ORIGINAL ARTICLE

Ecological drivers of intraspecific variation in seed dispersal services of a common neotropical palm

Therese Lamperty[1,2] | Jordan Karubian[3,4] | Amy E. Dunham[1]

[1]Department of Biosciences, Rice University, Houston, TX, USA

[2]Department of Biology, University of Washington, Seattle, WA, USA

[3]Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA, USA

[4]Fundación para la Conservación de los Andes Tropicales, Quito, Ecuador

Correspondence
Therese Lamperty, Department of Biology, University of Washington, Seattle, WA, USA.
Email: jtl28@uw.edu

Abstract

Through frugivory and seed dispersal, vertebrates influence plant demography and forest regeneration. Variation in local habitat surrounding fruiting plants can influence frugivore foraging decisions, thereby creating intraspecific variation in seed dispersal services. However, we have little knowledge of drivers of local variation in frugivory. Here, we investigate factors that may influence frugivore diversity and fruit removal at the level of individual plants. We focus on a common understory palm within a continuous Chocó forest with mixed land-use histories in Ecuador. The density of pioneer tree species in the genus *Cecropia* around focal palms was negatively related to fruit removal and the diversity of frugivores visiting palms. This may relate to the fact that the presence and abundance of *Cecropia* species often indicate the existence and severity of past disturbances. Local *Cecropia* density was also related to an overall shift in the frugivore community that corresponded with an increase in fruit removal by lower-quality seed dispersers (rodents). We also found that the local density of fruiting conspecifics was positively related to frugivore diversity, but not fruit removal. Our results provide information on drivers of intraspecific inequalities in plant populations across tropical forest landscapes. The reduction in fruit removal and frugivore diversity associated with local *Cecropia* abundance suggests that seed dispersal services can be sensitive to fine-scale variation in habitat structure. Furthermore, because *Cecropia* are often indicative of past disturbances, this indicates that even small-scale habitat degradation by humans can have lasting effects by creating localized pockets of forest unfavored by frugivores.

Abstract in Spanish is available with online material.

KEYWORDS
Choco forest, Ecuador, floral neighborhood, frugivore behavior, frugivory, local habitat effects, seed dispersal, tropical forest

1 | INTRODUCTION

The consumption of fruit by vertebrates facilitates seed dispersal for more than three-quarters of tropical plant species (Bascompte & Jordano, 2007; Howe & Smallwood, 1982). Frugivory comprises a critical step in forest regeneration by allowing propagules to escape distance- and density-dependent mortality concentrated under parent plants (Connell, 1971; Estrada & Fleming, 2012; Janzen, 1970) and by laying the spatial template for plant regeneration on the forest floor (Bagchi et al., 2018; Wandrag et al., 2017). Frugivore visitation and fruit removal are often positively correlated with seedling recruitment (Muñoz et al., 2017) and are the most commonly collected data on the seed dispersal process (Schupp et al., 2019). Yet we have limited knowledge of the drivers of variation in frugivore visitation and fruit consumption at the level of individual plants' (Hopson et al., 2020), even though such intraspecific variation in seed dispersal services has been proposed to affect plant population demography, evolution, and resilience to anthropogenic disturbances (Snell et al., 2019).

Plant traits and the ecological context surrounding individual plants can affect frugivore visitation and, consequently, seed dispersal and recruitment (Carlo & Morales, 2008; Ortiz-Pulido & Rico-Gray, 2000). Such intrinsic factors (traits associated with the plant individual) and extrinsic factors (the ecological context surrounding the plant) that can influence frugivore visitation include fruit crop size, the abundance of surrounding fruiting resources, and habitat characteristics such as canopy density and the presence of old-growth trees versus pioneer trees (Carlo & Morales, 2008; Donoso et al., 2017; Kirika et al., 2008; Schupp et al., 2019). However, the effects and relative importance of extrinsic and intrinsic drivers of intraspecific variation in seed dispersal are not fully understood (Schupp et al., 2019).

Most existing knowledge on drivers of intraspecific variation in fruit removal and seed dispersal comes from studies of how fruit crop size and the local density of neighboring fruiting plants influence frugivore foraging decisions (Blendinger et al., 2008; Fontúrbel et al., 2017; García & Ortiz-Pulido, 2004; Guerra et al., 2017; Hopson et al., 2020; Moreira et al., 2017; Pizo & Almeida-Neto, 2009). In general, studies find that fruit crop size can increase visitation to individual plants. However, the effect that the density of surrounding fruiting plants has on visitation and fruit removal varies. This indicates the effect is mediated by other variables such as landscape-scale fruit availability and localized habitat disturbance levels. Some studies report what appears to be a dilution effect, whereby the abundance of surrounding fruiting individuals decreases individual-level visitation and fruit removal because frugivore visitation is spread across a larger number of fruiting trees (e.g., Hopson et al., 2020; Pizo & Almeida-Neto, 2009). Other work has found that fruiting neighborhood density increased frugivory at the individual plant level instead and indicates resource tracking whereby frugivores are attracted to patches of higher resource concentration and all plants within a patch benefit from increased visitation (Blendinger et al., 2008; Guerra et al., 2017).

In addition to variable resource availability, changes in forest structure and plant composition, such as those caused by past disturbances, can influence the movement and behavior of the local frugivore community, potentially affecting visitation rates and driving intraspecific variation in plant seed dispersal services (Durães et al., 2013; Fontúrbel et al., 2015; García & Martínez, 2012; Kirika, Farwig, et al., 2008; Kirika et al., 2008). For example, some large-bodied avian frugivores exhibit foraging preferences for trees surrounded by relatively denser canopy cover (Mahoney et al., 2018). Factors such as lower canopy density, along with the presence of pioneer tree species and lower canopy heights, are common signs of past localized disturbances in forests from either human activities (e.g., selective logging) or natural disturbances (e.g., treefall; Alroy, 2017; Chazdon, 2014), which may deter frugivores. It is unclear how impactful local habitat heterogeneity can be relative to other factors such as fruit crop size in predicting fruit removal and visitation for individual plants.

