Vertical stratification of seed-dispersing vertebrate communities and their interactions with plants in tropical forests

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ABSTRACT

Vertical stratification (VS) is a widespread phenomenon in plant and animal communities in forests and a key factor for structuring their species richness and biodiversity, particularly in tropical forests. The organisms composing forest communities adjust and shape the complex three-dimensional structure of their environment and inhabit a large variety of niches along the vertical gradient of the forest. Even though the degree of VS varies among different vertebrate groups, patterns of compositional stratification can be observed across taxa. Communities of birds, bats, primates, and non-flying small mammals are vertically stratified in terms of abundance, species richness, diversity, and community composition. Frugivorous members of these taxa play important roles as seed dispersers and forage on fruit resources that, in turn, vary in quantity and nutritional value along the vertical gradient. As a consequence, plant–seed disperser interaction networks differ among strata, which is manifested in differences in interaction frequencies and the degree of mutual specialization. In general, the canopy stratum is composed of strong links and generalized associations, while the lower strata comprise weaker links and more specialized interactions. Investigating the VS of communities can provide us with a better understanding of species habitat restrictions, resource use, spatial movement, and species interactions. Especially in the face of global change, this knowledge will be important as these characteristics can imply different responses of species and taxa at a fine spatial scale.

Key words: stratum, plant–animal interactions, seed dispersal, frugivory, birds, bats, primates, non-flying small mammals, fruits, tropical forests

CONTENTS

I. Introduction .................................................................455
(1) VS as a guiding principle in ecology .................................455
(2) VS of tropical forests ......................................................455
(3) Importance of vertebrate seed dispersers in tropical forests 456
(4) The threat of global change ..............................................456
(5) Challenges to be resolved ...............................................456
II. Methods: literature research ..............................................456
III. Species diversity and distribution across forest strata ............457
(1) Bat communities ..............................................................457
(2) Bird communities ............................................................457
(3) Non-flying small mammal communities ............................458

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“One of the outstanding general principles of community organization is that of stratification. Nearly all communities share a well-defined lamination into a column of strata upon a vertical organismal gradient” (Allee et al., 1949, p. 442).

I. INTRODUCTION

(1) VS as a guiding principle in ecology

The vertical organization of structures, microclimate, and biota in ecosystems has been a recurring topic in scientific research and ecosystem description since the 1950s (Allee et al., 1949; Richards, 1952; Geiger, 1965; Smith, 1973; Bongers, 2001) and the concept of vertical stratification (VS) is one aspect of this (Richards et al., 1996). In science, the general term ‘stratification’ is used to describe distinct, but closely related and interconnected phenomena. VS can refer to the vertical layering of microclimate, leaf mass, food resources, or animal communities. Allee et al. (1949) perceived VS as a general phenomenon of plant and animal communities in terrestrial (forests, deserts, grasslands) and aquatic (oceans, intertidal zones, lakes) environments. For example, fresh- and saltwater environments exhibit gradients of water pressure, temperature, light intensity, wavelength absorption, and other abiotic factors (Allee et al., 1949). Grassland can be divided into subterranean, floor, and herbaceous layers. Forest communities mostly have six vertical strata: soil, forest floor, herbaceous, shrub, tree, and emergent layers. Organisms composing these communities adjust to the vertically stratified environment (Allee et al., 1949). Whereas for aquatic environments and grasslands many early studies described the VS of abiotic and biotic factors (Shelford & Gail, 1922; Wollereck, 1932; Henrici, 1939; ZoBell, 1946), knowledge about forest stratification was for many years more or less restricted to the lower layers (Allee et al., 1949). During the last 30 years, improved access to the forest canopy has changed our understanding of key ecosystem processes substantially (Ozanne et al., 2003).

The vertical pattern of microenvironmental conditions such as temperature, light, humidity, and wind on the forest is determined by its plant species composition and three-dimensional structure (Geiger, 1965; Parker, 1995). Vertical climatic gradients within forests are more pronounced than those defined by latitude and elevation. Climate may vary by as much as 4°C and 10% humidity along a 20–30 m vertical forest gradient, which is equivalent to over 400 m in altitude and hundreds of kilometres in latitude (Scheffers et al., 2013). In general, circadian climatic variations of the upper canopy are much stronger than those in the lower layers. For instance, the canopy temperature of a tropical lowland rainforest in Costa Rica ranges during the day from 20.5°C to 27°C, compared to 22°C to 25°C in the understory (Fetcher, Oberbauer, & Strain, 1985). Also, the vapour pressure deficit in the understory is stable at around 0.2 kPa, but ranges from 0.3 to 0.9 kPa in the canopy (Fetcher et al., 1985). Forest type and structure influence microclimatic profiles, light quality, and light quantity (Shaw, 2004). Evergreen forests, for example, allow less light through the canopy than deciduous hardwoods, affecting forest floor biota and lower-canopy environments (Kato & Yamamoto, 2002). In submontane evergreen forests and tropical dry forests, foliage shows the highest density in the canopy and the understory, with more open spaces in the midstorey (Terborgh & Weske, 1969; Pearson, 1971; Terborgh, 1980). Vertically organized plant structures comprise leaves, reproductive parts, trunks, branches, butts, roots, and deadwood (Shaw, 2004). For instance, in different types of temperate and tropical forests, flowers and fruits show higher abundance in the canopy, whereas tree trunks and dead leaves dominate under- and midstorey levels (Terborgh, 1980; Marra & Remsen, 1997).

(2) VS of tropical forests

Due to their diversity and structural complexity, tropical forests are of particular interest for the study of VS of ecological communities. Their canopies can reach heights of >50 m, spanning from the lowest herbs to the emergent layers
(Richards, 1952). Their complex three-dimensional structure and the diversity of microenvironments along the vertical gradient provide ample opportunities for niche diversification (Ozanne et al., 2003). Thus, VS has been considered a pivotal factor shaping the species richness and diversity of tropical forests (Condit et al., 2002; Wright, 2002; Ozanne et al., 2003; Pennington & Dick, 2010; Sedio, Wright, & Dick, 2012). Furthermore, their canopies are considered to be hotspots of biological diversity (Ozanne et al., 2003; Nakamura et al., 2017).

