

# Vertically stratified frugivore community composition and interaction frequency in a liana fruiting across forest strata

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## Abstract

Vertical stratification is a key feature of tropical forests and structures plant–frugivore interactions. However, it is unclear whether vertical differences in plant–frugivore interactions are due to differences among strata in plant community composition or inherent preferences of frugivores for specific strata. To test this, we observed fruit removal of a diverse frugivore community on the liana *Marcgravia longifolia* in a Peruvian rain forest. Unlike most other plants, *Marcgravia longifolia* produces fruits across forest strata. This enabled us to study effects of vertical stratification on fruit removal without confounding effects of plant species and stratum. We found a high number of visits of a few frugivore species in the understorey and a low number of visits of many different frugivores in the canopy and midstorey. Whereas partial and opportunistic frugivores foraged across strata with differing frequencies, obligate frugivores were only found eating fruits in the higher strata. Avian frugivores foraging in the canopy were mainly large species with pointed wings, whereas under- and midstorey avian foragers were smaller with rounded wings. Our findings suggest a continuous shift in the frugivore community composition along the vertical gradient, from a few generalized frugivores in the understorey to a diverse set of specialized frugivores in the canopy. This shift in the frugivore community leads to correlated, reciprocal changes from specialized to generalized plant–frugivore interactions. Thus,

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we conclude that vertical niche differentiation between species in tropical forests persists even when food resources are available across strata. This highlights its role for promoting biodiversity and ecosystem functioning.

Abstract in Spanish is available with online material.

#### KEYWORDS

bird traits, diet specialization, frugivory, plant–animal interactions, rain forest, seed dispersal

## 1 | INTRODUCTION

Vertical stratification is a wide-spread phenomenon in plant and animal communities and a key factor for structuring biodiversity, particularly in tropical forests (Basset et al., 2003; Chmel et al., 2016; Thiel et al., 2021). Plants, fungi, and animals inhabit a variety of niches along the vertical forest gradient (Allee et al., 1949; Bongers, 2001; Izuno et al., 2016; Richards, 1952; Smith, 1973). Many studies have observed patterns of vertical stratification for birds, bats, primates, and small non-flying mammals in terms of species abundance, richness, and community composition (Buchanan-Smith et al., 2000; Chmel et al., 2016; Kalko & Handley, 2001; Thiel et al., 2021). Consequently, vertical structure also affects associated ecological processes such as frugivory and seed dispersal, as many animal species from these taxa feed on fruits and disperse their seeds (Fleming, 1993; Fleming & Kress, 2013; Howe & Smallwood, 1982; Jordano, 2000). This is particularly important in tropical rain forests, where up to 90% of woody plant species produce fleshy fruits (Fleming, 1993; Howe & Smallwood, 1982).

However, there are very few studies that not only report the presence or absence of frugivores across strata but focus on actual interactions. One of the few network studies carried out across vertical strata in a Kenyan rain forest by Schleuning et al. (2011) found that the degree of specialization in a plant–frugivore network is vertically stratified. They hypothesized that this was due to differences in foraging behavior among bird and small non-flying mammal species. Notably, they found differences in the use of strata according to the feeding specialization, particularly their dependence on fruit. In the understorey, opportunistic frugivores were abundant and, due to limited fruit availability, rather specialized in their fruit choice (Schleuning et al., 2011). By contrast, obligate frugivores moved predominantly within the canopy, where they foraged on a large range of plants with fleshy fruits (Schleuning et al., 2011). Consequently, the canopy network was composed of strong interaction links and generalized associations, whereas the understorey was characterized by weak links and more specialized associations (Schleuning et al., 2011). In line with these findings, Shanahan and Compton (2001) reported trait-mediated vertical stratification in the dispersal of various *Ficus* species. The small fruits of understorey trees were mainly consumed by small non-flying mammals and bulbs, whereas the larger figs of the canopy attracted a more diverse

assemblage of large-bodied bird and mammal species. Generally, assemblages of canopy-feeding frugivorous birds are dominated by large-bodied species, whereas those in the understorey of tropical forests comprise mainly small species (Bell, 1982; Fleming, 1988; Fleming & Kress, 2013).

It becomes apparent that vertical stratification plays an important role in the diversification of plant and animal traits and thereby also in structuring mutualistic interactions (Bender et al., 2018; Blendinger et al., 2008; Jordano, 1995; Muñoz et al., 2017). For instance, plant height affects the foraging behavior of frugivores that have preferences for particular forest strata (Muñoz et al., 2017; Schleuning et al., 2011; Shanahan & Compton, 2001). In turn, the wing shape of avian frugivores is strongly related to plant height and beak size is further strongly related to fruit size. (Bender et al., 2018). While rounded wings allow birds to forage in the dense forest understorey, birds with pointed wings are better equipped to forage in the canopy and move over long distances, at the cost of reduced maneuverability (Moermond & Denslow, 1985).

However, all studies on vertical stratification of plant–animal communities focused on plant communities where the investigated plant species presented fruits within a single stratum (Schleuning et al., 2011; Shanahan & Compton, 2001). Thus, fruit resources are also vertically stratified, and plant species and stratum are confounding variables. As a consequence, existing studies do not allow to resolve whether foraging is limited due to the preference for a specific vertical niche or because the preferred fruit resources are only available within a certain stratum.

Therefore, for our study, we focused on the Neotropical liana *Marcgravia longifolia* (Marcgraviaceae), which provides infructescences from the understorey to the canopy. As such, *M. longifolia* is an ideal study organism to investigate the vertical stratification in plant–frugivore interactions since it enables us to investigate changes in frugivore community composition and interaction frequencies across forest strata for one particular fruit resource and thus eliminating the confounding effect of plant species and stratum. With this system, we want to test whether there are inherent preferences of frugivores for a specific stratum that result in vertical stratification in plant–animal interactions irrespective of plant community composition. We test three hypotheses: H1: Frugivores preferentially forage in a distinct vertical niche. Because previous studies have not been able to unequivocally test

whether the use of vertical space is driven by differing resource availability or due to an inherent preference for a certain vertical niche, our unique study system will allow us to test this in the presence of the same resources along the entire vertical gradient. If such a preference exists, we expect that visitation rate, frugivore diversity, and community composition differ among strata in our study system. H2: Bird species with different degrees of specialization on fruits differ in their vertical niche specificity. Here, we want to test whether the observation of Schleuning et al. (2011) that obligate frugivores primarily feed on fruits in the canopy, and that partial and opportunistic frugivores are less specialized on a particular stratum can be confirmed even if the same resource is available across all strata. In addition, our study allows for an independent test of the hypothesis H3 that functional traits of birds play an important role in determining their vertical foraging niche, again by eliminating the confounding effect of plant species and stratum. Specifically, we expect that large-bodied species with large bills and pointed wings forage preferentially in the canopy, whereas smaller frugivores with smaller bills and rounded wings feed predominantly in the understory.

