands and agricultural croplands (Kappelle and Juárez, 1994, 1996, 2006).

2.2. Vegetation sampling

In order to quantify anthropogenic habitat disturbance in the study area, different aspects of vegetation structure were recorded at each study site along the disturbance gradient. Vegetation characteristics were recorded at 10 m radius sampling stations, randomly established along the transects used for the bird census, totaling 87 sampling stations (2.73 ha). At each sampling station, girth of all trees >10 cm diameter at breast height was measured and total tree height and height of first major branching was estimated to the nearest meter and subsequently ordered in classes. Trees having their first major branching above half their height have probably grown up under a closed canopy and were considered 'primary' trees, whereas trees having their first branching below half

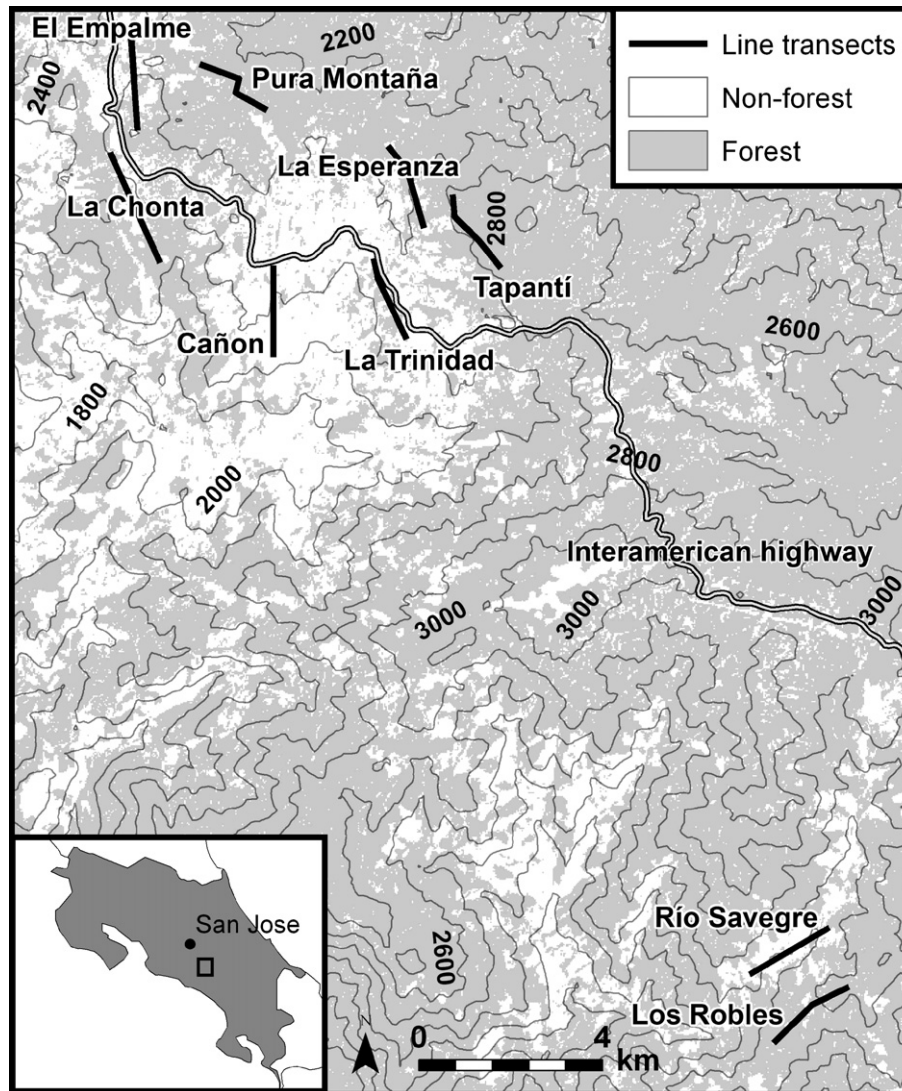


Fig. 1 – Map of study area showing the location of nine study transects in relation to forest cover in the Talamanca Mountains, Costa Rica.

their height have probably grown up under an open canopy and were thus considered ‘secondary’ trees (Jones et al., 2003; Nijman, 2004). At each sampling station five smaller (1.0 m radius) plots were evenly distributed. Within these plots, percentage ground cover of leaf litter, bare soil, dead material, grass, and ground vegetation was estimated to the nearest 5%. In addition, within these plots shrub density was assessed by counting numbers of ‘shrubs’ at breast height in the following categories: palms, tree ferns, ferns, bamboos, stems, young trees, blackberries and other shrubs. Young trees were defined as trees taller than 5 m, with a diameter at breast height ≤ 10 cm, and stems were defined as trees smaller than 5 m.

