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# FRUIT REMOVAL BY LARGE AVIAN FRUGIVORES VARIES IN RELATION TO HABITAT QUALITY IN CONTINUOUS NEOTROPICAL RAINFOREST

**Michael C. Mahoney**[1] · **Luke Browne**[1,2,3] · **Zoe Diaz-Martin**[1,2] · **Jorge Olivo**[2] · **Jacqueline Cabrera**[2] · **Monica Gonzalez**[2] · **Jenny Hazlehurst**[4] · **Jordan Karubian**[1,2]

[1] Department of Ecology and Evolutionary Biology, Tulane University, 400 Boggs Building, New Orleans, LA 70118, USA.

[2] Fundación para la Conservación de los Andes Tropicales, Mariano Hurtado y Vicente Heredia N-5089, Quito, Ecuador.

[3] UCLA La Kretz Center for California Conservation Science, Institute of the Environment and Sustainability, Los Angeles, CA 90095, USA.

[4] Department of Entomology, University of California Riverside, 900 University Ave., Riverside, CA 92521, USA.

E-mail: Jordan Karubian · jk@tulane.edu

**Abstract** · Animal-mediated seed dispersal shapes key ecological processes including seedling recruitment and demography. Anthropogenic activities have substantively impacted tropical habitats, yet the degree of sensitivity exhibited by different frugivores to changes in habitat quality and how this may impact seed dispersal outcomes remains poorly understood. This is particularly true in contexts of low to moderate habitat alteration. To address this knowledge gap, we characterized the diurnal disperser community for an ecologically important canopy palm, *Oenocarpus bataua,* in continuous forest with differing degrees of human modification in northwest Ecuador. Our specific goal was to assess the degree to which visitation and fruit removal rates vary in relation to fine-scale forest structure. Frugivory and seed dispersal (i.e., removal of fruits with intact seeds) was dominated by three large bird species; smaller birds and some mammals visited fruiting trees but did not substantively contribute to seed dispersal. One of the three effective dispersal agents, the Long-wattled Umbrellabird (*Cephalopterus penduliger*), an endangered species threatened by habitat loss and degradation, exhibited higher visitation and fruit consumption rates in areas characterized by denser canopies, suggesting preference for foraging in undisturbed habitat. In contrast, two relatively common toucan species, Chocó Toucan (*Ramphastos brevis*) and Chestnut-mandibled Toucan (*R. swainsonii*), exhibited no variation in foraging behavior in relation to the habitat metrics we assessed. These findings highlight the degree to which differences in sensitivity to habitat disturbance among frugivore species may impact foraging ecology and suggest that variation in forest structure within continuous forest can impact seed removal and seed dispersal processes.

**Resumen · La remoción de frutas por aves frugívoras de gran tamaño varía con respecto a la calidad de hábitat en bosques continuos Neotropicales**

La dispersión de semillas mediada por animales moldea procesos ecológicos claves como la posterior supervivencia y demografía de plántulas. Las actividades antropogénicas han afectado substancialmente los hábitats tropicales, sin embargo, el nivel de sensibilidad que presentan los diferentes frugívoros a cambios en la calidad del hábitat y cómo esto afecta a la dispersión de semillas, sigue siendo poco conocido. Esto es particularmente cierto en un contexto de poca a moderada alteración de hábitat. Para lograr comprender este vacío de conocimiento caracterizamos la comunidad de dispersores diurnos de una palma de dosel de importancia ecológica, *Oenocarpus bataua*, en bosques continuos con niveles diferentes de afectación humana en el noroccidente del Ecuador. Nuestro objetivo principal era de conocer el nivel en el cual las visitas y las tasas de remoción de frutas varía en relación a la estructura del bosque a escala muy fina. La frugivoría y la dispersión de semillas (es decir remoción de frutos con semillas intactas) fue dominada por tres especies de aves de gran tamaño; las aves más pequeñas y ciertos mamíferos visitaron palmas en fruto pero no contribuyeron substancialmente a la dispersión de semillas. Uno de los tres agentes de [illegible] y degradación de su hábitat – realizó un mayor número de visitas y tasa de consumo de frutos en áreas caracterizadas por doseles más densos, lo cual sugiere una preferencia de forrajeo en hábitats no alterados. Por el contrario, dos especies relativamente comunes de tucanes, Tucán del Chocó (*Ramphastos brevis*) y Tucán de Pico Castaño (*R. swainsonii*), no presentaron diferencias en el comportamiento de forrajeo con respecto a las métricas de hábitat que nosotros utilizamos. Estos hallazgos resaltan el nivel en el cual diferencias en la sensibilidad a la alteración del hábitat entre especies frugívoras pueden impactar la ecología de forrajeo. Sugiere también que la variación en la estructura del bosque dentro de bosques continuos puede impactar la remoción de semillas y el proceso de dispersión de las mismas.