Local habitat structure (e.g., canopy openness) and floristic composition (e.g., presence of pioneer species) may alter frugivore visitation to individual plants in a predictive way. For example, higher resilience to local habitat degradation is often exhibited by smaller, lower-quality seed dispersers (e.g., rodents) that either predate seeds or are not likely to facilitate transportation beyond the crowns of parent plants (Galetti et al., 2015; Pérez-Méndez et al., 2015; Rosin & Poulsen, 2016). Large-bodied, more effective long-distance seed dispersers (e.g., large birds) often show heightened sensitivity to habitat disturbance or degradation (Mahoney et al., 2018; Walter et al., 2017). Alternatively, habitat characteristics relating to fine-scale disturbance may have a negligible effect on intraspecific variation in fruit removal (Mahoney et al., 2018; Moreira et al., 2017) given that many frugivores are highly mobile.

To better understand the drivers of intraspecific variation in seed dispersal services for plants, we examined how frugivore visitation and fruit removal from a neotropical palm species was mediated by individual-level variation in crop size, the density of surrounding fruiting conspecifics, and forest vegetation structure and composition associated with small-scale disturbances. Although frugivore visitation and fruit removal are not direct measurements of seed dispersal and recruitment success, they are readily measurable precursors to establishment (Schupp et al., 2019). It is important to note, however, that fruit removal does not necessarily lead to successful establishment or affect population dynamics, and our results should be evaluated with this in mind. Still, understanding factors influencing frugivore visitation and foraging behaviors informs both our knowledge of drivers of forest regeneration dynamics and our knowledge of how current global change patterns may alter plant-animal interactions and, subsequently, future forest regeneration (Albert et al., 2020; Snell et al., 2019). We used camera traps on a dominant understory palm species, *Prestoea decurrens* (Arecaceae), within a continuous Chocó forest of mixed land-use history in northwestern Ecuador. Our objectives were to (1) identify frugivore visitors to *P. decurrens* and to quantify fruit removal at each focal palm, (2) assess

whether fruit removal varies in relation to surrounding habitat structure and composition as well as variation in the focal palm's crop size and neighborhood-level conspecific fruit availability, and (3) examine how frugivore visitation, species richness, and community composition respond to neighborhood variation and how these responses mediate changes in net fruit removal rates.

Rather than testing specific hypotheses, our goal was to better understand the relative role of factors thought to be important mechanisms driving individual variation in frugivore visitation. Previous work has shown that many frugivores avoid or decrease in abundance in disturbed areas (Gray et al., 2007; Kirika, Bleher, et al., 2008; Markl et al., 2012), so we expected to find reduced fruit removal rates, fewer large-bodied frugivore visitors [body size being a proxy for sensitivity to disturbance (Sodhi et al., 2004; Velho et al., 2012)] and reduced abundance of frugivore visitors at palms in areas with local habitat characteristics indicative of past disturbance such as the number of surrounding pioneer tree species. However, we also considered that if frugivore visitation rates are unaffected by fine-scale habitat differences or if declines in some frugivore species are compensated by increases in others, we may not find an effect of habitat variables on net fruit removal, and if frugivores are mobile enough to not be influenced by fine-scale neighborhood variation, intraspecific variation will instead be driven by crop size and the density of fruiting conspecific plants in the focal individuals' surrounding neighborhood.

2 | METHODS

2.1 | Study system

Our study was conducted at Bilsa Biological Station in northwest Ecuador (79″45′W, 0″22′N; 350–750 m elevation; 2–3 m precipitation annually), a 3500-ha private reserve of humid evergreen rainforest located within the Chocó biogeographic region (Durães et al., 2013). The Chocó forest has exceptionally high levels of endemism in both plant and animal species and is recognized as one of the most biologically diverse regions on the planet (Myers et al., 2000). The study area consists of continuous forest that is composed of a complex matrix of undisturbed forest with patches of varying size that have been regenerating naturally for the past 24–34 years after selective logging and small-scale farming (Durães et al., 2013).

Our focal plant species, *Prestoea decurrens* (Arecaceae), is a monoecious, insect-pollinated understory palm that is common in our study area (Browne & Karubian, 2016) and throughout lowland tropical forests ranging from Bolivia to Nicaragua (Ervick & Bernal, 1996; Steege et al., 2013). The palm is clonal, and individuals form distinct clusters of stems with a mean height of approximately 4 m (±1.4 standard deviation (SD), *N* = 252). *Prestoea decurrens* produces fleshy animal-dispersed fruit 2–3 cm in diameter, with a purple epicarp, that contain a single seed measuring 6–7 mm in diameter. Fruits are arrayed on infructescences, each holding approximately 100–600 fruits, and individual trees may hold up to six separate infructescences concurrently

(T. L. Lamperty, unpublished data). We selected this focal palm species because it is a widespread and abundant fruiting resource in the understory environment and important for many frugivores across a large proportion of neotropical forests. The size and characteristics of *P. decurrens* fruits are common among many tropical plants, which makes it possible to extrapolate relevant information from our results into a broader context across tropical forests.