2.3. Bird census

The well-established line transect distance sampling method (Buckland et al., 1993) was applied to assess bird densities at

nine study sites. Despite challenging terrain, line transects rather than point counts were used as they yield more data per unit field time (Buckland et al., 1993; Rosenstock et al., 2002) and are therefore more suited for surveying species with a large home range occurring at low abundances. At each study site a transect was established with average distances between sites ranging from 1.5 to 25.0 km. Together the nine study sites covered a habitat disturbance gradient not related to their geographic location. This gradient ranged from undisturbed mature oak forest to intensively grazed pastures. Although being relatively close to small rural settlements, sampled mature forests had no to very limited human presence and were close to or continuous with larger forest tracts of the Amistad Biosphere Reserve. Sites with intermediate levels of disturbance consisted of a mosaic of remnant mature forests, successional forest, and actively used habitats (ranging from pastures to blackberry fields). The heavily disturbed sites mainly consisted of pastures with no legal

protected status used for cattle grazing. The latter contained a high number of remnant and often isolated mature forest trees and secondary trees, as well as small patches of successional forest. Each transect was 2.0 km in length as measured by using a GPS receiver or a tape measure and by counting paces. The minimum distance between transects was 1.0 km. Transects were laid out in a straight line through the landscape, avoiding human paths and roads (Bibby et al., 1992). All transects were surveyed six times (by L.G.L.G. and V.O.), with the exception of the Río Savegre (five times) and Tapantí (four times) transects, with a total effort of 102 km. Transects were walked at 1 km h⁻¹, bird surveying was restricted to the period between 6:00 and 8:00 AM. The direction at which transects were walked was alternated between replicates. All data were collected under fair weather conditions (light winds, no rain, no mist). Birds were both visually and aurally identified. For all observations the perpendicular distance of the bird individual to the transect line was estimated. Accuracy was assured by frequently calibrating distance estimates outside survey hours. Fully aerial bird individuals were not included, as they were not observed using the habitat. Birds that were observed flushing from the vegetation were recorded at the distance of perching prior to flushing. Diet and body mass of birds were determined according to Stiles and Skutch (1989), with large, medium and small frugivores being defined as larger than 140 g, between 50 and 140 g and smaller than 50 g, respectively. Both obligate and opportunistic frugivores were included. Prior to analysis 11 species were excluded, as these were primarily seed predators, were rare migrants or were only observed <3 times.

2.4. Distance analysis

The program Distance (Thomas et al., 2004) was used to estimate bird densities (cf. Marsden et al., 1997; Jacobs and Walker, 1999; Creswell et al., 1999; Shaw and Shewry, 2001; Riley, 2002, 2003; Marsden and Pilgrim, 2003). This program plots a histogram of the distribution of observations against their perpendicular distance to the transect line. A detection function is fitted to the histogram describing the probability of detection as a function of distance. This detection function is used to calculate densities (see Buckland et al., 1993). In our study a variety of models with different series expansions were fitted to the histograms and selection of detection functions was based on Akaike's Information Criterion (AIC; see Buckland et al., 1993). Detection functions were computed separately for each bird species for two different habitat types, being forest (50 km) and non-forest (56 km). Visual and aural observations were pooled prior to analysis. Right-hand truncation (of most distant records) was performed to increase accuracy by removing outliers from the data set. Remaining data was grouped in distance intervals to avoid rounding errors at greater distances and, for the Black-faced Solitaire (*Myadestes melanops*) and the Mistletoe Tyrannulet (*Zimmerius vilissimus*), to account for observer effects at smaller distances (Buckland et al., 1993).

In five cases, the number of records in one of the habitat types was too small to model a habitat specific detection function. Here we conservatively used the detection function of one habitat to estimate densities in the other habitat. For the Barred

Becard (*Pachyramphus versicolor*), Black-faced Solitaire, Black-cheeked Warbler (*Basileuterus melanoenys*) and the species group of the Large Frugivores (see below) we used the detection functions from forest habitats to estimate those of non-forest habitats and calculate densities correspondingly. For the Flame-colored Tanager (*Piranga bidentata*) we did the reverse. For several species the number of records of each species was too small to model a species-specific detection function. Following Marsden et al. (1997), we pooled distance data of 14 species into four groups, for each habitat type separately, to produce a common detection function and density estimate for each group. Grouping of species was based on similarity in body mass, diet and detectability, as evaluated by similarity in the distribution of distance records (cf. Marsden et al. 1997; Shaw and Shewry 2001; Riley 2002). The groups were as follows: Large Frugivores (Black Guan (*Chamaepetes unicolor*), Resplendent Quetzal (*Pharomachrus mocinno*) and Emerald Toucanet (*Aulacorhynchus prasinus*)), Large Ground-dwellers (Highland Tinamou (*Nothocercus bonaparte*), Buffy-crowned Wood-parttridge (*Dendrortyx leucophrys*) and Spotted Wood-quail (*Odonthophorus guttatus*)), Medium-sized Frugivores (Collared Trogon (*Trogon collaris*), Prong-billed Barbet (*Semnormis frantzii*) and Black-and-yellow Silky-flycatcher (*Phainoptila melanoxantha*) and Small Frugivores (Swainson's Thrush (*Catharus ustulatus*), Slaty-backed Nightingale-thrush (*Catharus fuscater*), Spangled-cheeked Tanager (*Tangara dowii*), Yellow-throated Brush-finch (*Atlapetes gutturalis*) and Chestnut-capped Brush-finch (*Atlapetes brunneinucha*)). For all bird species and habitat types for which detection functions have been made in this study, detection functions fitted the data well and conditions for reliable density estimates were always met.