**Key words:** *Cephalopterus penduliger* · Chocó rainforest · Ecuador · Forest structure · Frugivory · *Oenocarpus bataua* · *Ramphastos brevis* · *Ramphastos swainsonii* · Seed dispersal

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## INTRODUCTION

Seed dispersal, the movement of a seed away from its parent plant, is a key ecological and evolutionary process that facilitates colonization of new habitats, provides escape from density dependent mortality factors such as pathogens, predators, and intraspecific competition near parent trees, and shapes patterns of gene flow structure within and between populations (Harms et al. 2000, Wang & Smith 2002, Comita et al. 2010, Franziska et al. 2014). Frugivores and the seed dispersal services that they provide have an outsized influence on plant demography and genetics in many systems (Wenny & Levey 1998; Karubian et al. 2010, 2012; García & Grivet 2011). For example, in the tropics an estimated 85% of tree species are dispersed by vertebrates (Terborgh 1990, Almeida-Neto et al. 2008). Human activities such as habitat degradation may perturb these mutualisms, with potentially important consequences for ecological and microevolutionary dynamics in plant populations (Kirika et al. 2008, Markl et al. 2012, Galetti et al. 2013, Menezes et al. 2016). For this reason, better understanding the ways in which habitat degradation impacts frugivory and seed dispersal is a timely research topic for tropical ecologists and conservation biologists.

Habitat conversion is an increasingly prevalent source of disturbance in tropical landscapes. Between 1950 and 2000, more than 50% of the terrestrial area in the tropics experienced some level of anthropogenic disturbance, including selective logging (removal of certain trees), fragmentation, or clear-cutting (ITTO 2002). Much attention has been given to how habitat conversion via deforestation and forest fragmentation has impacted species diversity and composition (Mesquita et al. 2001, Wright 2005, Barlow et al. 2007a, Chazdon et al. 2009, Newbold et al. 2015, Arroyo-Rodríguez et al. 2017). Relatively less attention has been paid to potential impacts of more subtle forms of habitat degradation on ecological processes (Gray et al. 2007, Norden et al. 2009), and available results are mixed (Barlow et al. 2007b, Gardner et al. 2007, Gibson et al. 2011, McConkey et al. 2012, Durães et al. 2013).

Frugivorous birds play a key role in forest maintenance and regeneration because of the seed dispersal services that they provide (Gorchov et al. 1993, Jordano 2000, Gray et al. 2007, Arroyo-Rodríguez et al. 2017). Small-bodied generalist birds have the potential to disperse large numbers of seeds (Carlo & Morales 2008). In contrast, large-bodied birds may disperse fewer seeds in terms of absolute numbers but play a disproportionately important role in dispersing high volumes of seeds and relatively large seeds (Jordano 2000, Markl et al. 2012, Galetti et al. 2013, Muñoz et al. 2016). They may also move longer distances, thereby providing long distance seed dispersal (Holbrook et al. 2002, Van Houtan et al. 2007, Lees & Peres 2009). However, large-bodied frugivores are often more heavily impacted by tropical forest loss and habitat disturbance (Renjifo 1999, Barlow et al. 2007b, Markl et al. 2012, Reid et al. 2012), which may in turn impact the reproductive biology and dispersal dynamics of the plants they disperse (Galetti et al. 2013).