To test these hypotheses and expectations, we recorded removal of *M. longifolia* fruits by diurnal frugivores across forest strata (understorey, midstorey, canopy). We classified frugivorous visitors into guilds according to their dietary specialization and recorded functional morphological traits for birds at the species level.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

The study was conducted at the Estación Biológica Quebrada Blanco in north-eastern Peruvian Amazonia (4°21'S 73°09'W). Annual precipitation is ca. 3000mm, with December–May being the wettest and July–August being the driest months (Lüffe et al., 2018). Mean monthly temperature in the area ranges between 25 and 27°C (Klingbeil & Willig, 2008). For further details of the study site see Heymann et al. (2021) and Heymann and Tirado Herrera (2021).

### 2.2 | Studied plant species

*Marcgravia longifolia* (Marcgraviaceae) is a woody liana species known from western Amazonia (Tropicos, 2020). It produces long pedunculate and flagelliflorous inflorescences/infructescences arising from the unbranched stem of the liana all the way from ground level up to the canopy, which is an extremely rare phenomenon within the Marcgraviaceae and for plants in general. Foliage, on the contrary, is exclusively produced in the canopy. Within each infructescence 15–25 fruits are arranged in a circle. When fruits are ripe, the brownish husk is dehisced and the intense red fruit pulp is exposed (Figure 1). Fruits of *M. longifolia* contain hundreds of seeds with a diameter of ca.



**FIGURE 1** Fruits of *Marcgravia longifolia* (© Niklas Jedowski). When fruits are ripe, the brownish husk is dehisced and the intense red fruit pulp is exposed.

0.06 cm (Tirado Herrera et al., 2003). Infructescences are produced throughout the year, but with a clear fruiting peak from October to December (Paciência, 2014; Tirado Herrera et al., 2003). The individuals produce a large number of fruits (Paciência, 2014) and compared to other fruits at the study site, *M. longifolia* fruits have a high content of sugar, lipids, and proteins (Ripperger et al., 2014). They are consumed by a large assemblage of different frugivore species. Paciência (2014), for instance, observed 59 bird species feeding at *M. longifolia* of which 26 can be classified as frugivores. These 59 bird species represent around 18% of the observed 324 bird species at our study site (Pomara & Socolora unpubl. data quoted in Heymann & Tirado Herrera, 2021). Out of these, 163 were classified as invertebrate feeders, 10 as nectarivores, 43 as omnivores, 13 as seed/plant feeders, 20 as scavengers, and 59 frugivores (18 obligate frugivores, 33 partial frugivores, and 8 opportunistic frugivores; inventories made by Lars Pomara in 2004–2005 and Jacob Socola in 2014). Moreover, *M. longifolia* fruits are consumed by diurnal and nocturnal mammal species (Paciência, 2014; Ripperger et al., 2014; Tirado Herrera et al., 2003). Fruit production throughout the “dry season” (when other fruit resources are rare), high fruit abundance, nutritional content, and the large number of visitors suggest that it represents a seasonally (and locally) highly important resource (Paciência, 2014). All observed *M. longifolia* individuals grow on plain or slightly undulating terrain at our study site.

### 2.3 | Observations

#### 2.3.1 | Selection of *M. longifolia* individuals

The entire study site was surveyed for adult *M. longifolia* individuals along the trails and within the quadrants of the grid system. Out of the 97 recorded *M. longifolia* individuals, we selected 24 individuals for further observations based on resource availability (sufficient number of ripe fruits across strata) and visibility or on accessibility of the host tree with climbing equipment, respectively. Observations of fruiting *M. longifolia* individuals were conducted from October to December of 2015, 2018, and 2019.

### 2.3.2 | Classification of height, canopy cover, forest strata, and fruit availability

We determined host tree height for each selected individual, either visually by two persons independently (to exclude estimation biases—as estimations were similar in all cases, we calculated mean values), or—for 13 individuals that were accessible with climbing equipment—the host tree was marked at 4 m-intervals up to the height of the first canopy branch and the total height was then estimated. For these individuals, we additionally characterized canopy cover along the vertical gradient by collecting diagonal hemispherical color photographs with an iPhone SE 2016 equipped with a 12 MP built-in camera and a 198° fisheye lens in order to assess canopy cover. We took pictures at 4 m intervals—starting at 0 m on the ground up to between 16 and 20 m aboveground and used ImageJ to calculate canopy cover from the pictures (Rueden et al., 2017). We classified three forest strata (understorey, midstorey, and canopy) in relation to the vertical distribution of foliage and density of the surrounding vegetation. We found that vegetation density was clearly distinct among these strata, and we assume that frugivores rather orientate themselves along the vegetation structure than based on absolute height (McCaig et al., 2020). The understorey was classified according to the height of the dense surrounding shrub and palm tree layer (0 m until up to between 3 and 10 m). For the classification of the canopy stratum, the height of the first canopy branch of the host tree and the height of the surrounding canopies was decisive (starting between 9 and 22 m, until up to between 12 and 32 m). The midstorey was then defined as the space between the understorey and the canopy, where vegetation density was lower (starting between 3 and 10 m, until up to between 9 and 22 m).

For all 24 *M. longifolia* individuals (each individual fruiting in all strata), the number of ripe fruits was estimated for each height class of 4 m, on each observation day, and then assigned to strata. We calculated mean fruit number per stratum of each *M. longifolia* individual across observation days. To determine crop mass, we collected 195 fruits from the 13 *M. longifolia* individuals being accessible with climbing equipment ( $n = 15$  from each individual). Fruits were selected evenly across strata by climbing the host trees. Fruits were weighed on the day of collection to determine the fresh mass in grams and we calculated mean fresh mass per fruit per stratum. We then calculated mean crop mass per stratum of each *M. longifolia* individual as the product of mean fruit number of this *M. longifolia* individual and mean fresh mass (Table S1).