2.5. Data analysis

Classification of the nine transects in three disturbance types was based on a Euclidian distance hierarchical cluster analysis of normalized vegetation data. The vegetation based cluster analysis was then compared to a Euclidian distance hierarchical cluster analysis based on absence/presence of all (40) frugivorous bird species observed during four surveys per transect. A principal component analysis (PCA) was performed on the normalized vegetation data, and best-fit linear regression models were calculated for relations between the first two PCA axes and bird densities. Significance was accepted when $p < 0.05$. Differences in bird densities between the three disturbance types were tested with one-way analysis of variance (ANOVA). A post hoc Tukey's HSD test was performed to identify specific differences between disturbance regimes.

3. Results

3.1. Vegetation

Mature forest differed from disturbed sites in 20 of 32 vegetation variables measured. Vegetation sampling and analysis (Table 1) revealed that even though the most heavily disturbed sites consisted mostly of pastures with secondary trees, values for tree density and basal area continued to be

high. Sites with intermediate disturbance levels had intermediate values for tree density, basal area and shrub density.

Analysis of vegetation data revealed high levels of correlation between vegetation variables. Vegetation variables correlating positively with the first PCA axis corresponded with low disturbance habitat conditions (e.g., tree density, basal area, shrub density and leaf litter cover). Negatively correlated variables corresponded with high disturbance habitat conditions (e.g., grass cover and bare soil). The first PCA axis was thus interpreted as a measure of disturbance. The second PCA axis was positively correlated with basal area per stem, relative density of trees with a height of 20–30 m, and of trees with a diameter at breast height ranging from 70 to 115 cm. It was negatively correlated with trees with a height of 10–20 m.

3.2. Frugivorous bird community

A total of 51 obligate and opportunistic frugivorous bird species was observed during 102 h of survey time. This corresponds to 57% of all frugivorous bird species known from the area (L.G.L.G. and V.O., unpublished data). Of these 51 species, 40 species were considered relevant frugivores as they include fruit in their diet on a regular basis (Appendix A). Total number of observed frugivorous bird species per site varied from 21 to 34. No differences in numbers were found for the three disturbance categories. The 35 species that occurred at sites with low disturbance levels (i.e. mature forest) are considered to be native to the undisturbed cloud forest. Of these native species 29 (83%) occurred under all disturbance regimes. Of the 36 species occurring at high disturbance sites, 5 (14%) did not occur at low disturbance sites at all, and are considered not native to the forest interior. Classification of sites based on vegetation data (Fig. 2a) shows similar relationships between sites to classification based on species composition (Fig. 2b). The gradient of disturbance, as observed along the nine different sites is thus reflected in the composition of the frugivorous species community at these sites. An exception is the La Chonta site which had vegetation characteristics strongly related to highly disturbed sites and a species composition closely related to intermediate levels of disturbance.

The highest number of observed species is also found at this site (34).

3.3. Density comparisons

Of the 40 bird species that are considered relevant frugivores in this study, we obtained density estimates for 33 species. Densities of ten individual bird species and of Large Frugivores and Small Frugivores showed a significant relation (linear regression, $p < 0.05$) with the first PCA axis as a measure of disturbance (Table 2). Six individual species and Large Frugivores responded negatively to disturbance and four individual species and Small Frugivores responded positively. Density of the Mountain Robin (*Turdus plebejus*) showed a significant negative relation with the second PCA axis (linear regression, $p < 0.05$; Table 2). The ecological significance of this relation is unclear. Its high densities under all disturbance regimes suggest that its preference might not necessarily be related to disturbance.

Most species that showed a significant response to disturbance (linear regression; Table 2) also showed a significant preference for one of the three disturbance regimes (ANOVA, $p < 0.05$; Table 3). We found species occurring at highest densities at undisturbed habitats (species preferring forest) as well as species occurring at highest densities at habitats with severe levels of disturbance (species avoiding forest). For some of these species densities at intermediately disturbed habitats were similar (ANOVA, post hoc Tukey's HSD test; Table 3) to either densities at undisturbed habitats (e.g. Sooty-capped Bush-tanager (*Chlorospingus pileatus*)) or densities at severely disturbed habitats (e.g. Barred Becard). For other species densities at intermediately disturbed habitats were in-between densities at undisturbed and severely disturbed habitats (e.g. Large Frugivores, preferring forest; Flame-colored Tanager, avoiding forest). Additionally, other species had highest densities at intermediately disturbed habitats (e.g. Mountain Robin). It is clear that the suitability of intermediately disturbed habitats for frugivores is highly species-dependent. A total of 15 species did not show a significant preference for one of the disturbance regimes. Several of these species reveal a certain degree of tolerance since they