(3) Importance of vertebrate seed dispersers in tropical forests

The vertical pattern of microenvironmental conditions within forests is crucial as it affects the distribution of forest biota, the behaviour of vertebrates, and numerous other aspects of ecosystem functioning (Shaw, 2004). For instance, many studies have observed VS for birds, bats, primates, and small non-flying mammals in terms of community composition, species diversity, richness, and abundance (e.g. Buchanan-Smith et al., 2000; Kalko & Handley, 2001; Cunha & Vieira, 2002; Vieira & Monteiro-Filho, 2003; Buzzard, 2006; Chamel et al., 2016; Gregorini et al., 2017; Dinanti, Winarni, & Supriatna, 2018). In tropical rainforests, these vertebrates are among the most important seed dispersers (Fleming, 1993; Fleming & Kress, 2013). Up to 90% of tropical rainforest plant species produce fleshy fruits that are consumed and their seeds dispersed by birds, bats, primates, and non-flying small mammals (Howe & Smallwood, 1982; Lobova, Geiselman, & Mori, 2009). Sekercioglu (2006) suggested that birds disperse the seeds of more than 70% of the woody plants bearing fleshy fruits. Furthermore, seed dispersal by primates has been associated with the maintenance of tropical rainforest diversity (Link & Di Fiore, 2006). Lastly, frugivorous bats are the most important seed dispersers in highly disrupted forests, as fragments are better reached by bats than by birds and primates, due to the lack of appropriate perching and nesting sites (Medellín & Gaona, 1999; Melo et al., 2009; Muscarella & Fleming, 2007, but see Farwig, Böhning-Gaase, & Bleher, 2006). Rainforest plants may profit substantially from seed-dispersing vertebrates, as these move over longer distances and thus maintain gene flow among populations on larger spatial scales, enable escape from high mortality near mother plants, and allow the colonization of new sites (Nathan & Muller-Landau, 2000). Hence, seed dispersal is vital for maintaining plant biodiversity and thus is the foundation for survival and sustainability (Cordeiro & Howe, 2003; Sekercioglu, 2006). Since plant and vertebrate communities show VS, it is plausible to assume differences among strata in the patterning of plant–animal interactions such as seed dispersal.

(4) The threat of global change

Tropical forests are under immense pressure due to anthropogenic factors such as forest degradation, land-use changes, and climate change (Lewis, 2006). These factors alter forest structure and constitute serious threats to the biological diversity of the tropics. Understanding their consequences for the persistence of native populations and communities remains a daunting challenge (Dobson, 2005). To date, studies have revealed that susceptibility to changing conditions varies among focal taxa and functional species groups (Medellín & Gaona, 1999; Lewis, 2006; Philpott et al., 2008; Ranganathan et al., 2008; Kirika et al., 2008a; Kirika, Farwig, & Böhning-Gaase, 2008b; Grass, Berens, & Farwig, 2014). It is highly probable that these changes will also affect the vertical distribution of communities. Thus, it is evident that we need a better resolved understanding of species characteristics and interactions to be able to understand how vertically stratified tropical forests and their affiliated species and ecosystem functions will perform under global change.

(5) Challenges to be resolved

VS of tropical forest biota has both ecological and evolutionary consequences for biodiversity and ecosystem functioning. Investigating VS of single taxa but also of essential species interactions such as seed dispersal should be a focal point of research to understand the underlying abiotic and biotic factors structuring diversity at a finer scale. It can provide a more detailed picture of vertical patterns exhibited by forest biota and the effects on species habitat preferences, resource use, spatial movement, and species interactions.

Herein, we review current knowledge about VS of species communities and resources, with particular emphasis on vertebrate taxa acting as seed dispersers in tropical forests. Further, we summarize existing literature on the VS of plant–seed disperser interactions and species networks and discuss its evolutionary and ecological implications. We conclude with a consideration of the implications of global climate change and outline directions for future research.

II. METHODS: LITERATURE RESEARCH

Our literature search was based on Google Scholar (https://scholar.google.de/) and Web of Science (https://apps.webofknowledge.com/) using all available years and a combination of the following key words: “vertical stratification” OR “forest strata” AND “tropics” OR “rainforest” AND “birds” OR “bats” OR “primates” OR “mammals” OR “fruits” OR “plant–animal interactions” OR “frugivory” OR “seed dispersal”. The online database search was last performed in September 2020 on titles, abstracts, and key words in both databases. From the list of studies obtained, we used their titles to identify relevant studies and scanned their abstracts for information on VS. In order to be included in this review, the study had to be conducted in one of the main tropical forest types (following the definition of Thomas & Baltzer, 2002) and provide information on VS of canopy communities of seed-dispersing birds, bats, primates, or other small non-flying mammals, VS of fruit crops,
or VS of plant–seed disperser interactions with animals belonging to the groups mentioned above in the tropics. For all relevant studies, we consulted the main text and extracted information regarding taxon, diet (only frugivores and omnivores were included), geographic region, height division of strata, the VS parameters examined, morphology of plant and animal traits, and possible drivers and benefits of VS. We use the terms ‘stratification’, ‘lower/middle/higher strata’, or respectively ‘understorey’; ‘midstorey’, and ‘canopy’ accordingly to the respective paper. However, as the usage of these terms is often very vague and differs among studies (for a more detailed analysis, see Parker & Brown, 2000), we only included studies that used ‘stratification’ as a synonym for height and that specified height division of strata. Studies consistently divided the forest into 2–4 strata (see online Supporting Information, Table S1) and even though emergent trees could be considered as an additional stratum, most studies either assigned them to the canopy stratum or did not include them in their observations. We also searched the references and citation records of the included studies for other studies that could provide additional data.

We found 15 papers published between 1994 and 2020 targeting bats, 15 papers published between 1969 and 2018 targeting birds, 16 papers published between 1977 and 2019 targeting non-flying small mammals, 31 papers published between 1972 and 2010 targeting primates (Table S1), three papers published between 2002 and 2014 targeting plants, and four papers published between 2001 and 2018 targeting plant–animal networks (Table S2). Even though we may not have found all studies targeting our question, and given that the file drawer problem (studies with significant results are published more often than those finding no significant patterns; Aronps & Wooster, 1995) may be relevant to our study, our search criteria were intended to be exhaustive. We did not include any unpublished results.