### 2.3.3 | Observations of frugivore visits

To record frugivorous animal species, five researchers equipped with binoculars (Leica Ultravid HD 10×42 or Pentax DCF—CS 10×42) recorded animal visits to the 24 *M. longifolia* individuals in the morning (06:00–11:00 h) and in the afternoon (12:00–17:00 h). Observations only took place under suitable weather conditions, that is, no heavy rain or wind. Each individual was observed multiple

times by different observers, resulting in  $16.7 \pm 0.5$  h (mean  $\pm$  SE) per fruiting *M. longifolia* individual and a total of 418 h of observations (Table S2). During observations, only feeding animals were recorded (frugivores that pecked, swallowed, or carried a fruit away) and counted per stratum. If a frugivore fed in more than one stratum during a single visit, it was counted once per stratum. Diurnal arboreal mammals (all known from previous research at the study site) and birds (according to Schulenberg et al., 2010) were determined to species level. If bird species could not be determined to species level, they were marked as “unidentified” and excluded from the analyses (10 frugivore visits, i.e., 1.1%). Number of visits of each frugivore species were calculated per stratum of each *M. longifolia* individual and summed across years. We also recorded the number of fruits that an individual consumer removed, and the estimated feeding heights (number of fruits for each feeding height). We calculated the number of remaining fruits per stratum by subtracting the number of consumed fruits per feeding height from the number of ripe fruits being available on this particular day. This was also calculated per *M. longifolia* individual but individually for each observation day (to enable the consideration of fruit availability on a daily basis).

Further, to estimate the availability of other fruit resources close to the observed *M. longifolia* individuals, we searched for other plant species bearing fleshy fruits in a radius of 15 m around the *M. longifolia* individuals at the same day observations took place. We determined the species, as well as their fruit abundance (in categories from one to three with one implying a low fruit abundance) and the height where fruits were produced. Lastly, we collected information on the observed frugivores' diet from literature (Wilman et al., 2014) and classified frugivore species according to their dietary specialization into partial, opportunistic, and obligate frugivores (Garber, 1988; Kissling et al., 2009; Myhrvold et al., 2015). Following the classification by Kissling et al. (2007), the main food item of obligate frugivores are fruits (90%–100% of their diet consists of fruits), whereas major food items of partial frugivores also include non-fruit resources, for example, invertebrates (50%–80% fruit consumption). Opportunistic frugivores supplement their diet only occasionally with fruits (<40% fruit consumption).

### 2.3.4 | Morphological bird traits

For frugivorous birds, we quantified four morphological traits, which previous studies have identified as key traits influencing interactions in plant–frugivore networks (Bender et al., 2018; Dehling et al., 2014), that is, bird body mass (g), bill length (mm), bill width (mm), and wing shape (i.e., Kipp's index as a measure of the pointedness of the wing). Body mass was collected from the literature (Dunning, 2007; Myhrvold et al., 2015), whereas the other traits were measured on at least four museum specimens per species (Museo de Historia Natural, Bogota; Natural History Museum, Tring; Natural History Museum, London; Senckenberg Natural History Museum, Frankfurt & Dresden; Natural History Museum of Denmark, Copenhagen; Zoological Research Museum Alexander Koenig, Bonn; for details

on the trait measurements see Dehling et al., 2014). Kipp's index was calculated by dividing Kipp's distance (the distance between the tip of the first secondary and the wing tip, measured on the folded wing, Leisler & Winkler, 1991) by wing length (which is analogous to the hand-wing index; Sheard et al., 2020). A low Kipp's index indicates rounded wings that are especially suited for high maneuverability in dense vegetation, whereas a high Kipp's index indicates a wing shape which enables birds to fly over long distances (Rayner, 1988). We calculated the species mean of body mass, bill length, bill width, and Kipp's index and then used these values for calculating community weighted means (CWMs) with the function *functcomp()* in R package FD 1.0-12 (Laliberté et al., 2019) for each subset of birds that fed in each stratum of each *M. longifolia* individual. In order to estimate the CWMs, trait values were weighted by the number of visits of each bird species in each stratum of each *M. longifolia* individual.

## 2.4 | Network analyses

We built an interaction matrix between frugivorous species and the three different forest strata (understorey, midstorey, canopy) for each *M. longifolia* individual. That is, we calculated interaction frequencies of each animal species with each stratum of each *M. longifolia* individual. We defined interaction frequency as the number of feeding animals within a particular forest stratum, independent of fruit handling. Following traditional network analyses, we analyzed the interaction matrix using the *bipartite* package (Dormann et al., 2009) in R (R Development Core Team, 2019). The total frequency of an animal species was defined as the number of visits to all strata, whereas the total frequency from the perspective of a particular stratum was given as the number of all animal visits to this stratum. Thus, we utilized the marginal totals of the interaction matrix to estimate total species' frequencies (Blüthgen et al., 2007).

First, to test if frugivores forage in distinct vertical niches (H1) and if frugivores of different dietary specialization differ in their niche specificity (H2), we calculated the Shannon's H diversity of interacting partners for each stratum. We further determined the relative frequency of an animal species across strata defined as the number of interactions between animal species *j* and stratum *i* divided by the number of visits of animal species *j* to all strata.

## 2.5 | Statistical analysis

To test if frugivores forage in distinct vertical niches (H1), we first analyzed whether fruit abundance and canopy closure differed among strata. Therefore, we calculated linear mixed effect models with crop mass or canopy closure, respectively, as response variables, stratum as explanatory variable, and IDs of individual lianas as random factors. To compare frugivore visitation among strata, we used a generalized linear mixed effect model with number of frugivore visits as response variable, stratum and crop mass as explanatory variables, and IDs of individual lianas as random factors. We

also added a zero-inflation term for stratum (to account for the zero-inflated count data) and an offset for observation hours (to account for differing observation hours among *M. longifolia* individuals), and fitted the model with a negative binomial distribution. For the comparison of fruit removal of *M. longifolia* among strata, we used a generalized linear mixed effect model with a binomial denominator of number of removed fruits (numerator) and number of not-removed fruits (denominator) as response variable, stratum as explanatory variable, and the day of observation (to account for differing observation days among *M. longifolia* individuals) and IDs of individual lianas as random factors. We also included observation level random effects to account for overdispersion of the data (OLREs, Harrison, 2014) and fitted the model with a binomial distribution (and a logit link). To compare the Shannon diversity of interacting partners among strata, we calculated a linear mixed effect model with Shannon diversity as response variables, stratum as explanatory variable, and IDs of individual lianas as random factors. For the analyses, crop mass and observation hours were log-transformed to approximate normal distribution of residuals. For all models, we used a contrast to compare among strata. To quantify the differences in the frugivore community among forest strata, we computed pairwise Bray-Curtis distances among strata and analyzed differences in community composition among strata using a MANOVA approach on our interaction matrix. We tested significance by permuting the raw data (1000 permutations) using the function *adonis()* in R package Vegan 2.5-6 (Oksanen et al., 2019).