Table 1 – Summary of characteristics of nine sites in the Talamanca Mountains, Costa Rica

| Name | Site characteristics | | | | Vegetation variables (mean ± SD) | | | |
|--------------|----------------------|----------------------------------|-----------------------------------|-------------|------------------------------------|---------------------------------|------------------------------------|-----------------------|
| | Altitude (m.a.s.l.) | Conservation status ^a | Level of disturbance ^b | Effort (km) | Tree density (# ha ⁻¹) | Basal area (m ² /ha) | Shrub density (# m ⁻²) | Sampling stations (n) |
| Tapantí | 2500–2600 | NPT | Low | 8.0 | 437 ± 111 | 83 ± 77 | 3.26 ± 0.96 | 7 |
| Pura Montaña | 2200–2300 | RMFR/NPT | Low | 12.0 | 532 ± 229 | 43 ± 27 | 3.50 ± 1.73 | 7 |
| Los Robles | 2300–2400 | LSFR | Low | 12.0 | 420 ± 112 | 43 ± 42 | 2.93 ± 1.13 | 10 |
| La Esperanza | 2380–2460 | None/RFRM | Intermediate | 12.0 | 312 ± 255 | 21 ± 17 | 2.91 ± 2.79 | 10 |
| El Empalme | 2340–2420 | None/RFRM | Intermediate | 12.0 | 332 ± 261 | 39 ± 40 | 1.74 ± 1.5 | 14 |
| Río Savegre | 2220–2300 | LSFR | High | 10.0 | 127 ± 190 | 18 ± 32 | 0.68 ± 0.93 | 15 |
| La Chonta | 2320–2440 | None | High | 12.0 | 127 ± 104 | 11 ± 8 | 0.68 ± 1.52 | 10 |
| Cañon | 2300–2500 | None | High | 12.0 | 105 ± 110 | 15 ± 23 | 0.50 ± 0.79 | 7 |
| La Trinidad | 2380–2540 | None | High | 12.0 | 218 ± 278 | 15 ± 19 | 0.12 ± 0.22 | 7 |

a LSFR: Los Santos Forest Reserve; RMFR: Río Macho Forest Reserve; NPT: Tapantí – Macizo de la Muerte National Park.

b Classification based on a Euclidian distance hierarchical cluster analysis of 32 vegetation variables.

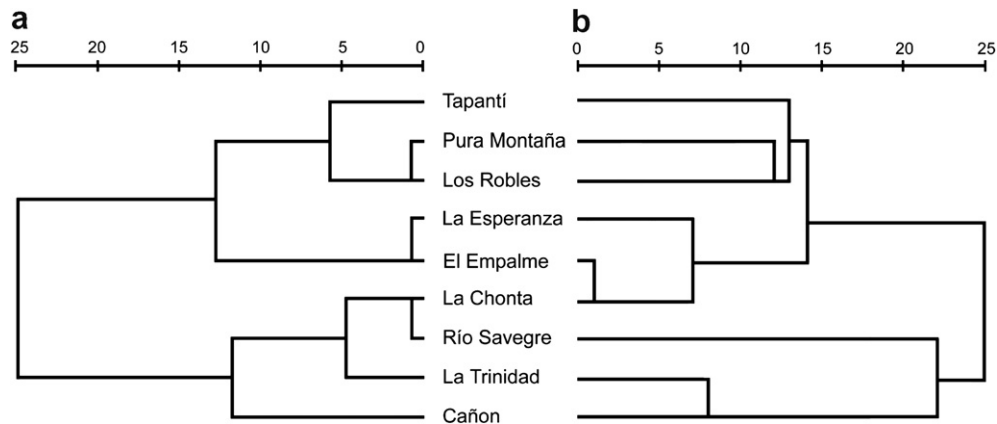


Fig. 2 – Euclidian distance hierarchical cluster analyses of sites based on vegetation data (a) and absence/presence of frugivorous bird species (b), showing generally similar classifications.

Table 2 – Linear regression models of habitat characteristics (principal components 1 and 2 of vegetation variables) and frugivorous bird densities

| Bird species | Model ($y = ax + b$) | | Independent variable (x) | R ² | p-Value |
|--|------------------------|-----|--------------------------|----------------|---------|
| | a | b | | | |
| Barred Becard (<i>Pachyramphus versicolor</i>) | 5 | 7 | PCA1 | 0.54 | 0.03 |
| Tropical Kingbird (<i>Tyrannus melancholicus</i>) | -14 | 13 | PCA1 | 0.61 | 0.01 |
| Mountain Elaenia (<i>Elaenia frantzii</i>) | -156 | 240 | PCA1 | 0.69 | 0.01 |
| Mountain Robin (<i>Turdus plebejus</i>) | -108 | 265 | PCA2 | 0.48 | 0.04 |
| Black-faced Solitaire (<i>Myadestes melanops</i>) | 15 | 17 | PCA1 | 0.62 | 0.01 |
| Ruddy-capped Nightingale-thrush (<i>Catharus frantzii</i>) | 18 | 44 | PCA1 | 0.48 | 0.04 |
| Black-billed Nightingale-thrush (<i>Catharus gracilirostris</i>) | 16 | 44 | PCA1 | 0.56 | 0.02 |
| Long-tailed Silky-flycatcher (<i>Ptilogonys caudatus</i>) | -28 | 32 | PCA1 | 0.84 | 0.00 |
| Flame-colored Tanager (<i>Piranga bidentata</i>) | -15 | 16 | PCA1 | 0.76 | 0.00 |
| Sooty-capped Bush-tanager (<i>Chlorospingus pileatus</i>) | 162 | 230 | PCA1 | 0.74 | 0.00 |
| Yellow-thighed Finch (<i>Pselliophorus tibialis</i>) | 49 | 95 | PCA1 | 0.68 | 0.01 |
| Large frugivores ^a | 4 | 6 | PCA1 | 0.85 | 0.00 |
| Small frugivores ^a | -26 | 48 | PCA1 | 0.50 | 0.00 |