2.2 | Frugivore observations

We deployed camera traps on 31 fruiting *P. decurrens* palms located across approximately 40 ha of continuous, but heterogeneous, forest in Bilsa from August to November 2018, a period that coincided with high fruit production in this species (J. Karubian, unpublished data). We selected focal palms with mature fruits in locations that represented the spectrum of past-habitat use found in the 130-ha study area. Focal palms were geolocated by GPS (Garmin model 64s) with 3–7 meters accuracy. We deployed Browning Strike Force® HD motion-sensor trail cameras (2014 and 2018 models) with nighttime capability in front of the mature infructescences of each palm. In most cases (all but 2), all mature infructescences on an individual palm were included in the camera frame, generally 1–3 infructescences. Palms were located in most cases before fruits were ripe, and cameras were installed once fruits ripened. A small proportion of focal palms were already ripe when found, and camera traps were immediately set in front of them. Palm crop size was estimated for each infructescence by counting the number of fruits on three rachilla, averaging them, and multiplying the average by the number of rachilla on an infructescence, then summing the estimate for all infructescences on a given palm.

Cameras were deployed for approximately 25 days or until all fruits were removed. Cameras were programed to capture 30-s videos with a 5-s delay between videos and as such recorded most or all visitation events during the sampling period. Because the maximum continuous recording time allowed by our cameras was only a few minutes, we did not have the ability to record and compare the full length of foraging events by frugivores. However, we can draw conclusions about relative rates and visitation frequencies through our 30-s capture method.

Visitors were identified to the species level, using Ridgely et al. (2001) *The Birds of Ecuador* and Tirira (2017) *A field guide to the mammals of Ecuador*. The majority of the toucans we recorded were Chocó toucans (*Ramphastos brevis*); however, Chestnut-mandibled toucans (*R. swainsonii*) are also common in the area, and due to the similarity in appearance, we categorize these birds broadly as "toucans" here. We recorded the number of fruits handled, removed, or dropped by each visitor in each video. We summed the total fruit removed from each focal palm and calculated the mean percentage of overall fruit removal that each frugivore species contributed. We also calculated for each frugivore species the mean percentage of fruit it swallowed/carried away versus dropped (which can provide information on disperser quality).

2.3 | Local habitat characterization

To understand how local habitat might influence visitation and fruit removal, we selected habitat metrics known to influence frugivore habitat use at this site: (Durães et al., 2013; Mahoney et al., 2018): canopy density, canopy height, the number of large trees [>50 cm diameter at breast height (DBH)] within 20 m of each focal palm, the number of trees belonging to the genus *Cecropia* within 10 m of each focal palm, and the presence of conspecifics fruiting in the understory within 20 m of focal palms. Variation in neighborhood fruit availability was estimated by counting conspecifics because *P. decurrens* was the only observed fruiting plant in the understory near focal plants during the study period. We recorded *Cecropia* species abundance because these prevalent neotropical pioneer trees indicate past disturbance (Mesquita et al., 2001; Zalamea et al., 2008, r2012). We estimated canopy density as percentage canopy cover using a spherical densiometer (Forestry Supplies no. 43888), and canopy cover measurements were taken 0.5 m from the base of the focal palm in each cardinal direction and averaged. Canopy density as well as canopy height and the presence of large trees are typically attributed to lower disturbance levels. We quantified canopy height as the tallest tree within 10 m around the focal palm; this height was estimated individually by the same two observers for each palm and averaged.

2.4 | Analysis

2.4.1 | Models

Prior to building models, we tested our predictor variables (canopy cover, canopy height, *Cecropia* density, fruiting conspecific density, old-growth tree density, and crop size) for collinearity by calculating variance inflation factors (VIF). VIF was problematic (>2; Craney & Surles, 2002) between local canopy height and old-growth tree abundance; this was solved by omitting the old-growth tree variable from models. Because the number of days that cameras were in front of focal palms varied with the period of time that ripe fruit was present on each palm, we also included an offset of log(days) in our models (Geyer et al., 2003).

We tested how our habitat and palm variables affected the diversity of frugivore visitors at palms with linear mixed-effects models and diversity metrics based on Hill numbers (or effective number of species; Hill, 1973). Hill number calculations can be categorized by their Hill order "q," for which the importance of the abundance distribution increases with increasing Hill order. For $q = 0$, the Hill number is a metric akin to species richness, which places weight on rare species because rare and common species are treated the same. For $q = 1$, the metric is the exponential of Shannon entropy and weights species by their proportional abundance. For $q = 2$, the metric is the Gini–Simpson index which places more weight on common species and strongly discounts rare species (see Hill, 1973 for equations; Chao et al., 2014; Ellis et al., 2019; Jost, 2006). Hill number estimation was done with the hill_taxa function in the package hillR (Li, 2018).

We used a generalized linear mixed-effects model (GLMM) fit with a negative binomial error distribution [function glm.nb in the package MASS (Venables & Ripley, 2002)] to test the effects of our predictors on overall fruit removal. We also ran a multivariate covariance generalized mixed-effects model (McGLMM; Wagner, 2018) to test how our predictor variables affected fruit removal by individual frugivore species in our study. This analysis was only possible for the most common frugivores (large occurrences of zeros for the rarer frugivores were prohibitive in testing relationships): aracaris, toucans, motmots, and toucanets.

While there was no significant collinearity found among variables used in our models, we additionally re-ran our models by incorporating habitat variables as outputs generated from a principal component analysis (PCA; for details see Figure S1). This conservative approach allowed us to include all habitat variables in our models as two principal components rather than as multiple, potentially related variables.

2.4.2 | Non-metric multidimensional scaling (NMDS) and community composition relationships with environmental vectors

To gain a comprehensive perspective on how the frugivore communities visiting individual focal palms may shift in relation to habitat variables, we used NMDS based on Bray–Curtis dissimilarity values generated from our visitation data. We used the "envfit" function in the "Vegan" package to analyze how *Cecropia* density, the only environmental variable revealed to be a significant predictor of fruit removal and visitation by preceding analyses (above), affected the frugivore community composition. This approach allows us to incorporate the presence (or absence) of all frugivore visitors recorded in our study and their contribution to overall frugivore community composition visiting each focal palm, despite some of those frugivores not being recorded as frequent enough visitors in our study to be analyzed within our other analyses. All analyses were done in R version 3.6.3 (R Core Team, 2020).