To test if the niche specificity of frugivores of different dietary specialization differs among strata (H2), we first compared visitation and relative frequency of partial, opportunistic, and obligate frugivores among strata separately for each dietary guild to account for the statistical problem that we did not observe obligate frugivores in the understorey (zero-observation, Steel et al., 2013). Therefore, we calculated generalized linear mixed effect models with the number of visits of partial, opportunistic, or obligate frugivores, respectively, as response variables, stratum and crop mass as explanatory variables, and the IDs of individual lianas as random factors. We also added a zero-inflation term for stratum, an offset for observation hours, and fitted the model with a Poisson distribution (and a logit link). Then, we used generalized linear models with the relative frequency of partial, opportunistic, or obligate frugivores, respectively, as response variables and stratum as explanatory variable. In all models, we used a contrast to compare among strata.

To test if morphological traits differ among strata (H3), we compared CWM body mass, CWM bill length, CWM bill width, and CWM Kipp's index among strata calculating linear mixed effect models with birds' traits as response variables, stratum as explanatory variable, and the IDs of individual lianas as random factors. Further, we analyzed if the variation of these traits differed among strata using the function *asymptotic\_test()* in R package cvequality 0.2.0 (Marwick & Krishnamoorthy, 2019).

Linear mixed effect models and generalized linear mixed effect models were calculated using the function *glmmTMB()* in R package glmmTMB 1.0.2.1 (Brooks et al., 2020). We used the function *Anova()*

in R package *car* 3.0-10 (Fox & Weisberg, 2019) for Wald- $\chi^2$  tests and determined contrast comparisons with the function *emmeans()* in R package *emmeans* 1.4.7 (Lenth et al., 2020).

### 3 | RESULTS

We observed 862 interactions between 24 fruiting *M. longifolia* individuals and 43 frugivore species (41 birds, 2 primates). The most frequent frugivores on fruiting *M. longifolia* were the partial frugivores White-crowned manakin (*Dixiphia pipra*,  $n = 501$  observations), the Blue-crowned manakin (*Lepidothrix coronata*, 71), the Red-headed manakin (*Dixiphia rubrocapilla*, 54), the Green-and-gold tanager (*Tangara schrankii*, 37), and the Striped manakin (*Machaeroptus regulus*, 32; Table S3). According to their dietary specialization, 6 of the 43 frugivore species were obligate, 28 partial, and 9 opportunistic frugivores. Partial frugivores were more common than obligate frugivores and opportunistic frugivores.

Canopy closure significantly differed among strata with decreasing values from the understory to the canopy (Tables 1 and 2). Crop mass, on the other hand, did not significantly differ among strata (mean  $\pm$  SE: low =  $23.29 \pm 5.1$ , middle =  $22.12 \pm 3.27$ , high  $24.92 \pm 4.1$ ; Table 1, Figure 2a). We further found 10 individuals from eight different plant species with fleshy-fruits growing near the observed *M. longifolia* individuals (Table S4). However, in comparison to *M. longifolia*, they only produced a very low number of fruits and were thus not further considered in our analysis ( $n =$  six individuals with  $<25$  fruits,  $n = 2$  with  $<50$  fruits,  $n = 2$  with  $>50$  fruits). Seven individuals produced their fruits in the canopy and three in the understory.

#### 3.1 | Network specialization

Consistent with H1 (frugivores forage in distinct vertical niches), the number of frugivore visits significantly differed among strata with a higher number of visits in the understory than in the canopy (Tables 1 and 2, Figure 2b). Crucially, differences among strata in the number of frugivore visits were not correlated to crop mass, which did not differ among strata (Table 1, Figure 2b). Further, fruit removal did not differ among strata (Table 1, Figure 2c). The Shannon diversity of interacting partners with *M. longifolia* was significantly higher in the canopy and in the midstorey than in the understory (Table 1, Figure 2d). Also, frugivore community composition strongly differed among forest strata (Adonis:  $r^2 = .088$ ,  $F = 2.25$ ,  $p = .004$ ). Ten species exclusively foraged in the canopy and 17 species exclusively in the midstorey. Nine species foraged in the canopy and midstorey, three in the understory and midstorey and only four species foraged across all strata (Figure 3).

Consistent with H2 (niche specificity of frugivores of different dietary specialization differs among strata), number of visits (Table 1, Figure 4a) and the relative frequency of partial, opportunistic, and obligate frugivores (Table 1, Figure 4b) differed among strata and

was not correlated to crop mass (Table 1). Partial and opportunistic frugivores foraged across strata, but with a significantly decreasing number of visits of partial frugivores toward the canopy and a significantly higher number of visits of opportunistic frugivores in the midstorey than in the canopy (Tables 1 and 2, Figure 4a). The relative frequency of both partial and opportunistic frugivores was significantly higher in the midstorey than in the canopy and the understory (Tables 1 and 2, Figure 4b). This means that individual partial or opportunistic frugivores foraged relatively more often exclusively or with a relatively higher frequency in the midstorey (in relation to the other strata) than in the canopy and understory. Obligate frugivores foraged exclusively in the canopy and midstorey and were never detected in the understory. Among these two strata, their number of visits and relative frequency did not differ (Tables 1 and 2, Figure 4a,b).

#### 3.2 | Trait-based analysis

Consistent with H3 (morphological traits differ among strata), CWM of all measured traits (body mass, bill length, bill width, and Kipp's index) were significantly higher in the canopy than in the mid-, and understory (Tables 1 and 2). Further, the variance of all morphological traits was significantly greater in the canopy than in the mid-, and understory (Asymptotic test:  $p < .001$  for all traits; Figure 5).

### 4 | DISCUSSION

By offering fruits across the vertical gradient, the liana *M. longifolia* attracted a broad spectrum of avian frugivore species with different morphological traits. Crucially, frugivore visitation, diversity, and community composition significantly differed among strata with a high number of visits of a few partial frugivore species in the understory and a low number of visits of many different obligate frugivores in the canopy and midstorey. Even though the same resource was available across strata, most frugivore species did not exploit the whole vertical gradient but mainly stayed within a limited vertical foraging niche. These observations support the view that vertical stratification in plant–frugivore interactions is driven by inherent preferences of animal frugivores for particular forest strata. These preferences further seem to be associated with certain avian morphologies, where large species forage in the canopy, whereas smaller species mainly forage in the lower strata. Thus, our results highlight the importance of differentiating among forest strata and feeding guilds when analyzing plant–frugivore interactions. Since *M. longifolia* was the only plant species at our study site with abundant fruit production across strata that allowed for observations of frugivorous birds across strata, it would be highly relevant to identify and study similar plant systems and, where possible, include other taxa of frugivores that forage across strata such as bats or arboreal mammals.