^a Densities of 14 frugivorous bird species could not be estimated individually due to low number of records; combining data of these species into four groups yielded density estimates for each group of which two are here displayed (see main text for details).

had comparable densities for all disturbance categories (e.g. Mistletoe Tyrannulet, Medium Frugivores). Others did not have comparable densities, but due to large variation in densities for at least one disturbance category preferences were also not significant (e.g. Large Ground-dwellers).

4. Discussion

Our results indicate that the changes in vegetation structure associated with anthropogenic habitat disturbance have led to a complex response of the frugivorous bird community. While species richness of frugivores did not decline, community composition showed a gradual shift in response to disturbance. At the species level, we found both decreases and increases in densities in response to habitat disturbance. The frugivores that increased in densities were generally resilient forest species, occurring under all habitat disturbance regimes, and not species invading open lands. The frugivores that decreased in densities differed in their

habitat preference, with intermediately disturbed habitats harboring high, intermediate or low densities of frugivores. This suggests that some frugivores, though responding negatively to disturbance, can still be moderately tolerant to intermediate levels of disturbance. For the lumped species group of Large Frugivores this was the case, but not for the groups of Medium Frugivores and Small Frugivores. They appear more tolerant to both intermediate and severe disturbance and in the latter case even prefer habitat disturbance. A similar relation between body mass and tolerance to habitat disturbance seems to exist in other frugivores, with tolerance decreasing with increasing body mass. Exceptions are the large Band-tailed Pigeon (*Columba fasciata*) that is more tolerant to habitat disturbance than other large frugivores and several small frugivores that are less tolerant than others. At present, the frugivorous bird community appears to be relatively tolerant to intermediate levels of habitat disturbance, but less to high levels of habitat disturbance.

Table 3 – Differences in densities of 33 frugivorous bird species at sites with low, intermediate and high levels of disturbance

| Bird species | Bird density (ind. km ⁻²) per disturbance category (mean ± SD) | | | ANOVA p-value |
|--|--|----------------------|--------------|---------------|
| | Low (n = 3) | Intermediate (n = 2) | High (n = 4) | |
| Band-tailed Pigeon (<i>Columba fasciata</i>) | 8 ± 11 | 17 ± 10 | 28 ± 28 | 0.52 |
| Ruddy Pigeon (<i>Columba subvacea</i>) | 11 ± 18 | 4 ± 6 | 5 ± 6 | 0.76 |
| Acorn Woodpecker (<i>Melanerpes formicivorus</i>) | 13 ± 23 | 11 ± 11 | 20 ± 11 | 0.79 |
| Barred Becard (<i>Pachyrhamphus versicolor</i>) | 18 ± 2a | 3 ± 5b | 3 ± 5b | 0.01 |
| Tropical Kingbird (<i>Tyrannus melancholicus</i>) | 0 ± 0 | 3 ± 1 | 28 ± 19 | 0.07 |
| Mountain Elaenia (<i>Elaenia frantzii</i>) | 22 ± 24a | 310 ± 100b | 368 ± 133b | 0.01 |
| Mistletoe Tyrannulet (<i>Zimmerius vilissimus</i>) | 40 ± 29 | 34 ± 11 | 30 ± 14 | 0.79 |
| Mountain Robin (<i>Turdus plebejus</i>) | 120 ± 72a | 468 ± 80b | 272 ± 107ab | 0.02 |
| Black-faced Solitaire (<i>Myadestes melanops</i>) | 38 ± 21 | 11 ± 7 | 5 ± 5 | 0.04 |
| Ruddy-capped Nightingale-thrush (<i>Catharus frantzii</i>) | 55 ± 30 | 69 ± 5 | 23 ± 7 | 0.04 |
| Black-billed Nightingale-thrush (<i>Catharus gracilirostris</i>) | 55 ± 15ab | 64 ± 15a | 25 ± 11b | 0.02 |
| Long-tailed Silky-flycatcher (<i>Ptilogonys caudatus</i>) | 4 ± 6a | 15 ± 14a | 62 ± 15b | 0.00 |
| Flame-throated Warbler (<i>Parula gutturalis</i>) | 55 ± 11 | 39 ± 24 | 46 ± 28 | 0.75 |
| Black-cheeked Warbler (<i>Basileuterus melanogenys</i>) | 59 ± 51 | 37 ± 53 | 5 ± 7 | 0.24 |
| Golden-browed Chlorophonia (<i>Chlorophonia callophrys</i>) | 43 ± 37 | 18 ± 12 | 17 ± 20 | 0.41 |
| Flame-colored Tanager (<i>Piranga bidentata</i>) | 1 ± 1a | 10 ± 14ab | 32 ± 12b | 0.02 |
| Common Bush-tanager (<i>Chlorospingus ophthalmicus</i>) | 9 ± 16 | 84 ± 106 | 175 ± 123 | 0.16 |
| Sooty-capped Bush-tanager (<i>Chlorospingus pileatus</i>) | 345 ± 48a | 423 ± 146a | 46 ± 55b | 0.00 |
| Yellow-thighed Finch (<i>Pselliophorus tibialis</i>) | 139 ± 40a | 129 ± 42ab | 45 ± 39b | 0.04 |
| Large Frugivores ^A | 10 ± 2a | 8 ± 4ab | 1 ± 2b | 0.01 |
| Large Ground-dwellers ^A | 21 ± 16 | 7 ± 10 | 3 ± 4 | 0.15 |
| Medium-sized Frugivores ^A | 10 ± 7 | 17 ± 10 | 7 ± 9 | 0.42 |
| Small Frugivores ^A | 7 ± 3a | 70 ± 42b | 67 ± 20b | 0.02 |