3 | RESULTS

We obtained a total of 18,288 camera trap hours from 31 *Prestoea decurrens* individuals during 4 months in 2018. Mean sampling effort per focal palm was 25 days (9 days minimum, 30 days maximum) or 595 camera trap hours (±100 SD). This variation in camera trap hours reflects variability in the fruiting duration of palms. Palm fruit crop size and our recorded environmental characteristics are summarized in Table 1. We recorded 686 foraging events by seven bird taxa, one squirrel species, and unknown mice species (Figure 1; Table S1). Toucans (*Ramphastos brevis* and/or *R. swainsonii*), the pale-mandibled araçari (*Pteroglossus erythropygius*), and the

TABLE 1 Mean, standard deviation, and range of values measured for habitat and palm variables

Variable	Mean ± SD (min–max values)
Focal palm fruit crop size	229 ± 251.6 (23–900)
Trees in the genus *Cecropia*	2 ± 1.9 (0–7)
Canopy height	28 m ± 9 (12–45 m)
Percentage canopy cover	96 ± 2.8 (88–100)
Fruiting conspecifics	2.78 ± 3.35 (0–10)

Note.: Cecropia trees were counted within 10 m of the focal palms. Canopy height was the tallest tree within 10 m of the focal palm. Canopy cover was taken directly at focal palm (from four points around it and averaged). Fruiting conspecifics were counted within 20 m of focal palms.

rufous motmot (*Baryphthengus martii*) accounted for approximately 88% of all fruit removal and we, therefore, refer to these as the "dominant" frugivores in our study (Figure 1; Table S1).

Avian species either dropped fruits directly under the focal palm, swallowed fruits whole, or held whole fruits in their beaks and flew away (suggesting successful dispersal). Mice species either carried fruit away whole in their mouths or in cheek pouches. Although mice were recorded transporting intact seeds away from focal palms, the likelihood that this results in successful dispersal away from parent plants (e.g., >10 m) and/or seedling survival may be lower compared to avian frugivores as neotropical rodents are often granivorous seed predators or deposit clumps of seeds in caches where density-dependent mortality is increased (Brewer & Rejmánek, 1999; DeMattia et al., 2004; Galetti, Guevara, et al., 2015). Red-tailed squirrels (*Sciurus granatensis*) were only recorded chewing fruits on branches and dropping them. We posit the rodent visitors are relatively low-quality seed dispersal agents in our system compared with the avian visitors.

The diversity of frugivore species visiting individual plants varied significantly in relation to local habitat variables (Table 2; Figure 2a). *Cecropia* abundance was significantly negatively related to frugivore visitor diversity when the diversity index placed weight on rarer species (i.e., $q = 0$; Table 2; Figure 2a); however, the negative trend was non-significant when the diversity metric did not place weight on common or rare species (i.e., $q = 1$) or when the metric placed weight on common species (i.e., $q = 2$; Table 2; Figure 2a). The number of fruiting conspecifics surrounding focal palms and canopy height had significant positive effects on all metrics of species diversity (Table 2; Figure 2), while fruit crop size had no significant relationship with any frugivore diversity metric. A denser local canopy was significantly associated with lower values of frugivore visitor diversity (Table 2; Figure 2).

Total fruit removal was significantly positively related to frugivore visitor diversity when the diversity index placed weight on rarer species (i.e., $q = 0$; Table 3); however, a significant negative trend existed between fruit removal at individual palms and frugivore visitor diversity when diversity was measured by not placing weight on common nor rare species (i.e., $q = 1$). A near-significant positive trend existed between fruit removal and diversity when diversity was measured placing weight on the occurrence of common species (i.e., $q = 2$; Table 2; Figure 2a).

The total number of the fruit removed and transported away from individual focal palms was negatively related to the density of trees in the pioneer genus *Cecropia* (negative binomial GLM, $b = -0.26 \pm 0.03$, $p < 0.001$ ***; Table S1). This pattern was driven primarily by the two most commonly visiting frugivore species, toucans, and aracaris (Tables 2 and S2; Figure 2c). Fruit crop size had a very weak but significant positive effect on total fruit removal (negative binomial GLM, $b = -0.001 \pm 0.0002$, $p < 0.001$ ***; Table S1). No other local habitat predictors had significant effects on overall fruit removal (Table S1; Figure 2b), despite some significant associations found with removal rates by individual frugivore species (Tables 2 and S2; Figure 2c). Results from our PCA were qualitatively similar to the models incorporating variables independently and are reported along with PCA methodological details in our supplementary materials Figure S1 and Tables S1–S6.

A weak but significant association existed between fruit removal by motmots, aracaris, and toucans and denser overhead canopy cover, while toucanets showed the opposite trend (Figure 2c; Table S2). The density of local fruiting conspecifics was positively related to fruit removal from focal palms by toucanets and had a weak negative association with fruit removal by aracaris and motmots, while toucan fruit removal had no variation associated with conspecific fruiting neighbors (Figure 2c; Table S2).

Fruit crop size had no effects outside of a very weak positive association with toucan fruit removal. The height of the overhead canopy at focal palms was positively associated with toucanet fruit removal rates and negatively associated with fruit removal from motmots, aracaris, and toucans (Figure 2c; Table S2). These individual associations, however, were not strong enough to alter overall fruit removal patterns from the perspective of the plant.