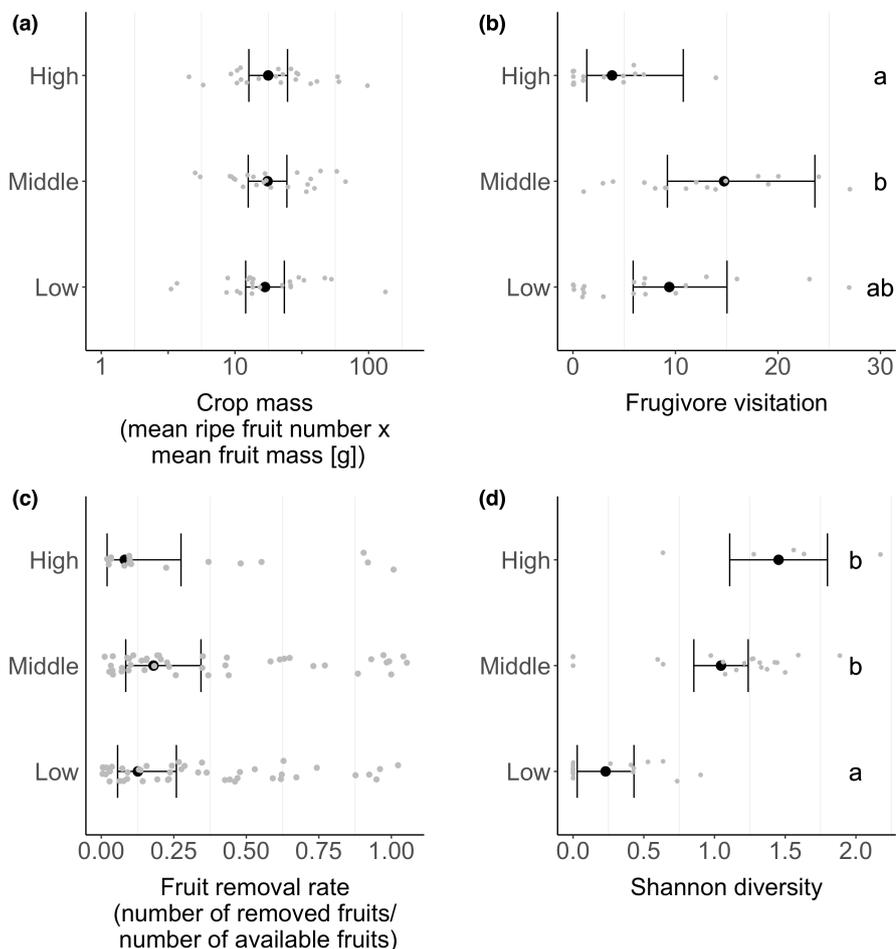
**TABLE 1** Results of the linear and generalized linear mixed-effect models ( $\chi^2$ , degrees of freedom, and  $p$  derived from the *glmmTMB()* function, respectively) examining differences in canopy closure, crop mass, fruit removal, frugivore visitation, Shannon diversity, relative frequency, and birds' traits among strata with *Marcgravia longifolia* individuals, observation days, observation level random effects (number of fruit removal events), respectively, included as random factors.

Model	Variable	$\chi^2$	df	$p$
<b>Canopy closure</b>				
Canopy closure ~ Stratum + (1 Marcgravia ID)	Stratum	41.82	2	<.0001
<b>Crop mass</b>				
Crop mass ~ Stratum + (1 Marcgravia ID)	Stratum	0.07	2	.97
<b>Fruit removal</b>				
Fruit removal ~ Stratum + (1 Marcgravia ID) + (1 Observation day) + (1 olre), family = binominal (link = logit)	Stratum	1.795	2	.41
<b>Frugivore visitation</b>				
Number of visits ~ Stratum + log(Crop mass) + (1 Marcgravia ID) + offset (logHours), zi = ~Stratum, family = nbinom1	Stratum	8.2	2	.017
	Crop mass	0.008	1	.97
<b>Shannon diversity</b>				
Shannon diversity ~ Stratum + (1 Marcgravia ID)	Stratum	75.76	2	<.0001
<b>Visitation of frugivores of different dietary specialization</b>				
Number of visits of partial frugivores ~ Stratum + log(Crop mass) + (1 Marcgravia ID) + offset (logHours), zi = ~Stratum, family = poisson	Stratum	36.1	2	<.0001
	Crop mass	1.68	1	.19
Number of visits opportunistic frugivores ~ Stratum + log(Crop mass) + (1 Marcgravia ID) + offset (logHours), zi = ~Stratum, family = poisson	Stratum	25.41	2	<.0001
	Crop mass	0.47	1	.49
Number of visits obligate frugivores ~ Stratum + log(Crop mass) + (1 Marcgravia ID) + offset (logHours), zi = ~Stratum, family = poisson	Stratum	2.4	1	.12
	Crop mass	2.64	1	.10
<b>Relative frequency (RF)</b>				
RF of partial frugivores ~ Stratum + log(Crop mass) + (1 Marcgravia ID) + offset (logHours)	Stratum	38.03	2	<.0001
	Crop mass	11.33	1	.8
RF of opportunistic frugivores ~ Stratum + log(Crop mass) + (1 Marcgravia ID) + offset (logHours)	Stratum	32.89	2	<.0001
	Crop mass	1.28	1	.26
RF of obligate frugivores ~ Stratum + log(Crop mass) + (1 Marcgravia ID) + offset (logHours)	Stratum	1.07	1	.30
	Crop mass	2.23	1	.14
<b>Frugivorous birds' traits</b>				
CWM Body mass ~ Stratum + (1 Marcgravia ID)	Stratum	34.63	2	<.0001
CWM Bill length ~ Stratum + (1 Marcgravia ID)	Stratum	28.04	2	<.0001
CWM Bill width ~ Stratum + (1 Marcgravia ID)	Stratum	19.59	2	<.0001
CWM Kipp's index ~ Stratum + (1 Marcgravia ID)	Stratum	14.56	2	.0007

#### 4.1 | Vertical stratification of plant–frugivore relationships and potential drivers

The observed differences in community composition among strata and the higher species diversity in the canopy and midstorey are

in agreement with the findings of previous studies, even though those focused on many different plant species offering different resources among strata (Thiel et al., 2021 and references therein). We further observed vertical differences among partial, opportunistic, and obligate frugivores, in line with the study by Schleunig



**FIGURE 2** Differences among strata of the liana *Marcgravia longifolia*. (a) Crop mass (mean ripe fruit number  $\times$  mean fruit mass [g]), (b) frugivore visitation, (c) fruit removal rate (number of removed fruits/number of available fruits), and (d) Shannon diversity of interacting partners shown for the understorey (“Low”), the midstorey (“Middle”), and the canopy (“High”). The letters (“a” and “b”) indicate significant or, respectively, non-significant differences among strata. Shown are the predicted means with their 95%-confidence intervals derived from the linear, or generalized linear mixed effect models, respectively. Dots are individual raw datapoints of *M. longifolia* individuals. Note the log scale for crop mass.