III. SPECIES DIVERSITY AND DISTRIBUTION ACROSS FOREST STRATA

(1) Bat communities

Bat communities in forests of the Paleo- and Neotropics show similar patterns of VS (Table S1). Species are heterogeneously distributed between the canopy and the understorey with the canopy being intensively used (Francis, 1994; Sampio et al., 2003; Rex et al., 2008; Gregorin et al., 2017). Whereas numbers of individuals are generally higher in the understorey, species richness and diversity are higher in the canopy with distinct differences in community composition (Bernard, 2001; Kalko & Handley, 2001; Silva et al., 2020). Most of these differences in habitat use can be explained by differences in echolocation and wing morphology, which are intimately linked to foraging behaviour and diet, as well as roost-site preferences (Kalko, Handley, & Handley, 1996; Hodgkinson et al., 2004; Olaya-Rodríguez, Pérez-Torres, & Londoño-Murcia, 2019). In bats, echolocation is an important sensory system that determines profoundly the interaction of animals with the surrounding habitat structure (Denzinger, Tschapka, & Schnitzler, 2018).

The echolocation and wing morphology of bat species with short, high-frequency signals and short, broad wings (Fig. 1) are adapted to foraging in the dense understorey of tropical forests (Duya, Fidelino, & Ong, 2017; Denzinger et al., 2018). For example, many well-sampled species of the Neotropical genera *Carollia* and *Sturnira* (Kalko & Handley, 2001; Delaval, Henry, & Charles-Dominique, 2005; Pereira, Marques, & Palmeirim, 2010) or the African genus *Epomops* (Henry et al., 2004) are solely found in the understorey. They mostly feed on fruit produced by shrubs and treelets of the families *Clusiaceae, Piperaceae*, and *Solanaceae* and use day roosts near the ground (Fleming & Heithaus, 1986). Frugivores with short, high-frequency signals, but long and narrow wings (Fig. 1) are better adapted to hunt in the less-chuttered canopy (Denzinger et al., 2018; Olaya-Rodriguez et al., 2019). For example, phyllostomid bats of the Neotropical subfamily *Stenodermatinae* (e.g. *Chiroderma, Uroderma*, *Platyrrhinus* [*Vampyrops]*) and some species of the African and Asian subfamily *Pteropodinae* (e.g. *Micropteropus, Desmalopex, Eonycteris*) primarily forage in the canopy (Lim & Engstrom, 2001; Henry et al., 2004; Carvalho, Fabián, & Meneghetti, 2013; Duya et al., 2017). Here, they feed on figs and other Moraceae and utilize day roosts in the sub-canopy (Bernard, 2001; Kalko & Handley, 2001; Henry et al., 2004).

(2) Bird communities

With improved access to the canopy of tropical forests and the development of new techniques such as the use of canopy cranes or ground-to-canopy mist nets (Walther, 2002b, 2003; Naka, 2004; Chmel et al., 2016; Klimento & Richards, 2018), researchers have obtained detailed data on the VS of bird guilds and a fuller picture of bird diversity. Overall abundance (Orians, 1969; Pearson, 1971; Bell, 1982; Dinanti et al., 2018), species diversity (Jayson & Mathew, 2003; Chmel et al., 2016), and community composition (Terborgh, 1980; Walther, 2002a) clearly differ among the strata of tropical forests (Table S1).

The vast majority of studies showed a VS of trophic bird guilds with an increasing abundance and diversity of frugivorous and omnivorous birds towards the canopy (Greenberg, 1981b; Firth, 1984; Shanahan & Compton, 2001; Naka, 2004; Dinanti et al., 2018). Body mass and wing size appear to be structuring factors as they can to some extent constrain the use of vertical strata (Fig. 1). Canopy-feeding seed dispersers are mainly large-bodied species such as toucans, trogons, hornbills, fruit pigeons, or birds of paradise, for which moving in the dense vegetation of lower forest strata and resting on the mostly thin branches there is difficult (Bell, 1982; Fleming & Kress, 2013). The seed dispersers feeding in the understorey of tropical forests are primarily smaller species such as manakins, bulbuls, and flowerpeckers (Karr, 1976; Fleming, 1988; Chmel et al., 2016).
Foliage density in combination with the availability of food resources seems to be an important driver of the vertical distribution of bird communities. There seems to be a link between foliage density and bird diversity and abundance in tropical forests all over the world (MacArthur, 1964; Pearson, 1971; Bell, 1982; Jayson & Mathew, 2003). Species from strata with lower vegetation density have larger vertical foraging niches than species foraging in strata with dense vegetation (Walther, 2002a). Frugivorous birds are far less abundant in the understorey, where vegetation density is high, whereas the high fruit availability in the canopy leads to increased abundance and diversity of frugivorous and omnivorous birds (Terborgh, 1980; Bell, 1982; Chmel et al., 2016). Nevertheless, available food density for entire avian communities is difficult to assess accurately, as diet composition is still unknown for many tropical bird species (Hutto, 1990; Chmel et al., 2016).

(3) Non-flying small mammal communities

VS of rodents and marsupials is extremely common in tropical rainforests (Table S1; Stallings, 1989; McClearn et al., 1994; Voss, Lunde, & Simmons, 2001; Helder, Macedo, & Cruz Loss, 2019). Community composition and abundance differ among strata (Charles-Dominique et al., 1981; Voss & Emmons, 1996; Grelle, 2003). The majority of species seem to use only one stratum, whereas others move across the vertical gradient (Adam, 1977; Malcolm, 1991; Rader & Krockenberger, 2006). Didelphid marsupials like Caluromys philander and Geacrinanus agilis, for instance, generally constitute the most common group in the canopy of Neotropical forests (Vieira & Monteiro-Filho, 2003), whereas other species like Marmosa incana or Marmosa marina are typical understory foragers (Cunha & Vieira, 2002; Vieira & Monteiro-Filho, 2003; De Faria Calazans & Bocchiglieri, 2019). Body size and locomotor behaviour define the use of vertical space in small mammal communities (Fig. 1). The ability of species to deal with branches of variable diameters and inclination can restrict their use of vertical strata (Cunha & Vieira, 2002).

Availability and access to food resources are important factors for the differential use of forest strata (Vieira & Monteiro-Filho, 2003; Lambert, Malcolm, & Zimmermann, 2005; Rader & Krockenberger, 2006). Species living in the canopy have a higher proportion of fruits in their diet than species of the understory (Malcolm, 1991; Emmons, 1995; Cunha & Vieira, 2002). By foraging on canopy resources, species may reduce competition at ground level (Passamani, 1995). Especially when resources are scarce, canopy access can translate into increased efficiency in finding resources, as canopy-dwelling species can access fruits that are only accessible to competitors on the ground after they fall (Layne, 1970; Rader & Krockenberger, 2006). Predator avoidance is considered to be another driver of canopy use (Schoener, 1974; Passamani, 1995).