The multivariate correlation analysis revealed that *Cecropia* density surrounding focal palms had a significant overall effect on the composition of frugivore communities (evaluated through Bray–Curtis values) visiting a given palm ($R^2 = 0.25$, $p = 0.03$; Figure 3). Our NMDS ordination of frugivore communities visiting focal palms revealed an overall trend of decreasing frugivore visitor diversity and specifically the decreasing presence of higher-quality dispersers (such as umbrellabirds (Karubian et al., 2010, 2012)) with increasing local abundance of *Cecropia* trees. The NMDS analysis suggests rodents (squirrels and the mouse species we recorded) may increase in prevalence as frugivores at focal palms with higher abundances of trees in the genus *Cecropia* in their surrounding neighborhoods.

4 | DISCUSSION

Continuous tropical rain forests are not homogenous; rather, they are composed of variable or patchy resource distributions and are marked by frequent, small-scale disturbances caused by natural events and human activities that can affect forest structure long after a perturbation has ceased (Brown & Gurevitch, 2004). Understanding how habitat heterogeneity influences frugivore foraging at individual plants can help our understanding of drivers
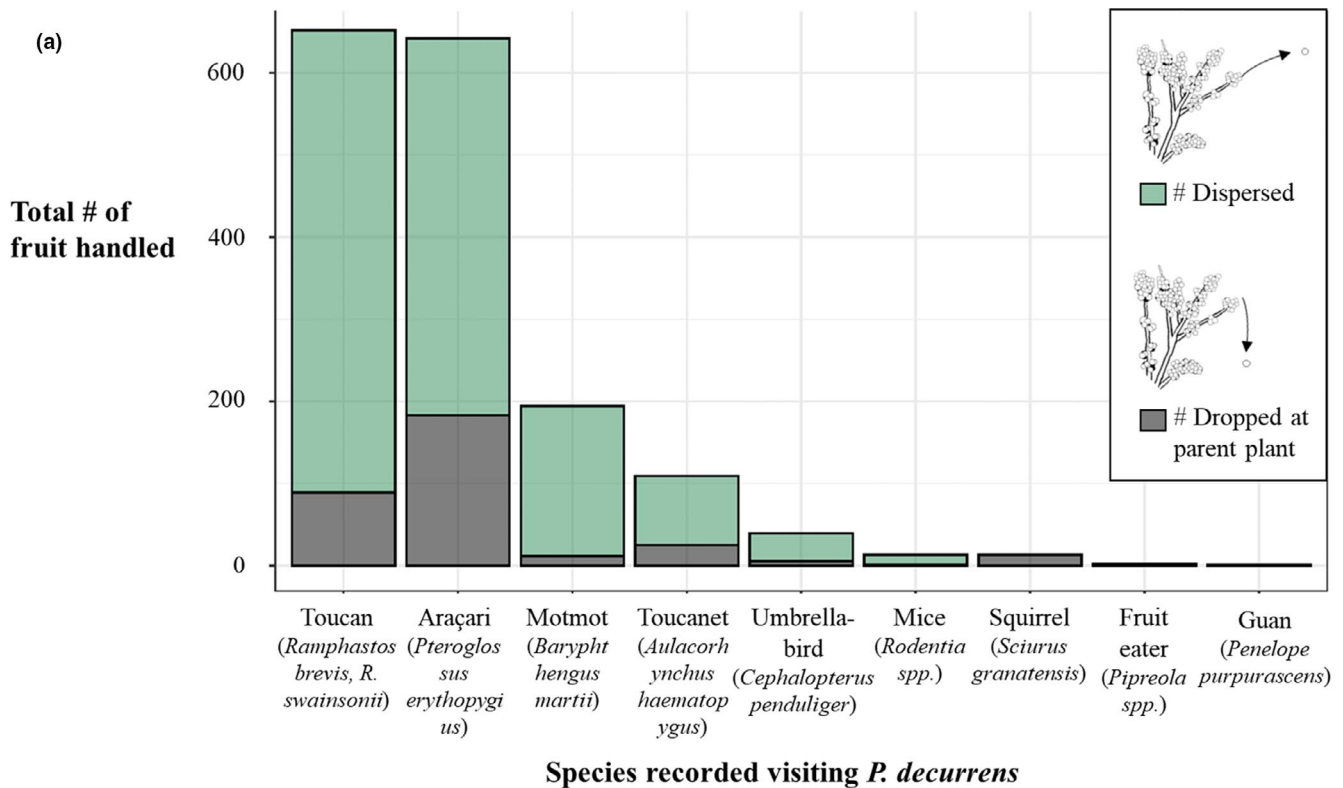
FIGURE 1 Foraging information for frugivore species recorded feeding on *P. decurrens*. (a) The cumulative total number of fruits that were handled by each species during the study. The gray portion of the bars shows the number of handled fruit that each species dropped directly below the parent tree, while green indicates the number of fruits carried away from parent trees. (b) The mean contribution to fruit removal by each frugivore, shown as a percentage calculated for each individual focal palm and then averaged across all focal palms to quantify the relative portion of fruit removal each frugivore contributed for *P. decurrens*. The number of our 31 individual focal palms each frugivore was recorded foraging on is also presented

of inequalities in seed dispersal services across a landscape. For an abundant understory palm (*Prestoea decurrens*) in northwestern Ecuador, we observed less fruit removal, lower diversity of visiting frugivores, and a shift in the visiting frugivore community in relation to local *Cecropia* density. The number of nearby fruiting conspecifics around focal palms had a weak but significant positive association with the diversity of visiting frugivores, but this did not result in more overall fruit removal from individual palms. Because *Cecropia* is a group of pioneer trees well known as indicators of past disturbance in the Neotropics (Berg et al., 2005; Zalamea et al., 2012), we posit that our results mean frugivore preferences and seed dispersal success at the level of individual plants can be negatively influenced by even low-intensity anthropogenic activity or natural disturbance

that occurred decades prior. In our study site and many similar tropical forest regions, this would include prevalent activities like small-scale selective logging by locals but also natural tree fall or storm damage.