We studied how frugivory by birds may be influenced by forest structure and microhabitat composition in continuous forest, with a focus on fruit removal of the large-seeded and widespread tropical canopy palm (*Oenocarpus bataua*, Arecaceae). Our first objective was to quantify visitation and dispersal rates by diurnal frugivores in our study area in northwest Ecuador, where previous studies have been conducted on *O. bataua* population genetics and one of its dispersal agents, the Long-wattled Umbrellabird (*Cephalopterus penduliger*) (Browne et al. 2015, Karubian et al. 2012). We predicted that large-bodied species, such as *Ramphastos* toucans and the Long-wattled Umbrellabird, would reliably remove whole fruits with seeds and provide seed dispersal services. Our second objective was to determine the degree to which variation in foraging patterns by avian frugivores can be explained by surrounding forest structure and microhabitat. Chestnut-mandibled Toucans (*Ramphastos swainsonii*), Chocó Toucans (*Ramphastos brevis*), and Long-wattled Umbrellabirds respond negatively to disturbance (Holbrook & Loiselle 2009, Karubian et al. 2012, BirdLife International 2016), but evidence from our own and other systems suggests toucans may be relatively more resilient (O'Dea & Whitaker 2007, Durães et al. 2013, Walter et al. 2017). We therefore predicted that, in continuous forest where habitat quality varies, Long-wattled Umbrellabirds, but not toucans, would remove *O. bataua* seeds from trees in more degraded habitat less often than in areas of old growth forest.

## METHODS

**Study area.** We conducted fieldwork at Bilsa Biological Station (BBS, 00°21’33”N, 79°42’02”W, elevation 300–750 m a.s.l., 3000 ha; Figure 1), a private reserve nestled within the 119,172 ha federal Reserva Ecológica Mache-Chindul (REMACH) located within the Chocó biogeographic zone, Esmeraldas province, northwest Ecuador (BirdLife International 2018). Bilsa Biological Station and surrounding areas exhibit high endemism, high diversity for plants and animals, and high rates of deforestation and conversion to agricultural land by local landowners (Dodson & Gentry 1991, Orme et al. 2005). The region exhibits seasonality with a relatively cool dry season from July to December, and a warm wet season from January until July, with an average yearly rainfall of 2000–3000 mm (Durães et al. 2013). Data were collected in a 130-ha study area that ranged in elevation from 435–615 m. This study area contains a continuous mosaic of forest types including primary old-growth forest, 19–30 year old secondary forest regenerating from clear-cut pasture, and selectively logged forest all with subtle but observable differences in structural composition as a result of previous modification regime (Durães et al. 2013). This continuous variation in habitat types allowed us to investigate how fruit removal might vary across different microhabitats in a continuous forest reserve. We did not expect that elevation would impact our findings as the potential frugivores identified in an earlier census (see Carrasco et al. 2013) of the avian community in BBS and the surrounding region exhibit much wider documented elevation ranges than the study parcel exhibits (Ridgely & Greenfield 2001, Carrasco et al. 2013, Walter et al. 2017).

**Study species.** Our first objective was to determine the primary diurnal frugivores of *Oenocarpus bataua,* a long-lived monoecious canopy palm in the family Arecaceae. *Oenocarpus bataua* is considered a 'hyperdominant' species, with a distribution that includes both the Amazon Basin and Chocó