a,b Differences in bird densities between the three disturbance types were tested with one-way analysis of variance (ANOVA), with different letters within each row indicating significant differences between disturbance categories, as identified by a post hoc Tukey's HSD test.

A Densities of 14 frugivorous bird species could not be estimated individually due to low number of records; combining data of these species into four groups yielded density estimates for each group (see main text for details).

4.1. Response to disturbance

Both positive and negative responses of bird communities to habitat disturbance have been reported from the Neotropics. Compared to intact forest, heavily disturbed habitats tend to be especially poor in terms of species numbers and abundance (Estrada et al., 1993; Petit et al., 1999; Daily et al., 2001; Dunn, 2004; O'Dea and Whittaker, 2007). Species numbers and abundance in agricultural areas with higher tree cover are generally much higher (Estrada et al., 1993, 1997; Reitsma et al., 2001; Hughes et al., 2002; Matlock et al., 2002; Lindell et al., 2004; Sekercioglu et al., 2007). In southern Mexico, Guevara and Laborde (1993) have found frugivorous forest birds to be frequently using isolated pasture trees, even for nesting. Propagule movement between forest and such trees appears substantial. In the Talamanca mountain forest region, high densities of remnant and successional trees in disturbed habitats are likely to contribute to the relative tolerance of frugivores to intermediate disturbance and to a lesser degree to heavy disturbance. Species composition in heavily disturbed habitats is often a mixture of resilient species originating from the intact forest and open area species, which invade from other disturbed areas. In some heavily disturbed areas, the local avifauna consists mostly of resilient species (Daily et al.,

2001; Barrantes and Pereira, 2002; Hughes et al., 2002; Lindell et al., 2004; Stouffer et al., 2006; this study) while other heavily disturbed areas have few remaining forest species and are dominated by open area species (da Silva et al., 1996; Estrada et al., 1997; Petit and Petit, 2003; O'Dea and Whittaker, 2007).

Previous studies in the Neotropics report increased species richness or bird densities in response to moderate habitat disturbance (Johns, 1991; Blake and Loiselle, 2001; Woltmann, 2003; O'Dea and Whittaker, 2007; but see Thiollay, 1997; Lees and Peres, 2006). Moderately disturbed habitats consist of degraded forest or patchy landscapes with open and closed forest habitat. Heterogeneity of vegetation structure is typically high, which is often favorable for bird diversity (MacArthur and MacArthur, 1961). In moderately disturbed habitats bird species from both sides of the disturbance gradient occur (Connell, 1978). This was also the case in our study. Fruit abundance might be higher in moderately disturbed habitats because of improved light conditions for fruiting trees. This might partially explain the relative tolerance of frugivores to intermediate levels of disturbance found in this study. Throughout the Neotropics tolerance of frugivorous birds to habitat disturbance is a frequently seen phenomenon (Johns, 1991; Mason, 1996; Estrada et al., 1997; Petit et al., 1999; Blake and Loiselle, 2001; Barrantes

and Pereira, 2002; Woltmann, 2003; but see also Stouffer et al., 2006). However, differences can arise when body mass (or body size) is related to tolerance to disturbance. A larger body mass is generally associated with increased vulnerability to disturbance for birds in the tropics (e.g. Keane et al., 2005; Feeley et al., 2007; Gray et al., 2007). In a bird study on fragmentation in the Colombian Andes at only a marginally lower altitude than our study, Renjifo (1999) has found that while extra vulnerability to disturbance is not clearly pronounced for large birds of other guilds, it is certainly present for large frugivores. Similarly, he found small frugivores more resilient to disturbance. These findings are in line with our findings that large frugivores are among the least tolerant to habitat disturbance. However, intolerance to disturbance also occurs among several small frugivores in our study.