Fig 1. Schematic representation of a vertically stratified tropical forest and its inhabitants. Even though the degree of vertical stratification (VS) differs among different seed-dispersing vertebrate groups, all reviewed studies reported significant patterns of compositional stratification across taxa. The bar plots indicate the number of studies that found significant patterns of VS for bats, birds, non-flying small mammals, and primates in Africa (black), Asia (dark grey), Australia (grey), and the Neotropics (light grey).

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Therefore, VS contributes to reducing interspecific competition and to enable the co-existence of many sympatric species and thus the maintenance of diverse communities of small mammals in tropical forests (Schoener, 1974).

(4) Primate communities

VS of sympatric species emerges as a consistent pattern in primate communities, particularly in the Neotropics and in Africa (Table S1; Pook & Pook, 1982; Cords, 1987; Gautier-Hion, 1988; Lopes & Ferrari, 1994; Kaplin & Moermond, 2000; Pozo-R & Youldatos, 2005). Body mass and locomotion seem to be structuring factors for VS in African and Neotropical primates (Youldatos, 1999; Buchanan-Smith et al., 2000; Heymann et al., 2002). Larger species usually occupy higher strata, where they rarely use vertical supports and commonly jump from branch to branch (Fig. 1). Smaller species, by contrast, live in lower forest levels, use vertical substrates like vines, branches, and twigs extensively, and perform vertical clinging and leaping between trunks to locomote (Fleagle & Mittermeier, 1980; Buchanan-Smith et al., 2000; Heymann et al., 2002). An exception are large terrestrial or semi-terrestrial species like *Mandrillus leucophaeus* and *Cercoptetus campbelli* that occupy lower strata of African tropical forests than sympatric guenon species (Gartlan & Struhsacker, 1972; Buzzard, 2006). The role of body mass in VS is less pronounced for African, Asian, and Malagasy primate communities (MacKinnon & MacKinnon, 1980; Ungar, 1996). This difference between the Neotropics and other regions could be a consequence of Neotropical primates being on average significantly smaller than their Paleotropical counterparts (Kappeler & Heymann, 1996). However, more detailed studies of Paleotropical primate communities are needed to examine this question.

Differences in diet composition between primate species ranging at different heights suggest that VS facilitates niche segregation (ecological partitioning), thus allowing their sympatric coexistence. For instance, *Cercoptetus diana* generally forage on fruits in higher strata, *Cercoptetus petaurista* mostly feed on foliage in the middle stratum, and *Cercoptetus campbelli* mainly eat fruits and animal prey in lower strata of African tropical forests (Buzzard, 2006). The Neotropical species *Ateles paniscus* and *Chiroptotes satanas* are very similar in their use of forest strata but differ in diet: the former consuming primarily fruit pulp, the latter being a seed predator, while *Pithecia pithecia*—also a seed predator—occupies lower strata than *C. satanas*.

The role of VS for niche segregation becomes particularly obvious in interspecific associations (mixed-species groups) of closely related taxa. In associations formed by species of the Neotropical tamarin genera *Leontopithecus* (comprising what was previously considered subspecies of *Saguinus fasciolis*) and *Saguinus* (*S. imperator*, *S. labiatus*, *S. mystax*), the former occupies on average lower strata than the latter (Yoneda, 1980, 1984; Norconk, 1990; Buchanan-Smith, 1999). While they mainly feed on the same plant food resources, different foraging heights are associated with different prey-capture strategies (for example, use of the trunk surface, bark, and crevices versus use of foliage as foraging substrates) that reduce overlap in the animal portion of the diet (Peres, 1993b; Nickle & Heymann, 1996; Smith, 2000; Porter, 2001).

Apart from facilitating sympatric coexistence, vertical segregation in interspecific associations provides benefits in terms of complementary vigilance (Peres, 1993a), reduced individual efforts for vigilance (Cords, 1990; Oates & Whitesides, 1990; Hardie & Buchanan-Smith, 1997; Wolters & Zuberdüeßler, 2003), and increased foraging efficiency (Terborgh, 1983; Podolsky, 1990; Peres, 1992, 1996).

IV. VS OF FRUIT QUANTITY AND QUALITY

Food resource availability seems to be one of the key factors determining VS and canopy use of vertebrates in tropical forests. Naturally, there is a strong relationship between quality, quantity, and distribution of food and the number and density of fruit consumers (Smythe, 1982; Loiselle & Blake, 1991). Tropical rainforests are highly seasonal environments regarding phenology and fruit availability (Foster, 1982; Sabatier, 1985; Kinnaird, O’Brien, & Suryadil, 1996; Wikelski, Hau, & Wingfield, 2000). Whenever resources are limited, competition arises and the organization of animal assemblages and the coexistence of species are affected (Honuo, Vickery, & Chapman, 2006). This raises the question of whether fruit production, for instance in terms of quantity and quality of fruit crops in tropical forests also shows patterns of VS.

The quantity and quality of fruits do differ among forest strata (Table S2). In many tropical forests around the world, fruit abundance and density are higher in the canopy than in the lower strata (Shanahan & Compton, 2001; Schaefer, Schmidt, & Wesenberg, 2002; Houle, Chapman, & Vickery, 2007). Also, fruits of canopy trees are often larger and contain more water, sugar, and fruit pulp dry matter per fruit compared to fruits of understory trees (Shanahan & Compton, 2001; Houle et al., 2007). A study on diverse *Ficus* species in a Bornean lowland rainforest showed that canopy figs were produced in a greater size range than those of the understory. Furthermore, fig crops were considerably larger in the canopy than in the lower strata (Shanahan & Compton, 2001). The quality and quantity of fruits not only vary among species and trees of different forest strata, they can even vary within a fruit tree. For 13 tree species in the Kibale National Park of Uganda, canopy feeding sites produced a higher density and nutritional value of food than lower feeding sites on the same tree (Houle, Condlin-Brittain, & Wrangham, 2014).