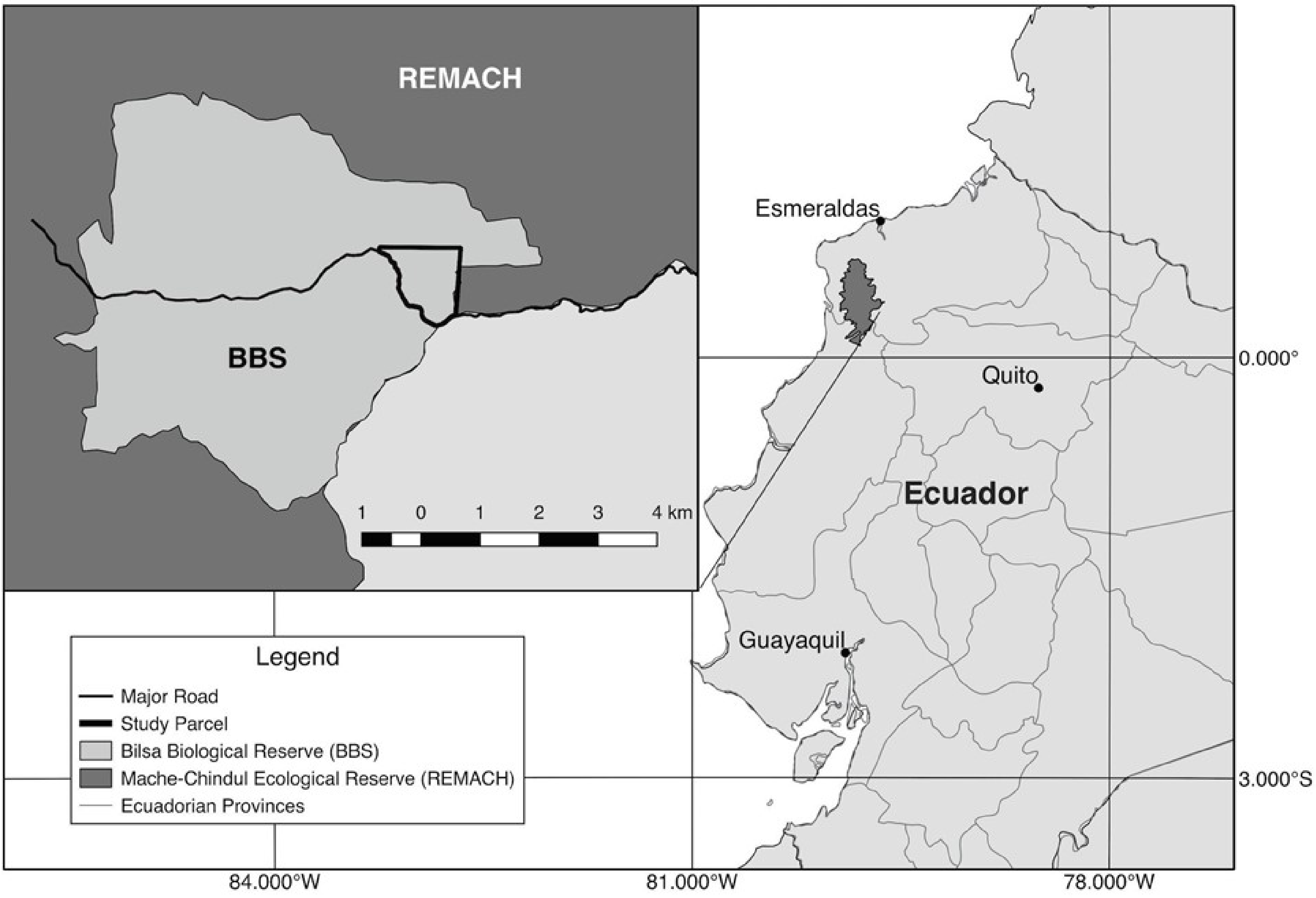

**Figure 1.** Map of the 130-ha continuous forest study area within Bilsa Biological Station (3000 ha) in the Mache-Chindul Reserve (119,172 ha), northwest Ecuador, at the southern extent of the Chocó Biogeographic Region. The main road passes along the southern boundary of the study parcel.

forests to the West of the Andes (Goulding & Smith 2005, ter Steege et al. 2013). *Oenocarpus bataua* exhibits a supra-annual cycle of fruit production, in that many adult trees synchronously flower and subsequently fruit on two-year intervals (Rojas-Robles & Stiles 2009). An adult tree can produce one or more infructescences of clustered fruit with > 2000 large-seeded (seed size: 39.7 ± 3.4 mm length × 22.7 ± 2.2 mm width; Browne et al. 2015), lipid rich fruits per infructescence. Ripe fruits are typically present on the infructescence for approximately four weeks (Rojas-Robles & Stiles 2009). *Oenocarpus bataua* is slow growing, taking up to 80 years or more to reach reproductive maturity, suggesting that the *O. bataua* trees in secondary forests within our study area are most likely remnants from before the area was clear-cut (Isaza et al. 2016; see also Browne et al. 2015). Adult *O. bataua* trees are found with similar densities across habitat types within our study area.