Frugivore diversity is often positively related to fruit removal and seed dispersal services (Bleher & Böhning-Gaese, 2001). At the scale of individual fruiting palms, canopy height was a weak but highly significant predictor of the diversity of visiting frugivores, suggesting areas across our study landscape characterized by lower past disturbances, which corresponds with higher canopy height (Holl et al., 2018; Zahawi et al., 2015), are associated with higher frugivore diversity. This agrees with the negative effect *Cecropia* density had on frugivore diversity, given that *Cecropia*

TABLE 2 Linear model outputs testing predictor effects on species diversity

Response	Predictor	Estimate ± SE	p
$q = 0$ (species richness)	Neighborhood abundance of *Cecropia*	−0.15 ± 0.04	<0.001***
	Percent canopy cover	−0.10 ± 0.03	0.003**
	Canopy height	0.03 ± 0.01	0.003**
	Fruit crop size	−0.0008 ± 0.0003	0.02*
	Neighborhood abundance of fruiting conspecifics	0.10 ± 0.02	<0.001***
$q = 1$ (Shannon entropy)	Neighborhood abundance of *Cecropia*	−0.06 ± 0.04	0.10
	Percent canopy cover	−0.11 ± 0.03	<0.001***
	Canopy height	0.02 ± 0.01	0.01**
	Fruit crop size	−0.001 ± 0.0003	0.08
	Neighborhood abundance of fruiting conspecifics	0.10 ± 0.02	<0.001***
$q = 2$ (Gini–Simpson index)	Neighborhood abundance of *Cecropia*	−0.04 ± 0.04	0.26
	Percent canopy cover	−0.11 ± 0.03	<0.001***
	Canopy height	0.02 ± 0.01	0.03*
	Fruit crop size	−0.0004 ± 0.0003	0.13
	Neighborhood abundance of fruiting conspecifics	0.09 ± 0.02	<0.001***

Note.: Species diversity was described through Hill numbers reported of order $q = 0$ (produces a species richness index which places weight on rare species), $q = 1$ (Shannon entropy, places weight on species neither common nor rare), and $q = 2$ (Gini–Simpson, places weight on common species; Ellis et al., 2019; Hill, 1973). See Section 2 for details.

occurs more often in disturbed areas characterized by lower canopies. Canopy cover, a metric often cited as a positive indicator of tropical forest intactness and frugivore diversity (Holl et al., 2018; Mahoney et al., 2018; Zahawi et al., 2015), was *negatively* related to frugivore diversity at the local scale of visitors to individual palms (Figure 2a), a pattern that toucanets appear to have substantially contributed to (Figure 2c; Table S2). This pattern of increased frugivore diversity at palms under more open canopies corresponded to (and was likely driven by) the positive association we found between frugivore diversity and the density of fruiting conspecifics surrounding focal palms. Indeed, the density of fruiting conspecifics was significantly related to a more open canopy (Poisson GLM, percent canopy cover as a predictor of fruiting conspecific abundance: $b = -0.03 \pm 0.01$, $p = 0.007$ **). This agrees with previous work showing frugivores can be attracted to a patch of higher resource concentration and all plants within the patch benefit from increased visitation (Blendinger et al., 2008; Guerra et al., 2017). Among the four most dominant frugivore species, toucanets are the only species that showed a significant preference for fruiting conspecific patches at the cost of more foraging time in less dense canopy (Figure 2c), while the other three most dominant frugivores (aracari, motmots, and toucans) foraged more in denser canopy areas and did not show a preference for conspecific fruiting patches (Figure 2c), indicating the trend of increased visitor diversity with increasing local fruiting resources was not driven by the most common frugivores in our study system.

Despite these multiple and varying effects of our measured habitat variables on frugivore diversity, the negative effect found from *Cecropia* abundance was the only one that also translated into an association with lower fruit removal from individual palms (Table 2;

Figure 2b). Our examination of how the most dominant frugivores (aracari, motmots, toucans, and toucanets) responded to variation in local habitat variables indicated this trend is substantially contributed to by toucans, which consumed more fruit in our study than any other frugivore, followed in kind by aracari and toucanets, while motmots did not show a significant association with *Cecropia* abundance (Figure 2c). Additionally, our ordination analysis showed that six of the nine frugivores recorded foraging on *P. decurrens* tended toward feeding on palms in neighborhoods characterized by fewer *Cecropia* (Figure 3), shifting the relative abundances and community composition of frugivores visiting individual palms.

Our results suggest that areas of small-scale past disturbances, colonized by pioneer species such as *Cecropia*, were less-favored by frugivores in our study system. Similar avoidance of edge or fragmented habitat by large-bodied frugivores has been previously documented (Babweteera & Brown, 2008; Gomes et al., 2008; Neuschulz et al., 2011; Rehm et al., 2018). However, evidence of frugivore sensitivity to more subtle habitat heterogeneities, as we present here, suggests frugivores may respond to habitat characteristics on a relatively fine-scale, and this has not been widely documented or studied. The lower levels of fruit removal and diversity of frugivore visitors we observed in areas with high local *Cecropia* density merit further investigation as they suggest a negative influence of localized past disturbance events on seed dispersal services. In our study, the effects of *Cecropia* density that we report cannot be extrapolated directly to past disturbance intensity or time since disturbance. This is because *Cecropia* density varies non-linearly with time since disturbance such that *Cecropia* numbers will peak and then decline as time since disturbance progresses. It should then be noted that greater *Cecropia* numbers in our study's context could mean a