These findings explain, at least partially, why some species show a pronounced preference for the canopy and why communities are vertically stratified. For instance, Schaefer et al. (2002) observed that most large avian frugivores fed in the middle strata where fruits were largest. Smaller frugivorous
birds like tanagers and warblers, by contrast, were mainly observed feeding on the smaller fruits in the canopy (Greenberg, 1981a; Thiollay & Jullien, 1998; Schaefer et al., 2002). These observations differ from the general pattern, that large fruits mainly occur in the canopy and that large seed dispersers thus mainly feed in the canopy and small ones in the understory, but demonstrate how fruit availability can shape VS of seed-disperser communities. However, differences in fruit production among forest strata in terms of abundance, size, and nutrient content may not only induce a VS of seed-dispersing species based on their resource requirements, but also have the potential to cause competition. For instance, all primate species in the Kibale National Park preferred to feed in higher strata when alone (Houle, Chapman, & Vickery, 2010). However, in the presence of dominant species that were able to monopolize the canopy as a feeding site, subordinates retreated to feeding sites in lower forest strata (Houle et al., 2010).

In summary, the availability of fruits in terms of fruit numbers, fruit sizes, and calorific value of fruits differ among forest strata. Many factors can potentially influence the actual patterns, including climatic conditions, phylogenetic diversity, and the floristic composition of the forest. Nevertheless, stratification of fruit resources obviously could influence the vertical niches of seed-dispersing species.

V. VS OF INTERACTIONS BETWEEN PLANTS AND SEED DISPERSERS

Understanding the structure of species interactions across vertical gradients is crucial in explaining global biodiversity patterns. Above, we have established that bird, bat, primate, and small mammal assemblages exhibit patterns of VS. Additionally, the quantity and nutritional value of fruits have been shown to vary along the vertical gradient. This leads to the assumption that these differences among forest strata may also affect plant–animal interactions, for instance in terms of interaction frequencies and mutual specialization, particularly concerning plants and their frugivorous seed dispersers.

Schleuning et al. (2011) reported that the degree of generalization in the plant–frugivore network in a Kenyan rainforest was vertically stratified, probably caused by the resource-oriented utilization of fruits. In the understory, opportunistic frugivores were abundant and, due to limited fruit choice and availability, were rather specific in their fruit choice. By contrast, obligate frugivores moved predominantly within the canopy, where they could forage on a large range of plant species with fleshy fruits (Schleuning et al., 2011). Consequently, the canopy network was composed of strong links and generalized associations, whereas the understory was characterized by weak links and more specialized associations (Schleuning et al., 2011). These findings are in line with a study of frugivore assemblages on Ficus trees (Shanahan & Compton, 2001). Figs of understory trees were mainly consumed by small non-flying mammal species and small bulbuls, whereas the larger figs of canopy species attracted a more diverse assemblage of large-bodied bird and mammal species (Table S2; Shanahan & Compton, 2001).

It becomes evident that seed-disperser and plant traits also differ among forest strata. Plant traits such as plant height, fruit morphology, and nutritional content are determinants of seed-disperser foraging behaviour and fruit-removal rates (Blendinger, Loiselle, & Blake, 2008; Muñoz et al., 2017). At the same time, seed-disperser traits such as body size, wing shape, and sensory and locomotory physiology determine their fruit choices and foraging height (Jordano, 1995; Bender et al., 2018). In mutualistic interactions such as seed dispersal, evolution will have favoured matching of traits between partners (Thompson, 2005). VS plays an important role in this diversification of plant fruit structures, dispersal devices, and disperser traits. First, plant height affects seed dispersers that have preferences for particular forest strata (Shanahan & Compton, 2001; Schleuning et al., 2011; Muñoz et al., 2017). In terms of trait matching, for instance, wing shape of avian seed dispersers was shown to be highly related to plant height (Bender et al., 2018). While rounded wings allow birds to forage in the dense forest understory, birds with pointed wings are better equipped to move quickly and forage in the canopy (Moermond & Denslow, 1985). Second, disperser seed consumption is also affected by fruit and seed size. Seed size can limit consumption due to morphological constraints of the frugivores (Jordano, 1995) and the importance of traits related to size matching in interaction networks is well established (Woodward & Warren, 2007; Maglianesi, Böhning-Gaese, & Schleuning, 2015; Bender et al., 2018). In vertically stratified forests, different sets of morphological traits have evolved among strata and VS appears to be an important factor shaping plant and seed-disperser traits and thus structuring the variety of their mutualistic interactions (see Table S2 and Section VI.2).

The VS of seed-disperser assemblages and their traits has implications for the plant species that depend on the dispersal of their seeds. In the canopy, the high abundance and diversity of obligate frugivores provides reliable seed-dispersal services for the trees (Schleuning et al., 2011) due to their generalized fruit choice (Loiselle & Blake, 1990; Carlo, Collazo, & Groom, 2003; Wallace, 2006). Dispersal by diverse frugivores might improve the quality of seed dispersal due to complementary effects (Fleming, 1993; Schleuning, Fründ, & Garcia, 2015; Rother, Pizo, & Jordano, 2016). Such complementary effects include different dispersal distances away from the mother plant and deposition in different microhabitats (Jordano et al., 2007). These effects are induced by differences in seed-disperser traits such as body size, feeding style, and mobility (Shanahan & Compton, 2001; Jordano et al., 2007; Kissling, Böhning-Gaese, & Jetz, 2009). Based on the diversity of seed-disperser traits in species-rich assemblages, canopy fruiting species were expected to achieve greater spatial homogeneity of seed rain (Shanahan & Compton, 2001). Furthermore, they were suggested to experience a higher dispersal probability and reliability (Shanahan & Compton, 2001). The larger fruits in

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the canopy tend to attract large-bodied frugivores (Lambert, 1989a; Kalko et al., 1996), which need to eat more fruits than small frugivores and thus are more reliable seed dispersers (Shanahan & Compton, 2001). Additionally, their gut passage time is longer and they travel further, whereby seeds are dispersed over larger distances (Lambert, 1989b). By contrast, plants in the understorey depend mainly on seed-dispersal services provided by rare and opportunistic frugivores, which are specialized on certain plant species which may result in a lower effectiveness of seed dispersal. Additionally, small understorey frugivores tend to have shorter gut passage times, resulting in shorter dispersal distances (Westcott & Graham, 2000).

The obligate and opportunistic frugivores of higher and lower forest strata, respectively, occupy a crucial ecological role as seed dispersers for tropical plant species. High abundance and generalized fruit choice of obligate frugivores could mitigate spatiotemporal variation in the abundance of consumer species and thus increase the robustness of seed-dispersal interactions (Schleuning et al., 2011). This might render canopy trees more resilient towards disruption such as habitat fragmentation, human interference, or the drop out of single dispersers (Farwig et al., 2006; Kirika et al., 2008a, 2008b). Seed-dispersal interactions in the under- and midstorey, by contrast, are far more sensitive towards species loss when they depend on fewer and more specialized species (Cordeiro & Howe, 2003; Schleuning et al., 2011).