**Frugivore observations.** We characterized avian visitation and seed dispersal at *O. bataua* trees in our study area via observations of fruiting trees between February 2009 and June 2016. During each observation, observers sat quietly on the ground approximately 20 m from a fruiting tree recording the number of individuals visiting the tree, the length of the bird's visit, and the number of intact seeds removed from the focal tree. Observers identified frugivores to the species level using Ridgely & Greenfield (2001). Observations of focal trees lasted 3 hours and were conducted during either the early morning or late afternoon on individual trees that had at least one infructescence with mature fruit. As our observations were restricted to daylight hours, nocturnal species were not considered in the current study. In addition, we did not record species that removed fruit and seeds from the forest floor (i.e., secondary dispersal agents). The number of focal trees observed per year ranged from 3–35 (average ± SD = 14.25 ± 9.93). Observations were balanced across wet vs. dry seasons and across the two halves of the study period, and we had at least one observation in each month of the year; however across the study period, the highest numbers of observations were conducted in July and December. Although we provide a summary of all species observed consuming *O. bataua* fruits, we limit our statistical analyses to those species that removed fruits with intact seeds from trees, and thus acted as viable seed dispersal agents for *O. bataua*, in sufficient numbers to allow statistical analysis. We calculated percent removal by a single species and a species-specific removal rate by dividing the total number of seeds eaten by the number of hours of observation.

**Habitat metrics.** For each tree included in the study, we measured habitat characteristics at various distances around focal trees that we have previously found to be useful in describing ecological pattern and process (e.g., Karubian & Carrasco 2008, Durães et al. 2013, Karubian et al. 2016), including percentage canopy cover, canopy height, number of trees in the genus *Cecropia* (Urticaceae), and number of large trees (> 50 cm DBH). We measured canopy cover from underneath the focal tree using a concave spherical densiometer that measured the amount of light hitting the forest understory (Forestry Suppliers no. 43888). To calculate this metric, we counted the number of light spots hitting the 96-point concave half sphere and multiplied the count by 1.04 to scale the metric to 100. We then subtracted that number (i.e., amount of light) from 100 to give us the percent coverage. We measured canopy height (m), indicated by the tallest tree in a 10-m radius around the *O. bataua* tree, using a digital range finder. In the case where the tree under observation was the tallest tree, the canopy height was equal to the height of the focal tree. We counted the number of adult trees in the genus *Cecropia* in a 10 m radius centered around the focal *O. bataua* tree as a proxy for recent disturbance, as these are pioneer tree species (Norden et al. 2009) and in past studies have been a useful index of habitat disturbance in BBS (Karubian & Carrasco 2008). Additionally, we counted the number of trees with a diameter at breast height (DBH) > 50 cm within a 20 m radius of each tree, to capture the number of large trees surrounding each focal tree. We used these continuous measures of microhabitat structure rather than a categorical measurement of habitat in order to parse out responses to habitat structure differences, as categorical descriptions have in the past not been effective indicators of response (Barlow et al. 2007b). We selected these habitat measurements for our study because previous studies in the area have used these habitat variables as indicators of forest structure (*sensu* Durães et al. 2013).