(a) Habitat effects on diversity of frugivores foraging at focal palms

(b) Habitat effects on fruit removal from focal palms
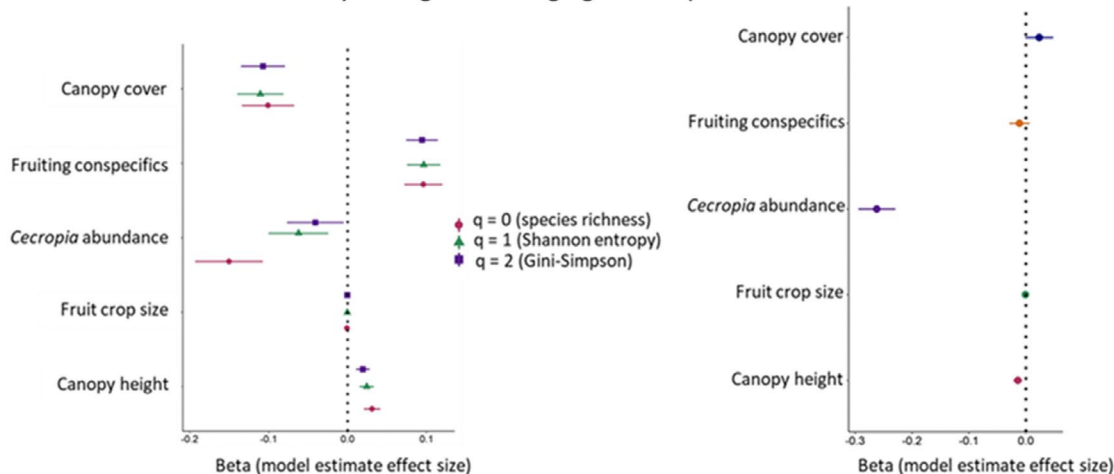
(c) Habitat effects on fruit removal by dominant frugivores
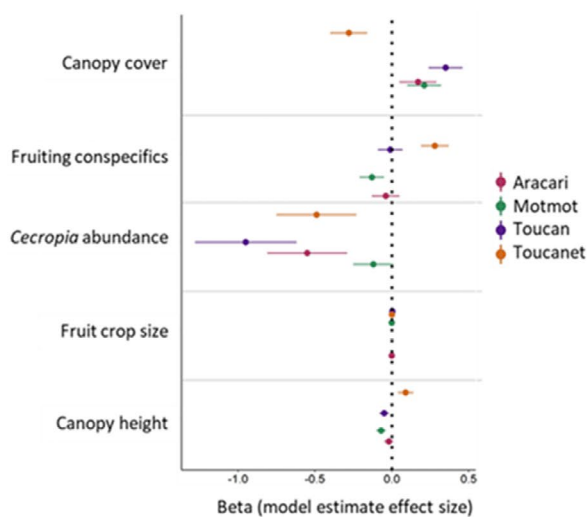
FIGURE 2 (a) Coefficient estimates from linear models testing the effects of local habitat variables on the diversity of frugivore species visiting individual palms. Species diversity was described through Hill numbers reported of order $q = 0$ (produces a species richness index which places weight on rare species), $q = 1$ (Shannon entropy, places weight on "typical" species neither common nor rare), and $q = 2$ (Gini–Simpson, places weight on common species; Ellis et al., 2019; Hill, 1973). See Section 2 for details. (b) Coefficient estimates from negative binomial generalized linear model testing effects of local habitat variables on the amount of fruit removed per palm. (c) Coefficient estimates from multivariate generalized linear model testing the effect of local habitat variables on fruit removal by the four dominant frugivore species in our study. In all plots, negative values correspond with negative effects while positive values show positive effects, and beta values within a plot show relative strength of those effects as estimated by our models. Lines through points show standard error

disturbance covered a slightly greater area around the focal palm, the disturbance was more intense, or the disturbance happened long enough ago to be at or near "peak" *Cecropia* colonization. However, our results support that any, small-scale, past disturbance leading to a change in forest composition (e.g., more *Cecropia*) can create areas less favored by frugivores for foraging.

Interestingly, our observed association between the diversity of visiting frugivores and the fruit removed from individual palms revealed significant and divergent results depending on the diversity metric used. We find that when diversity is quantified with weight placed on rare species (as with species richness, or Hill number

calculations to the order of $q = 0$), diversity is strongly and significantly associated with increased fruit removal. The result is the same when diversity is quantified with weight placed on the most common species (as with the Gini–Simpson index values, or Hill number calculated when $q = 2$). However, for diversity quantified as Shannon entropy, or $q = 1$, which places weight on the species in the community that are neither the rare nor the common individuals, we found a strong significant *negative* association between diversity and total fruit removed. This outcome may be driven by the substantial dominance the two most common frugivores—toucans and aracaris—had in driving fruit removal compared to other species (Figure 1a,b).

When rare species (e.g., umbrellabirds, guan, or the fruiteater species) visited palms, they did not replace the occurrence of the common frugivores rather supplemented and increased overall fruit removal. This leaves "typical" frugivore visitors neither common nor rare as those that cumulatively drove fruit removal the least and a diversity metric placing weight on them would result in a negative association between diversity and fruit removal.

TABLE 3 Negative binomial generalized linear model output testing effects of diversity measures on total fruit removed from individual focal palms

Response	Predictor	Estimate ± SE	p
Total fruit removed from focal palms	q = 0 (species richness)	1.24 ± 0.20	<0.001***
	q = 1 (Shannon entropy)	−1.71 ± 0.73	0.02*
	q = 2 (Gini–Simpson index)	1.00 ± 0.57	0.08

Note.: Species diversity was described through Hill numbers reported of order q = 0 (produces a species richness index which places weight on rare species), q = 1 (Shannon entropy, places weight on species neither common nor rare), and q = 2 (Gini–Simpson, places weight on common species; Ellis et al., 2019; Hill, 1973). See Section 2 for details.