VI. DISCUSSION AND OUTLOOK

(1) Patterns of VS across taxa and tropical regions

Communities of bird, bat, primate, and non-flying small mammal species are all vertically stratified in terms of abundance, species diversity, and community composition. When comparing patterns of VS across taxa, it becomes clear that these are influenced by different taxon-specific traits. For birds, body and wing size can to some extent constrain the use of certain vertical strata. Whereas birds are mostly active during daytime and visually oriented, bats are nocturnal and use of certain vertical strata. Whereas birds are mostly active during daytime and visually oriented, bats are nocturnal and constrained by their echolocation system in combination with their morphology. Finally, in primate and non-flying small mammal communities, VS, body size, and locomotor behaviour are strongly related (Fig. 1). So far, studies comparing VS among different seed-disperser taxa and examining, for instance, how they affect one another and how competition or interaction might shape their distribution across forest strata are very rare. One of the few examples of cross-taxa comparisons was conducted by Poulsen et al. (2002) who found that hornbills and primates utilize different kind of fruits, resulting in a rather low dietary overlap, and that hornbills feed in higher forest strata than primates.

In assembling studies for this review, a distinct geographical bias in favour of studies conducted in the Neotropics became apparent. Depending on the respective taxa, between 60 and 80% of all studies have been conducted in Neotropical forests (Tables S1 and S2). Although studies from Africa, Asia, and Australia report patterns of VS for communities of bird, bat, primate, and non-flying small mammal species comparable to those in the Neotropics, these conclusions are based on a relatively small number of studies. More research is needed to close this research gap on VS of seed-disperser communities in other tropical regions.

Nevertheless, despite the differences in biological characteristics of species, and incongruencies in sampling techniques, effort, and geographical distributional limits, it is evident that local species assemblages adjust to their vertically stratified environment.

(2) VS and trait evolution

VS influences the evolution of plant–animal trait pairs, for instance, plant height and wing shape, or crop size and body mass (Bender et al., 2018). Co-varying morphological character complexes (e.g. fruit size and colour) evolved in response to selection by particular groups of seed dispersers (Gautier-Hion et al., 1985; Fischer & Chapman, 1993; Shanahan et al., 2001; Hodgkison et al., 2007). It is conceivable that these character complexes respond also to VS of seed dispersers. Furthermore, additional fruit characteristics, for instance fruit odours, are likely to show patterns of VS. Different disperser groups like bats, birds, primates, and non-flying small mammals are attracted by different fruit scents. Primate-compared to bird-dispersed fruits, for instance, have especially rich odours, which are informative about ripeness (Nevo et al., 2016, 2018). Consequently, depending on the degree of specialization in plant–seed disperser networks, VS may also be expected in fruit odours.

Light environments are highly variable among forests and among forest strata (Endler, 1993). Perceived fruit colours depend on the interaction between the ambient light spectrum and the reflectance spectrum of fruits (Endler, 1993). Since the colour of fleshy fruits may have evolved to maximize visual detection by seed dispersers (e.g. Willson & Whelan, 1990; Schaefer, Schaefer, & Levey, 2004), and since fruit colour varies between bird- and primate-dispersed fruits (Valenta et al., 2018), VS in fruit colour can be expected.

Finally, plant species that provide fruits across all vertical strata (e.g. the Neotropical liana Marcgravia longifolia), and thus are subject to differential selection pressures from vertically stratified seed-disperser communities, represent test cases that allow the study of the role of VS on trait evolution.

(3) Effects of global change on vertically stratified forests and seed-disperser communities

(a) Local anthropogenic effects

Land-use changes – ranging from selective logging to habitat loss and fragmentation – are the main drivers of global change, threatening plant and seed-disperser communities
of tropical forest ecosystems (Vitousek et al., 1997; Sala et al., 2000). These drivers significantly alter forest structure, community composition of plants, sapling and tree densities, and understory density (Malcolm & Ray, 2000; Lelevre, Sharma, & Rodd, 2012). For instance, edge phenomena such as increased desiccation stress, wind shear, and wind turbulence (Laurance et al., 1997, 1998) sharply elevated the mortality of slow-growing, large-seeded, and high-canopy trees, and produced shifts in tree species composition and size distribution (Laurance et al., 2006). Large trees are also often removed in selectively logged forests, resulting in numerous openings in the forest canopy (Struhsaker, 1997). And while biological invasions are rare in undisturbed tropical forests, exotic species frequently invade disturbed tropical forests (Fine, 2002). Fast-growing pioneer tree and shrub species such as Syzygium jambos in Costa Rica (DI Stefano et al., 1998), Lantana camara in India (Joshi, Mudappa, & Shankar Raman, 2015), or Cecropia peltata in Malaysia (Putz & Holbrook, 1998) can rapidly change the structure and density of forest under- and midstoreys. Numerous studies have already shown that the susceptibility of seed dispersers to changes in forest structure and species composition differs among focal taxa and functional species groups (Medellin & Gaona, 1999; Farwig, Sajita, & Böhning-Gaese, 2008; Grass et al., 2014). Considering that global change affects the vertical structure of forest strata, these differences are likely even more pronounced in view of the VS of seed-disperser communities. However, studies investigating the effects of land-use changes on vertically stratified communities are very rare. In the Amazonian rainforest of Brazil, for instance, canopy-foraging bats were shown to be less sensitive to fragmentation than understory species, as they tend to be more mobile (Silva et al., 2020). Nevertheless, understory species also adapted to the higher post-fragmentation vegetation density of the understory by foraging higher (Silva et al., 2020). In the southwestern Central African Republic, decreased canopy cover following selective logging led to a shift in small-mammal biomass from the canopy stratum downward to the ground (Malcolm & Ray, 2000). In South India, a decline in tree cover with the subsequent invasion of L. camara selectively favoured avian seed dispersers adapted to lower vegetation, whereas forest specialists of the canopy declined (Aravind et al., 2010). Overall, understanding how global change effects impact the VS of seed-disperser communities of different taxa and functional groups remains an important challenge.