**Statistical analysis.** To test for associations between habitat characteristics (e.g., canopy height in a 10 m radius around tree (m), canopy cover, number of trees in the genus *Cecropia*, and number of trees > 50 cm DBH in a 20 m radius around tree) and fruit removal rates, we used multiple generalized linear mixed models (GLMMs) with a Poisson error structure (one for each species). Fruit removal rates were calculated as the total number of seeds removed by a species during an individual 3-hour observation period averaged across the seven years of observations. We chose a Poisson error structure because these models generally fit well to count or rate data (Bolker et al. 2009), which in our case was the number of fruits removed per 3-hour observation period. Because some trees had multiple observations, we added an individual level random effect of Tree ID to avoid pseudoreplication. To assess collinearity among our explanatory variables, we estimated the VIF (variance inflation factor) for each variable and found that all VIF values were < 1.3, which is less than the VIF = 3 threshold suggested by Zuur et al. (2010), where multicollinearity is a cause for concern in model formulation. We mean-centered and scaled predictor variables to standard deviation = 1 prior to analysis to facilitate comparison of regression coefficients (Schielzeth 2010). We ran all statistical analyses in R 3.4.0 (R Core Team 20171) using the 'lme4' package to fit the GLMMs (Bates et al. 2015).

## RESULTS

**Frugivore observations.** We completed 114 observation periods on 73 focal *O. bataua* trees, for a total of 342 hours of observation. We recorded six species feeding on fruits from *O. bataua* infructescences, five of which were birds (Table 1). Three avian frugivores dominated removal of fruits with intact seeds: Long-wattled Umbrellabird (*Cephalopterus penduliger*), Chestnut-mandibled Toucan (*Ramphastos swainsonii*), and Chocó Toucan (*Ramphastos brevis*). The Long-wattled Umbrellabird dispersed a total of 102 seeds (40.2% of total dispersal events), at a rate of 0.30 seeds per hour of observation; the Chestnut-mandibled Toucan dispersed 80 seeds (31.5%) at a rate of 0.23 seeds per hour of observation; and the Chocó Toucan dispersed 72 seeds (28.3%) at a rate of 0.21 seeds per hour of observation. Together the two toucan species accounted for 59.8% of all seeds dispersed. A Bronze-winged Parrot (*Pionus chalcolpterus*) and a squirrel (*Sciurus* sp.) were both observed to remove a single fruit with the seed intact, and a Rose-faced Parrot (*Pyrilia pulchra*) was observed to consume pulp without ingesting any seeds.

**Foraging preferences.** Long-wattled Umbrellabirds preferentially foraged in areas with more closed canopies (Table 2), indicative of less disturbed selectively logged and primary forests. Umbrellabird fruit-removal patterns did not correlate with any other microhabitat variables we measured (Table 2). Fruit-removal rates by the toucan species did not correlate with any of the microhabitat variables we measured (Table 2).

## DISCUSSION

Over the course of seven years of direct observation, we recorded a total of five frugivorous bird species and one squirrel consuming the fruit from *Oenocarpus bataua* infructescences. Of these, three birds removed the vast majority of fruits with intact seeds, thereby serving as primary seed dispersal agents for this large-seeded canopy palm: Long-wattled Umbrellabird (male length and body mass: 40–42 cm, 600 g), Chestnut-mandibled Toucan (53.5–56 cm, 665 g), and Chocó Toucan (43–45.5 cm, 412 g) (Ridgely & Greenfield 2001, BirdLife International 2016). We attribute this low richness of seed dispersers to the relatively large size of the O. *bataua* seed, which may make it difficult or impossible for smaller bird species to swallow the seeds (e.g., Muñoz et. al 2016). We also note that we made no observations at night and thus may be neglecting ecologically important nocturnal avian or mammalian frugivores. The Long-wattled Umbrellabird consumed fruits more frequently than did either species of toucan, but in aggregate the two toucan species consumed more fruit than did umbrellabirds. These findings support our first prediction that *O. bataua* fruits would be dispersed primarily by large-bodied frugivores. *Oenocarpus bataua* depends on large-seeded dispersers for effective propagule dispersal, and previous work at this field site has shown that when dispersal mutualisms are impacted through habitat loss and forest fragmentation, there are consequences for genetic structure and perhaps long-term survival of the population (Browne et al. 2015).