4.2. Consequences for natural regeneration

The success of restoration of anthropogenically degraded lands by the aid of frugivores depends, together with management objectives and available resources, on many ecological factors (Duncan and Chapman, 2002). The potential of frugivorous birds as seed dispersers to overcome the problem of limited availability of forest seeds is studied in different parts of the world (e.g. Carlo et al., 2003; Neilan et al., 2006; Cramer et al., 2007). In the present study, we focus on the tolerance of frugivorous birds to anthropogenic habitat disturbance as an integrated part of this problem. If frugivorous birds appear intolerant to habitat disturbance it is unlikely that they contribute to seed dispersal from the forest into degraded habitats since movement between forest and degraded habitats is limited and abundances in degraded habitats will be low. In our study, we find the frugivorous bird community to be relatively tolerant to habitat disturbance. However, there is less tolerance to severe habitat disturbance and several species appear rather intolerant to habitat disturbance. The potential of frugivorous birds as forest seed dispersers can be assessed by looking at the relative importance of the tolerant frugivores as seed dispersers and the degree of occurrence of the intolerant frugivores in disturbed habitats.

The relative importance of frugivores as effective dispersers of forest seeds depends on the quantity and quality of seed dispersal (Schupp, 1993) which is influenced by diet, behavior, habitat use, body size and morphology. A morphological constraint to maximum fruit size that can be handled related to body size is gape width. Frugivores with a small gape width are only capable of eating small fruits, whereas frugivores with a large gape width eat both large and small fruits (Wheelwright et al., 1984, 1985). This seems vitally important for dispersal of forest seeds to degraded habitats as Neotropical montane forest are dominated by large-seeded trees such as *Lauraceae* (Gentry, 1995). In a Costa Rican cloud forest at lower altitudes (ca. 1600 m) large seeds of a tree species of *Lauraceae* are reported to be primarily dispersed by only four large frugivores (Wenny, 2000a). These species, with the exception of one species that is not observed in our study area, together form the lumped species group of the Large Frugivores in our study.

Considering that the large frugivores are intolerant to severe habitat disturbance many forest seeds are unlikely to be dispersed into severely disturbed habitats in any significant amount. Given the moderate tolerance to intermediate habitat disturbance forest seeds will be dispersed into intermediately disturbed habitats in a reduced amount. The species group of the Large Ground-dwellers shows a similar response to disturbance, although it shows no significant habitat preference, due to high variation mainly among undisturbed habitats. Large Ground-dwellers are likely capable of handling fruits of similar sizes compared to other large frugivores, but behavior and other possible constraints (e.g. seed predation) imply that effectiveness of forest seed dispersal might be considerably different. The only large frugivore that appears tolerant to both moderate and severe disturbance is the Band-tailed Pigeon, likely a good quality disperser of a variety of forest seeds including *Quercus* (Stiles and Skutch, 1989). However, gape width is likely too small to disperse the larger forest seeds (Wheelwright et al., 1984).

For severely disturbed habitats efficient dispersal of forest seeds might strongly depend on the medium-sized frugivores. All medium-sized frugivores are tolerant to both moderate and severe disturbance. Although no dispersers of the largest forest seeds, all are high quality dispersers of smaller seeds including sub-canopy forest trees and *Quercus* (Wheelwright et al., 1984; Remsen et al., 1993; Wenny, 2000b). In intermediately disturbed habitats medium-sized as well as large frugivores will likely ensure dispersal of forest seeds. These habitats have good potential for natural regeneration by the aid of frugivores. Many small frugivores are likely to disperse a variety of forest seeds of the smaller sizes in both moderately and severely disturbed habitats, possibly indirectly stimulating future establishment of late-successional forest elements. Many questions on the effectiveness of natural regeneration by the aid of frugivorous birds remain unsolved. It is likely that once some vegetation has established, natural regeneration becomes a self-reinforcing process in which both conditions for seed germination and habitat preferences of important seed dispersers improve.

5. Conclusions

Combining our findings we conclude that moderately disturbed sites appear to have a good potential for natural regeneration aided by frugivorous birds. However, severely disturbed sites lack potentially important forest frugivores and may therefore have worse prospects. In our study disturbed habitats were always in the proximity of large tracts of continuous cloud forest. Therefore, bird populations in pasture areas could very well be sink populations not able to survive without a larger source population inhabiting the nearby forest. Deforestation in the study area is only of recent origin and the persistence of numerous birds in newly created pastures could be the effect of a time lag in local extinctions. Invasion of highland pastures by birds that prefer open areas, immigrating from different altitudes, and the competitive exclusion of the present pasture avifauna which originates from the intact forest may simply be a matter of time.

Our study suggests that moderately disturbed areas with a recent deforestation history and in close proximity to intact forests may have a good potential for natural regeneration, and consequently for restoration of landscape connectivity. They should be given high priority in restoration programs that include natural regeneration as a key strategy. However, the outlook for the more severely disturbed areas is less promising. We conclude that montane cloud forests are vitally important as they not only contain important viable seed sources essential for the success of natural regeneration, but also frugivorous birds needed to disperse those seeds to regeneration sites outside the intact forest. By promoting the use of frugivorous birds as key seed dispersal agents to speed up natural regeneration, we can significantly contribute to long-term restoration and conservation of cloud forests in a very cost-effective way.