Agroforestry – intentional management of agricultural crops with shade trees – could constitute a compromise that allows reducing deforestation in the tropics, while simultaneously improving rural livelihoods (Ashley, Russell, & Swallow, 2006). For instance, bat and bird assemblages occurring in banana and multistrata cacao agroforestry systems in Costa Rica are abundant, species rich, and very diverse (Harvey, & González Villalobos, 2007). Similarly, mixed fruit orchards in Thailand harbour up to 50% of the bird species inhabiting neighbouring forests (Round, Gale, & Brockelman, 2006). Williams-Guillén et al. (2006) reported that shade coffee plantations with a high diversity of shade trees provide suitable habitat and serve as corridors between forest fragments for mantled howler monkeys Alouatta palliata. These and many other examples across the tropics show that agroforestry systems with diverse canopy cover and less-intensive management have high species richness, harbour significant parts of the local fauna, and could thus play an important role in biodiversity conservation [see Bhagwat et al. (2008); Udawatta, Rankoth, & Jose (2019) and references therein]. However, the implications of the simplification of the vertical structure, with a thinned canopy and a less-dense stratum below, for vertically stratified communities have not been studied in detail. Neither are there studies examining whether the tree species composing this simplified canopy layer still offer sufficient resources for the large seed-dispersing species foraging in the canopy, nor whether those systems with complete suppression of native understory vegetation still sustain species normally inhabiting the dense vegetation of the lower forest strata. Additionally, studies investigating how the associated changes affect the ecological functionality in plant–animal networks are urgently needed. For instance, Bakermans et al. (2012) highlighted the need implicitly to consider attributes of various forest strata. VS of coffee plantations with shade trees in the Venezuelan Andes contributed to a high diversity of migratory birds. Upper-canopy foragers were positively associated with the number of large trees and tree canopy height, and low-canopy and ground foragers with the number of small and medium-sized trees and shade cover (Bakermans et al., 2012). Furthermore, bats and birds react in different ways to the structural and floristic simplification in agroforestry systems (Faria et al., 2006). In shade cacao plantations in Brazil, bat assemblages are as species rich, diversified, and abundant as in pristine forests, and maintain all species and feeding guilds (Faria et al., 2006). For bats, the combination of a less-dense although still vertically stratified habitat with the maintenance of major food resources may even be beneficial as they can move and forage more easily (Faria et al., 2006). For the bird community, by contrast, the complete suppression of native understory vegetation leads to a decrease in forest-dependent species of the forest interior and an increase in edge and open-field bird species (Faria et al., 2006). These results show that the habitat modification in agroforestry systems affects various biological groups, and groups inhabiting the different strata, in different ways. Agroforestry systems cannot truly substitute the original forest, and, even though the importance of multistrata agroforestry systems is increasingly recognized (Young, 2018), more research is needed examining the effects of these systems on vertically stratified communities.

Besides agroforestry systems, secondary forests and tree plantations are expanding rapidly in the tropics (Mace, Masundire, & Baillie, 2005; Wright, 2005). Their contribution to offset biodiversity loss from deforestation has been suggested, as they apparently allow the survival of some forest species and furthermore, provide complementary benefits in
terms of ecosystem goods and services (Myers, 1997; Lindenmayer & Franklin, 2002). For instance, in the northeastern Brazilian Amazon, surprisingly high numbers of primary forest mammal and bat species were found in areas of native regeneration and exotic tree plantations with an understorey of native shrubs (Barlow et al., 2007). However, these areas were still surrounded by an intact forest matrix and furthermore, variability across taxa was high. In contrast to the findings for bats and mammals, the species richness of birds was significantly lower in secondary forests and tree plantations than in primary forests. Also, community composition differed between primary and secondary forests for all focal taxa (Barlow et al., 2007). In a review of tropical forest regeneration, Dunn (2004) concluded that species richness can be predicted to resemble that of primary forests roughly 20–40 years after land abandonment. Nevertheless, the recovery of community composition differed among taxa. For birds, it took much longer than the recovery of species richness [Dunn (2004) and references therein]. However, considering the VS of communities, conclusions for entire animal taxa are unlikely to be reliable. For instance, the early stages of forest regeneration only contain shrubs and small trees, but no high canopy layer. As tall canopies provide additional resources and greater vertical foraging space, they provide more opportunity for the coexistence of species than low-stature forests (Bakermans et al., 2012). It can be predicted that these early succession habitats are unable to support species normally inhabiting the canopy layer of tropical forests. Furthermore, with a low canopy height and less VS, the understory environment shows marked differences in temperature, light, and moisture conditions compared to primary forests (Lebrija-Trejos et al., 2011). Therefore, investigations about how these different environmental conditions affect understory species are needed. Generally, more studies are necessary that examine the relationship between vertically stratified communities and forest regeneration.

(b) Global effects

Global climate effects such as changes in temperature, precipitation, humidity, or extreme weather events are predicted to increase the damage to tropical rainforests (Wright, 2003; Malhi et al., 2009), but they might not be uniform across all vertical strata. The available evidence indicates that the three-dimensional structure and community composition of tropical forests are going to change. Rapid increases of aboveground biomass, stem density, basal area, recruitment, mortality, and the relative importance of lianas and canopy tree species at the expense of understory tree species have been recorded and are considered to be linked to rising atmospheric CO₂ concentrations and an increase in photosynthetically active radiation, although the actual mechanisms are still unclear (Phillips et al., 2002, 2004; Baker et al., 2004; Laurance et al., 2004; Lewis et al., 2004). Such changes in tropical forest structure will affect the vertical distribution of the associated seed-dispersing vertebrate communities. Furthermore, climate change is predicted also to affect plant phenology. For instance, an exclusion experiment in an eastern-central Amazon forest examining the effects of severe drought episodes on canopy dynamics, emissions of greenhouse gases, and other ecological functions demonstrated a thinning of the canopy and a decline of fruiting in the treatment plots (Nepstad et al., 2002). Significant and unexpected changes or crashes of fruit availability will greatly impact frugivorous vertebrates and thus seed dispersal (Butt et al., 2015; Morellato et al., 2016). It has been suggested that vertical movement along the gradient might allow more-flexible species to tolerate changes in temperature and to seek buffered conditions within particular microhabitats (Scheffers et al., 2017; Scheffers & Williams, 2018). Canopy visitors, for instance, might shift their vertical distribution downwards in response to droughts (Bickford, 2005; Scheffers et al., 2013). Canopy species, however, which specialize on particular resources in this stratum or are restricted in their usage of space by morphological traits, cannot easily translocate their habitat downwards. They may reach their thermal limit due to increasing droughts and dry seasons and thus, depending on how harsh the conditions become, may face extinction from the canopy layer of tropical forests.