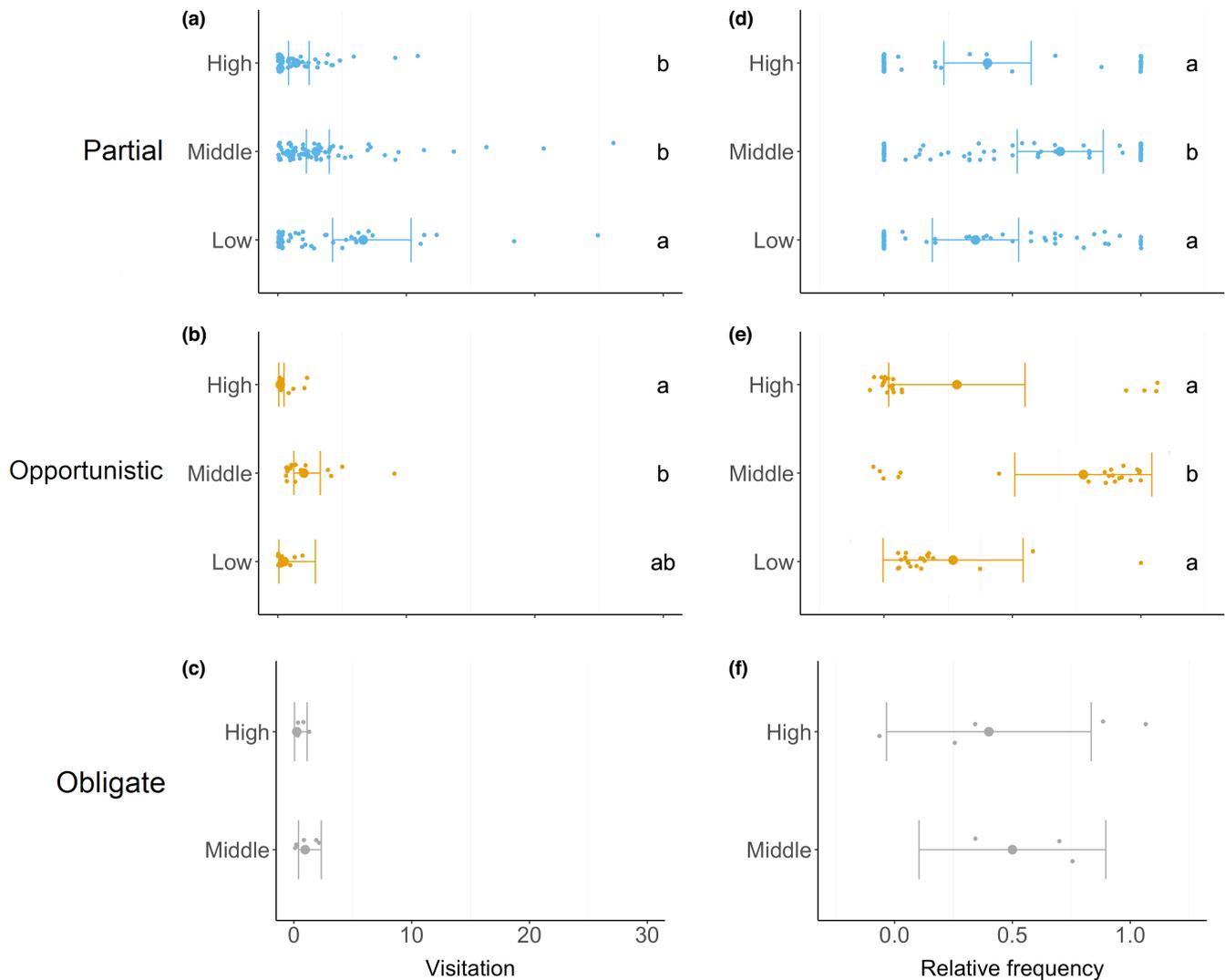
et al. (2011), where obligate frugivores primarily fed on fruits of canopy plants, whereas partial and opportunistic frugivores foraged across strata, but more frequently in the lower strata. In our system, most frugivorous species preferred certain strata for foraging, even though the same resource was available across all strata. These results suggest that the vertical stratification of the frugivore community cannot only be driven by a specialization on certain fruiting plant species (Dalsgaard et al., 2017), but that avian frugivores divide the vertical gradient into distinct vertical foraging niches based on inherent preferences. Thus, the vertical niche can be a strong structuring factor in plant-animal interactions.

Resource availability is considered as one of the most important drivers of network structure (Schleuning et al., 2011; Vázquez, Blüthgen, et al., 2009; Vázquez, Chacoff, & Cagnolo, 2009). Crucially, in our system the same resource was available across strata with no difference in crop mass, but we still found contrasting patterns of plant-frugivore interactions among strata. We assume that the differing avian traits among strata play a role in this pattern of vertical stratification. Large avian frugivores, such as

the red-billed toucan (*Ramphastos tucanus*) or the collared trogon (*Trogon collaris*) were exclusively observed in the canopy. Typical frugivores of the understorey were smaller species with rounded wings being especially suited for high maneuverability in dense vegetation, such as *D. pipra*, *D. rubrocapilla*, *L. coronata*, and *M. regulus*. Understorey foragers were closely related species from only two different families and, consequentially, more homogeneous in their traits. Species foraging in the canopy and midstorey, on the other hand, were from nine different families expressing a far higher diversity of traits. These findings are in line with the study by Shanahan and Compton (2001), where large bodied birds only fed on figs in the canopy and never descended into the lower forest strata to forage, whereas understorey frugivores were mainly small species. Species-specific traits such as avian body mass and wing size were already shown to influence horizontal bird movements within and across forest patches, with large-bodied species showing the highest movement abilities (Neuschulz et al., 2013; Ovaskainen et al., 2019). Still, as beak and fruit size are matching traits (Bender et al., 2018), the observation that birds foraging in

**FIGURE 3** Bipartite diagram depicting the interaction matrix of frugivores with *M. longifolia* in a tropical forest in north-eastern Peruvian Amazonia. In total, we observed 41 frugivorous bird and two frugivorous primate species removing fruits from the three strata of *M. longifolia*. The thickness of the gray lines connecting frugivore species and strata correspond to the interaction frequency with which frugivores fed in the respective stratum.