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Appendix A

Body mass and number of records of 40 frugivorous bird species at sites with low, intermediate or high levels of disturbance in the Talamanca Mountains, Costa Rica

| Bird species | Body mass (g) | Individuals per disturbance category (effort) | | |
|---|---------------|---|----------------------|--------------|
| | | Low (32 km) | Intermediate (24 km) | High (46 km) |
| Highland Tinamou (<i>Nothocercus bonapartei</i>) | 850 | 12 | 0 | 4 |
| Black Guan (<i>Chamaepetes unicolor</i>) | 950 | 13 | 4 | 0 |
| Buffy-crowned Wood-partridge (<i>Dendrortyx leucophrys</i>) | 350 | 23 | 3 | 2 |
| Spotted Wood-quail (<i>Odonthophorus guttatus</i>) | 300 | 71 | 49 | 36 |
| Band-tailed Pigeon (<i>Columba fasciata</i>) | 315 | 30 | 30 | 87 |
| Ruddy Pigeon (<i>Columba subvicia</i>) | 170 | 76 | 20 | 49 |
| Buff-Fronted Quail-dove (<i>Geotrygon costaricensis</i>) | 250 | 3 | 0 | 0 |
| Sulfur-winged Parakeet (<i>Pyrrhura hoffmanni</i>) | 75 | 7 | 2 | 54 |
| Resplendent Quetzal (<i>Pharomachrus mocinno</i>) | 210 | 28 | 5 | 3 |
| Collared Trogon (<i>Trogon collaris</i>) | 70 | 17 | 9 | 11 |
| Prong-billed Barbet (<i>Semnornis frantzii</i>) | 62 | 17 | 18 | 25 |
| Emerald Toucanet (<i>Aulacorhynchus prasinus</i>) | 180 | 4 | 13 | 6 |
| Acorn Woodpecker (<i>Melanerpes formicivorus</i>) | 85 | 54 | 28 | 94 |
| Barred Becard (<i>Pachyrhamphus versicolor</i>) | 14 | 49 | 7 | 12 |
| Tropical Kingbird (<i>Tyrannus melancholicus</i>) | 40 | 0 | 3 | 60 |
| Yellowish Flycatcher (<i>Empidonax flavescens</i>) | 12 | 9 | 2 | 4 |
| Mountain Elaenia (<i>Elaenia frantzii</i>) | 20 | 42 | 365 | 825 |
| Mistletoe Tyrannulet (<i>Zimmerius vilissimus</i>) | 9 | 129 | 86 | 144 |
| Silvery-throated Jay (<i>Cyanolyca argentigula</i>) | 65 | 7 | 0 | 1 |
| Clay-colored Robin (<i>Turdus grayi</i>) | 76 | 0 | 5 | 17 |
| Mountain Robin (<i>Turdus plebejus</i>) | 86 | 145 | 403 | 467 |
| Black-faced Solitaire (<i>Myadestes melanops</i>) | 33 | 160 | 37 | 31 |
| Swainson's Thrush (<i>Catharus ustulatus</i>) | 28 | 0 | 13 | 43 |
| Slaty-backed Nightingale-thrush (<i>Catharus fuscater</i>) | 35 | 5 | 3 | 11 |
| Ruddy-capped Nightingale-thrush (<i>Catharus frantzii</i>) | 28 | 118 | 147 | 101 |
| Black-billed Nightingale-thrush (<i>Catharus gracilirostris</i>) | 21 | 176 | 135 | 106 |
| Long-tailed Silky-flycatcher (<i>Ptilononyx caudatus</i>) | 37 | 15 | 31 | 231 |
| Black-and-yellow Silky-flycatcher (<i>Phainoptila melanoxantha</i>) | 56 | 7 | 23 | 0 |
| Yellow-winged Vireo (<i>Vireo carmioli</i>) | 13 | 24 | 11 | 17 |
| Flame-throated Warbler (<i>Parula gutturalis</i>) | 10 | 31 | 22 | 43 |
| Black-cheeked Warbler (<i>Basileuterus melanogenys</i>) | 13 | 48 | 13 | 6 |
| Golden-browed Chlorophonia (<i>Chlorophonia callophrys</i>) | 25 | 107 | 45 | 77 |
| Spangled-cheeked Tanager (<i>Tangara dowii</i>) | 20 | 3 | 14 | 17 |
| Flame-colored Tanager (<i>Piranga bidentata</i>) | 38 | 4 | 10 | 59 |
| Common Bush-tanager (<i>Chlorospingus ophthalmicus</i>) | 20 | 3 | 46 | 201 |
| Sooty-capped Bush-tanager (<i>Chlorospingus pileatus</i>) | 20 | 222 | 203 | 50 |
| Large-footed Finch (<i>Pezopetes capitalis</i>) | 56 | 16 | 19 | 11 |
| Yellow-thighed Finch (<i>Pselliophorus tibialis</i>) | 31 | 62 | 55 | 47 |
| Yellow-throated Brush-finch (<i>Atlapetes gutturalis</i>) | 33 | 0 | 5 | 2 |
| Chestnut-capped Brush-finch (<i>Atlapetes brunneinucha</i>) | 42 | 0 | 2 | 5 |

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