(c) Impacts on plant–animal interaction networks

Ultimately, the impacts of the main drivers of global change are predicted not only to affect species abundances, community composition, and organismal physiology but also to cause serious alterations to the networks of interactions among species (Sala et al., 2000; Tyllianakis et al., 2008). We discussed above that the differences in responses of plant and animal species to drivers of global change may favour certain species or growth forms over others. As plant and animal communities are linked by their mutualistic relationships, negative effects on the composition of plants may ultimately cause changes in seed-disperser communities and vice versa (Lefèvre et al., 2012). Differences in the susceptibility of interaction networks to drivers of global change have already been suggested (Schleuning et al., 2011; Grass et al., 2014). For instance, networks comprising strong links and generalized associations seem to be less prone to disruption than those characterized by weak links and more-specialized interactions (Schleuning et al., 2011). However, the consideration that species and network characteristics and traits also differ among strata adds an additional layer of complexity to the variability of responses to environmental change. For instance, habitat modification in agroforestry systems may not strongly affect the networks of the canopy stratum but may represent a particular threat to the plant–seed disperser networks of forest understoreys. As the native understory vegetation is suppressed in agroforestry systems, this will result in a loss of understory seed-dispersing species specialized on particular understory fruiting plants. Threats to the network of the canopy stratum, by contrast, may be induced by other drivers of global change. On one hand, it has been argued that canopy trees are especially vulnerable to forest degradation, fragmentation, and selective logging.
(Bello et al., 2015). They often produce fruits with a single, large seed (Roth, 1987), which can only be dispersed by a small number of large-bodied frugivores (Levey, 1987; Peres et al., 2016; Whitworth et al., 2019). As large-bodied arboreal species in general face disproportionately high threats of extinction due to hunting and habitat loss, dependent canopy trees are at particular risk of losing their dispersers (Peres, 2000; Whitworth et al., 2019). On the other hand, canopy trees have been suggested to be more robust towards disruption when interactions in the canopy are generalized and the seeds of canopy-fruiting trees are dispersed by many different dispersers. This should render the plants more robust to the loss of single disperser species (Shanahan & Compton, 2001). However, if increasingly extreme temperatures and droughts in the canopy, due to climate change, cause the loss of many seed-dispersing species from this stratum, the plant species fruiting there will also be left with a reduced spectrum or even without dispersers. The consequences may include lower seedling establishment and survival, and ultimately decreased abundance of such dependent plant species (Bleher & Böhning-Gaese, 2001; Makana & Thomas, 2004). These examples show that the effects of different drivers of global change are likely to be extremely variable and may also differ among strata.

(4) High variability of data quality among taxa

Due to different taxon-specific characteristics and behavioural patterns, different sampling methods have to be used, resulting in highly variable data quality among groups. For birds, focal observations from the ground and canopy towers, complemented by mist netting, have led to reliable and large data sets, including high numbers of species. By contrast, for bats, primates, and non-flying small mammals, small sample size is a common problem. Studies on primates mostly rely on behavioural observations. These may be more difficult than focal observations of birds, as primate groups need to be habituated in order to follow them consistently through the forest. Inherently, this type of data gathering leads to rather small data sets based on few species and a limited number of individuals. The same problem applies to the nocturnally active bats and the frequently crepuscular non-flying small mammals. In order to investigate these species, capturing devices such as mist nets and traps need to be installed at varying heights in the forest. Difficulties in the placement and configuration of these devices complicate the achievement of large and reliable sample sizes and allow in most cases sampling of only a part of the local fauna and frequently not over the entire vertical gradient (Kalko & Handley, 2001). However, a number of recent methodological advances are promising. For example, with increased access to the canopy of tropical forests enabled by the expansion of infrastructure such as canopy towers, new equipment for rope climbing, and the use of drones, data collection in the canopies of tropical forests is constantly improving (Nakamura et al., 2017). At the same time, recent technological improvements in monitoring systems now enable the collection of a wide range of ecological data for terrestrial wildlife. For instance, camera traps have proved to be a useful, cost-effective, and relatively low-effort technique (Gregory et al., 2014; Moore et al., 2020). Furthermore, the development of automated radio-tracking systems (Gottwald et al., 2019) will likely allow us to determine the vertical movement patterns even of small animals (see Ripperger et al., 2020) in the near future and thus will provide an increasingly detailed view of vertical movements of individual animals.

(5) Outlook

Understanding the importance of VS for mutualistic interactions requires data at a high resolution along the vertical gradient, and remains an important challenge particularly in the context of global change. Future investigations should focus on answering the following questions.

(1) How common is VS of interaction networks such as observed by Schleuning et al. (2011) across tropical forest ecosystems?

(2) Does VS in the vegetation structure exert selection pressures on associated seed dispersers (and other groups of animals)?

(3) What is the role of competition versus mutualistic interactions among taxa in shaping the distribution of plants and their seed dispersers among forest strata?

(4) Do seed-dispersing species shift strata at different times of the year in response to phenological changes in food availability?

(5) If an attractive food resource is available beyond the preferred stratum, do species acting as seed dispersers still remain within their preferred vertical niche?

(6) What are the consequences of changing interaction frequencies and degree of mutual specialization across strata for the species involved and for whole networks?

(7) Do networks in higher strata have higher robustness towards disruption and the drop out of single species? Does high biodiversity across strata enhance the resilience of seed-dispersal mutualisms to global change?

(8) How will global change affect VS, biodiversity, and species interactions such as seed dispersal, and are these effects similar or different among tropical regions and ecosystems?

VII. CONCLUSIONS

(1) The importance of VS as a crucial determinant of species richness and diversity in tropical forests is undeniable. The structural complexity of tropical forests creates vertically stratified ecosystems with a broad range of environmental conditions, for example, in microclimate and light. This allows for the coexistence of species with largely similar ecological requirements.
by forming stratified communities along the vertical gradient.

(2) Plant–seed disperser interaction networks and the degree of specialization and interaction strength within these networks change across the vertical gradient. In vertically stratified forests, different sets of morphological traits have evolved among strata and VS appears to be an important factor in shaping plant and seed-disperser traits and thus structuring the variety of their mutualistic interactions.

(3) Global change is likely to affect and alter patterns of VS in tropical forests, but further research is needed. Examining the links between species’ distribution, dispersal capabilities, and plant–seed disperser interactions at fine spatial scales and across the vertical gradient will be crucial. Answering these questions in complex tropical forests requires the establishment of long-term monitoring programs including vertically stratified surveys.

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