**FIGURE 4** Interaction of frugivores of different dietary specialization across strata. Visitation (a–c) and relative frequency (d–f) are depicted for partial (28 species), opportunistic (9 species), and obligate (6 species) frugivores in the understory (“Low”), the midstorey (“Middle”), and the canopy (“High”). The letters (“a” and “b”) indicate significant or, respectively, non-significant differences among strata. Shown are the predicted means with their 95%-confidence intervals derived from the generalized linear mixed effect models or linear models, respectively. Dots are raw datapoints of individual frugivore species.

the canopy have larger bills than species of the understory could be due to the fact that fruits of canopy trees are often larger compared to fruits of understory trees (Shanahan & Compton, 2001). In accordance with other studies, our results indicate that not only the horizontal, but also vertical movement of birds is strongly influenced by traits and that trait-associated habitat specialization of frugivores plays a decisive role in structuring the differences in plant–frugivore interactions among strata.

Further factors influencing the vertical foraging niche may be differences in the diversity of fruiting plant species rather than only resource abundance. For obligate frugivores, the importance of a mixed fruit diet was already shown (Wendeln et al., 2000; Whelan et al., 1998) and, in the canopy, they can feed on a wide array of different fleshy-fruited plant species (Schaefer et al., 2002) required to meet their dietary demands. Partial and opportunistic frugivores, on the other hand, forage in the lower strata, where fruit choice is comparably scarce (Schaefer et al., 2002; Schleuning et al., 2011;

Shanahan & Compton, 2001). They may be less dependent on a mixed fruit diet, as they only complement their invertebrate diet with fruits (Kissling et al., 2007). Structural factors such as vegetation density and light conditions have also been shown to shape the distribution of birds along the vertical forest gradient (Bell, 1982; Jayson & Mathew, 2003; MacArthur, 1964; Pearson, 1971; Walther, 2002a, 2002b). Also, in our system canopy closure and vegetation density differed among strata, and more plant species produced their fruits in the canopy than in the understory.

## 4.2 | Variability of network structure across strata

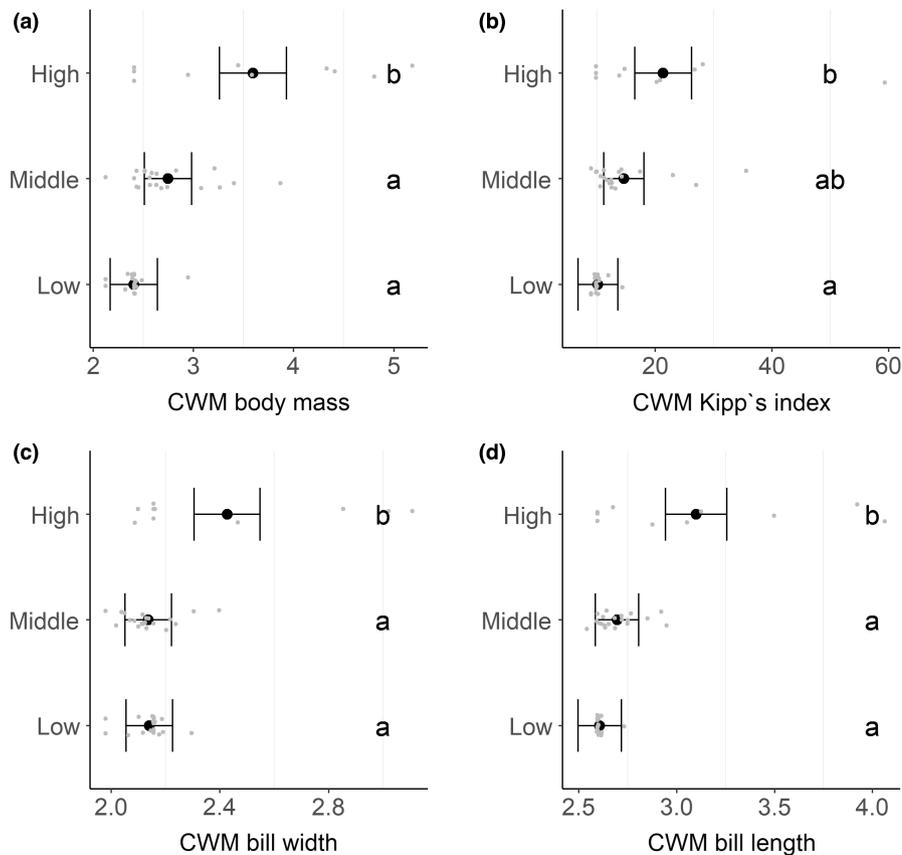
Our frugivore community was characterized by a high species diversity with few visits of the observed species in the canopy and midstorey, and a low species diversity with many visits of the observed species in the understory. Thus, our results show that the structure

**TABLE 2** Standard errors (SE), standardized estimates, and *P* values for all models derived from the *emmeans()* function, which were conducted for the *glmmTMB()* models with significant *p* values in Table 1 examining differences among strata on differences in canopy closure, frugivore visitation, relative frequency, and birds' traits with *Marcgravia longifolia* individuals as random factors.