Birds with similar functional traits like body size and feeding guild are often assumed to occupy similar functional groups and therefore are predicted to shift their foraging preferences to disturbance in similar ways (Barlow et al. 2007b). However, we found that umbrellabird fruit-removal rates vary in relation to canopy coverage, while toucans

**Table 1.** Vertebrate species recorded visiting *Oenocarpus bataua* trees with ripe fruit during diurnal focal tree observations in northwest Ecuador. Three avian species, Long-wattled Umbrellabird (*Cephalopterus penduliger)*, Chestnut-mandibled Toucan (*Ramphastos swainsonii)*, and Chocó Toucan (*Ramphastos brevis)*, dominated seed dispersal as assessed by swallowing fruit with intact seed.

| Family | Species | Number of visits recorded | Number of fruits with only pulp ingested | Number of seeds ingested |
|---|---|---|---|---|
| Sciuridae | Unidentified Squirrel (*Sciurus* sp.) | 3 | | 1 |
| Psittacidae | Bronze-winged Parrot (*Pionus calcholpterus*) | 1 | | 1 |
| Psittacidae | Rose-faced Parrot (*Pyrilia pulchra*) | 2 | 4 | |
| Ramphastidae | Chocó Toucan (*Ramphastos brevis*) | 60 | | 77 |
| Ramphastidae | Chestnut-mandibled Toucan (*Ramphastos swainsonii*) | 50 | | 87 |
| Cotingidae | Long-wattled Umbrellabird (*Cephalopterus penduliger*) | 116 | | 107 |

show no relationship to this or other measures of habitat quality that we investigated. Across the tropics, disturbed forests often have more open canopies (Guariguata & Ostertag 2001, Arroyo-Rodríguez et al. 2017), and this is also the case in our study area, in that canopy coverage in primary and selectively logged forests is considerably higher than in regenerating secondary forests (Durães et al. 2013). Local disturbance and changes in canopy coverage may shape frugivore communities by reducing visitation and removal rates by forest-dependent species (Kirika et al. 2008, Martínez & García 2015). Similarly, we found that the Long-wattled Umbrellabird, a species absent from most forest fragments in REMACH (Walter et al. 2017), appears to prefer to forage at trees in habitats with denser canopies, even within continuous forest. The reasons for this preference are unknown, but may relate to predator avoidance, the distribution of other fruit resources, or proximity to display sites (i.e., leks).

Compared to the Long-wattled Umbrellabird, both toucan species appear to be more general in their habitat requirements and foraging preferences. Additionally, both toucan species are relatively common in degraded forest types within BBS (JK unpubl. data), and also were detected in many of the forest fragments of varying sizes and distances from remnant forest that were sampled in surrounding REMACH (Walter et al. 2017). Yet excessive habitat degradation, hunting, and anthropogenic modification can reduce toucan numbers and also alter their behavior by reducing visitation time and seed removal (Hollbrook & Loiselle 2009).

Both umbrellabirds and toucans are widely considered to serve as high quality seed dispersal agents (Holbrook 2010, Karubian et al. 2012, Galetti et al. 2013, Jones 2017). The degree of overlap in their diets and dispersal services remains unclear, but we can make the following observations. Both species have the potential to move seeds long distances, with toucan dispersal distances estimated at 249–449 m from the parent tree (Holbrook 2010) and mean umbrellabird dispersal distances estimated at 257 m (Karubian et al. 2012) via radio tracking studies. One study notes that toucans may evenly disperse seeds across their home ranges (Jones 2017), while displaying umbrellabirds may generate high concentrations of seeds in lek sites (Karubian et al. 2012, Ottewell et al. 2018). A recent genetic study conducted in BBS suggests that clusters of seeds generated by lekking umbrellabirds may be more genetically heterogeneous than clusters of seeds putatively generated by toucans, but that toucans may move the seeds further from source trees (Browne & Karubian 2018). As such, any influence of canopy openness or other relatively fine grained parameters of habitat quality on visitation and fruit removal rates may have ecologically important consequences for *O. bataua* seed dispersal, seedling recruitment, and genetic structure (Wang & Smith 2002, Holbrook & Loiselle 2009).