There is some debate about whether seed dispersal mutualisms are robust to changes in frugivore communities due to functional overlap among frugivore species (Bueno et al., 2013; Moran et al., 2009) versus whether there is inadequate compensation by functionally similar species (Babweteera & Brown, 2008; Brodie et al., 2009; Fricke et al., 2018; McConkey & Brockelman, 2011; Pejchar, 2015). Our results support the latter since we documented a shift away from higher-quality seed dispersers toward lower-quality seed dispersers. For example, both toucans and umbrellabirds have been identified as highly effective seed dispersers; toucans can be effective long-distance dispersers (Holbrook, 2011), and umbrellabirds have been documented to disperse seeds from many individuals long distances in our system (Browne & Karubian, 2018; Karubian et al., 2010). In contrast, motmots, which according to our NMDS and model results, were the only dominant frugivore that did not exhibit significantly less foraging in relation to higher *Cecropia* density, often regurgitate seeds under fruiting plants and are not considered high-quality dispersers in the literature (Howe, 1993; Howe et al., 1985). However, in our study, we recorded motmots transporting seeds away from parent trees frequently (Figure 1) and as such they may be beneficial dispersers for *P. decurrens*. Our NMDS analysis indicated an increase in foraging by red-tailed squirrels in relation to *Cecropia* density, which also indicates a shift away from higher-quality dispersers in relation to *Cecropia* density because 100% of
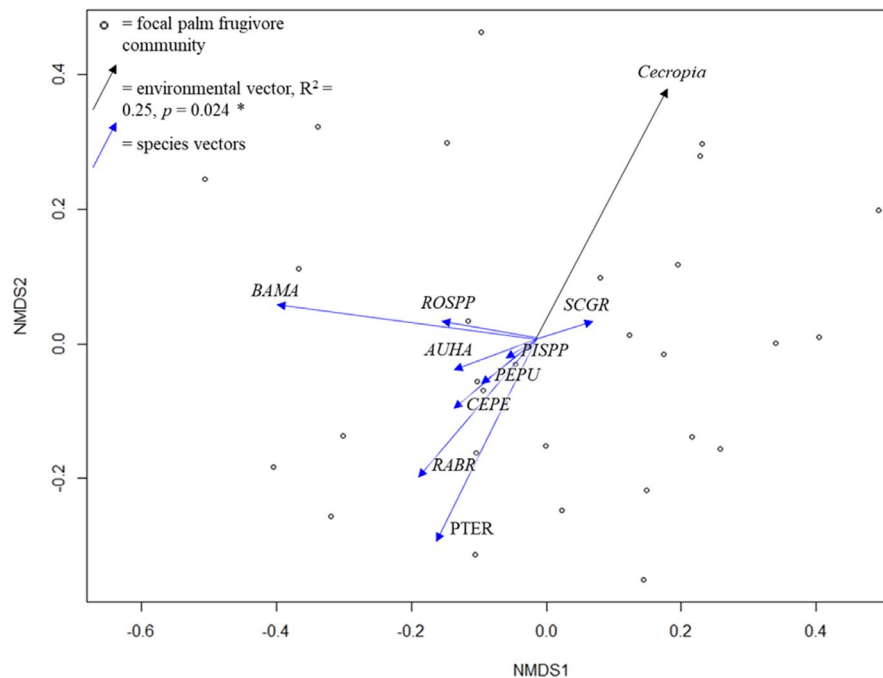
FIGURE 3 Multidimensional scaling of focal palm frugivore communities based on Bray–Curtis dissimilarity matrix with species vectors and the environmental vector for local *Cecropia* abundance plotted in the same two-dimensional space. Vectors for frugivore species are also plotted: BAMA, Baryphthengus *martii*; ROSPP, Rodentia spp.; SCGR, Sciurus *granatensis*; AUHA, Aulacorhynchus *haematopygus*; PISPP, Pipreola sp.; PEPU, Penelope *purpurascens*; CEPE, Cephalopterus *penduliger*; RABR, Ramphastos *brevis* (or *R. swainsonii*); PTER, Pteroglossus *erythropygius*. Arrow directions illustrate relative relationships between variables (e.g., PTER vector points nearly the complete opposite direction of the *Cecropia* environmental vector, indicating a negative relationship, while BAMA is almost perpendicular to the direction of the environmental vector, meaning minimal change occurs in BAMA abundance in relation to increasing local *Cecropia* abundance). R^2 and p values calculated from our multivariate correlation analysis of the effect of the environmental vector for *Cecropia* on Bray–Curtis community composition values

fruits removed by squirrels recorded in our study were dropped rather than carried away from parent plants.

Our study suggests that fine-scale heterogeneity in forested landscapes can influence frugivore foraging preferences with consequences for fruit removal. Although fruit removal does not necessarily lead to successful seedling recruitment, it is likely that lower fruit removal rates equate to reduced successful seed dispersal and seedling recruitment. We report that while diversity metrics and fruit removal had varying responses to local habitat variables, overwhelmingly the two most important factors in our system for predicting the diversity of frugivore visitors to focal palms were fruiting conspecific density and *Cecropia* abundance. Only local *Cecropia* abundance translated into a significant negative predictor of fruit removal, which can lead to diminished local dispersal services for fruiting plants. As this study takes information from a single species at in a single site, further research is needed on a broader array of plant species to tease apart the specific factors driving foraging preferences within continuous, mixed land-use history forests, how responses vary between frugivore species, and what the specific results are of this for successful dispersal and regeneration patterns of tropical forests.

AUTHORS' CONTRIBUTIONS

T.L., J.K., and A.E.D. conceived ideas. T.L. designed and carried out fieldwork and analyses, collected the data, and led the writing of the manuscript with inputs and revisions from A.E.D. and J.K. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.p2ngf1vqk (Lamperty et al., 2021).

ORCID

Therese Lamperty https://orcid.org/0000-0002-1245-489X

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Additional supporting information may be found online in the Supporting Information section.