Response variable	Stratum	SE	Standardized estimates	<i>p</i>
Canopy closure				
Canopy closure	High–Low	0.806	–5.01	<.0001
	High–Middle	0.8	–2.14	.0085
	Low–Middle	0.67	2.87	.0001
Frugivore visitation				
Number of visits	High–Low	0.519	–0.902	.09
	High–Middle	0.519	–1.353	.03
	Low–Middle	0.253	–0.451	.09
Shannon diversity				
Shannon diversity	High–Low	0.181	1.223	<.0001
	High–Middle	0.18	0.407	.03
	Low–Middle	0.111	–0.816	<.0001
Visitation of frugivores of different dietary specialization				
Number of visits of partial frugivores	High–Low	0.304	–1.717	<.0001
	High–Middle	0.226	–1.146	<.0001
	Low–Middle	0.245	0.571	.02
Number of visits of opportunistic frugivores	High–Low	0.953	–0.962	.32
	High–Middle	0.473	–2.368	<.0001
	Low–Middle	0.921	–1.406	.2
Relative frequency				
RF of partial frugivores	High–Low	0.056	0.047	.34
	High–Middle	0.059	–0.283	<.0001
	Low–Middle	0.057	–0.33	<.0001
RF of opportunistic frugivores	High–Low	0.125	0.141	.27
	High–Middle	0.124	–0.561	<.0001
	Low–Middle	0.131	–0.703	<.0001
Frugivorous birds' traits				
CWM body mass	High–Low	0.202	1.189	<.0001
	High–Middle	0.202	0.847	.0002
	Low–Middle	0.165	–0.342	.0445
CWM Bill length	High–Low	0.095	0.493	<.0001
	High–Middle	0.095	0.4037	.0002
	Low–Middle	0.078	–0.0892	.26
CWM Bill width	High–Low	0.071	0.286	.0003
	High–Middle	0.071	0.29	.0003
	Low–Middle	0.057	0.004	.944
CWM Kipp's index	High–Low	2.94	11.17	.0013
	High–Middle	2.94	6.74	.039
	Low–Middle	2.40	–4.43	.071

of the frugivore community can even differ among strata of a single plant species. Here, the partial frugivores, mainly foraging in the lower strata, played a core role, in particular the manakins *D. pipra*, *D. rubrocapilla*, *L. coronata*, *M. regulus*, and the tanager *T. schrankii*. The high visitation of a few partial frugivore species suggest that *M. longifolia* fruits are (at least seasonally) a very important resource

for them (Bender et al., 2018). The highly diverse obligate frugivores in our system, on the other hand, showed a low visitation and *M. longifolia* fruits only constitute a very small part of their fruit diet. It was further shown that they interact with many different plant species and thus fulfill more generalized roles in plant–frugivore interactions than bird species feeding on different food types



**FIGURE 5** Community weighted means (CWM) of morphological traits of bird communities for each forest stratum. (a) CWM body mass, (b) CWM Kipp's index, (c) CWM bill width, and (d) CWM bill length of frugivore communities foraging in the understory ("Low"), midstorey ("Middle"), and canopy ("High"). The letters ("a" and "b") indicate significant or, respectively, non-significant differences among strata. Shown are the predicted means with their 95%-confidence intervals of the linear mixed effect models. Dots are raw datapoints of *M. longifolia* individuals.

(Dalsgaard et al., 2017). Partial and opportunistic frugivores, on the other hand, interact across different types of interaction systems as they feed on different food resources (Mello et al., 2015; Schleuning et al., 2014) and might thus show a higher specialization on certain interaction partners within a single network. Numerous studies have already shown that variability among interaction systems in terms of individual specialization levels and species roles is highly context-dependent. For instance, the spatial scale on which biotic specialization is measured is highly relevant (Trøjelsgaard & Olesen, 2016). Dietary specialization across different interaction systems and niche partitioning among species within interaction networks shows varying spatial patterns (Dalsgaard et al., 2017). Changes in community composition and specialization of individual species were also observed at small spatial scales. For instance, hummingbird species in tropical wet, pre-montane, and lower montane wet forests of Costa Rica have been shown to be more specialized at low and mid than at higher elevations (Maglianesi et al., 2015). Our results now show that network structure and specialization can even vary among strata within a single plant species and thus, that variation of the interaction structure can occur on small spatial scales.

### 4.3 | Consequences for seed dispersal services

We have not studied seed dispersal directly, but our findings of differing frugivore-plant interactions across strata imply that the

resulting seed dispersal might as well differ among strata. Large-bodied birds feeding on *M. longifolia* fruits in the canopy have long gut passage times and are highly mobile, and therefore are likely to disperse seeds over large distances (Lambert, 1989). Average home-range size of *Ramphastos* toucans, for instance, is around 90ha (Holbrook, 2011). The small understory foragers, on the other hand, have shorter gut passage times and often have smaller home ranges, resulting in shorter dispersal distances (Westcott & Graham, 2000). Average home-range size of adult male manakins, for instance, is only between 2 and 3 ha, whereas female manakins have home ranges between 9 and 15ha (Théry, 1992). Dispersal by diverse frugivores improve the quality of seed dispersal due to complementary effects such as different dispersal distances away from the mother plant and deposition in different microhabitats (Bascompte & Jordano, 2007; Fleming, 1993; Rehling et al., 2022; Rother et al., 2016; Schleuning et al., 2015) For *M. longifolia*, the high species richness and wide range of avian frugivore traits may result in more complex dispersal kernels compared to plant species presenting fruits in a single forest stratum. Extending these observations to other plant species implies that plants that only present fruits in the understory experience much shorter dispersal distances than trees that exhibit most of their fruits in the canopy. For instance, Barry and Schnitzer (2021) observed differences in the conspecific negative density dependence between understory and canopy trees, where canopy trees were more overdispersed than understory trees.

## 5 | CONCLUSIONS

In our study, we found strong patterns of vertical stratification of plant–frugivore interactions at a single plant species. These results suggest that vertical stratification in plant–animal interactions might be a mechanism that is not primarily driven by differences in plant community composition among forest strata but by inherent preferences of animals for certain strata. It is a long-held tenet in ecology that tropical species are very specialized, that is, with a very fine-grained niche partitioning, which may facilitate the coexistence of high number of species (Schemske, 2002). Niche differentiation of species along the vertical gradient may be a key factor promoting diversity in tropical forests. Impairing this vertical structure due to anthropogenic disturbances such as selective logging of canopy trees would potentially result in a lower forest structure and a simplified vertical structure, that could be associated with altered patterns of visitation frequency and a loss of diversity of frugivores. Thus, a simplification of the vertical structure of agroforestry systems and forest regeneration areas needs to be carefully considered in tropical forest conservation.

### AUTHOR CONTRIBUTIONS

Sarina Thiel, Franziska Willems, Eckhard W. Heymann, Marco Tschapka, and Katrin Heer conceived the ideas and designed the methodology. Sarina Thiel, Franziska Willems, Till Töpfer, and NS collected the data. Sarina Thiel, Franziska Willems, Finn Rehling, Matthias Schleuning, Dana G. Schabo, Nina Farwig, and Katrin Heer analyzed and interpreted the data. Sarina Thiel, Eckhard W. Heymann, and Katrin Heer led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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### CONFLICT OF INTEREST STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available from: <https://doi.org/10.5281/zenodo.6799010>.

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