*Oenocarpus bataua* is a 'hyperdominant' species in the South American tropics found on both side of the Andes (ter Steege et al. 2013); the size of its range suggests that differences are likely to exist in the composition of frugivore and disperser community among *O. bataua* populations. In Colombia, diurnal primary fruit removal was observed in Red-tailed Squirrels (*Sciurus granatensis*), Western Dwarf Squirrels (*Microsciurus mimulus*), and capuchin monkeys (*Cebus apella*) (Franco-Quimaby & Rojas-Robles 2014). At Tiputini Biodiversity Station in the Ecuadorian Amazon, primary dispersal of *O. bataua* appears to be dominated by spider monkeys (*Ateles belzebuth*) (Karubian et al. 2015). These among site differences in frugivore community are likely associated with differences in seed movement and patterns of genetic structure, but very little comparative work addressing this issue currently exists. It also worth emphasizing that, because the current study only evaluates fruit removal directly from the infructescence during the day, we are potentially only capturing a portion of dispersal agents for *O. bataua*. Extending this study through the use of motion activated camera traps at night (to document nocturnal frugivores) and on the forest floor beneath fruiting trees (to document secondary seed dispersal by terrestrial vertebrates) may broaden the list of *O. bataua's* seed dispersal agents at this site by adding, e.g., agoutis (*Dasyprocta* sp.) and other rodents, peccary (*Pecari* sp.), terrestrial birds, and Oilbirds (*Steatornis caripensis*).

In general, large-seeded plants may be especially impacted by loss (locally or regionally) of large-bodied frugivores because small-bodied frugivores are unlikely to provide effective dispersal services if large-bodied frugivores are

**Table 2.** Influence of habitat quality on fruit removal rate based on generalized linear models with a Poisson error structure that evaluate the effect of habitat measures on fruit removal rates by each of the three main primary seed dispersal agents of the canopy palm (*Oenocarpus bataua*) in northwest Ecuador. Canopy density (i.e., more closed canopy) was positively associated with the rate fruit consumption at *O. bataua* trees by Long-wattled Umbrellabirds (*Cephalopterus penduliger)*. For both toucan species (*Ramphastos brevis, R. swainsonii*), there were no correlations between our selected microhabitat variables and the rate of fruit consumption. Std. = standard; * indicates significant difference (< 0.05).

| | *Cephalopterus penduliger* | | | | *Ramphastos brevis* | | | | *Ramphastos swainsonii* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Estimate Std. | Std. Error | Z value | Pr(>\|z\|) | Estimate Std. | Std. Error | Z value | Pr(>\|z\|) | Estimate Std. | Std. Error | Z value | Pr(>\|z\|) |
| Canopy height | 0.253 | 0.232 | 1.09 | 0.277 | 0.088 | 0.387 | 0.228 | 0.819 | 0.309 | 0.514 | 0.601 | 0.548 |
| Canopy density | **0.528** | **0.216** | **2.45** | **0.014*** | 0.457 | 0.359 | 1.27 | 0.203 | -0.269 | 0.453 | -0.594 | 0.553 |
| # trees > 50 cm DBH | 0.192 | 0.219 | 0.877 | 0.381 | -0.002 | 0.371 | -0.006 | 0.995 | -0.234 | 0.523 | -0.447 | 0.655 |
| *Cecropia* abundance | 0.218 | 0.120 | 1.09 | 0.276 | -0.541 | 0.392 | -1.38 | 0.167 | 0.228 | 0.485 | 0.469 | 0.639 |

absent (Markl et al. 2012, Saavedra et al. 2014). Local losses of frugivore services due to shifts in frugivore behavior to select individuals based on surrounding microhabitat may impact the evolutionary trajectory and genetic structure for plant populations lacking dispersers (Galetti et al. 2013, Browne et al. 2015, Giombini et al. 2017), potentially leading to reduced fitness and population viability. This study demonstrates that even relatively subtle variation in habitat quality - in this case variation in canopy openness within a continuous forest - may influence frugivore foraging patterns. More broadly, while there are certainly advantages associated with grouping species within guilds for ecological or conservation analyses (Bregman et al. 2014) ecologically important differences between species like those observed in our study may be lost with these groupings (McConkey et al. 2012). Additional information about natural history and foraging ecology of these key frugivores is likely to aid in management and conservation efforts (McConkey & Brockelman 2011).

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