Species Diversity of Canopy Versus Understory Trees in a Neotropical Forest: Implications for Forest Structure, Function and Monitoring

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ABSTRACT

Species composition and diversity of the canopy layer of tropical forests have rarely been described, yet they are important to many aspects of ecosystem structure and function. Species composition was compared among canopy trees (defined as sun-exposed crowns), understory trees, trees ≥10-cm diameter at breast height (DBH), and the tree community as a whole in a Neotropical moist forest. High-resolution stereophotographs were used to map all individual canopy tree crowns in 8.6 ha of a 50-ha forest dynamics plot on Barro Colorado Island (BCI), Panama. The canopy was found to have high species diversity in relation to the understory and the whole forest. Only 5% of the stems were found in the canopy, but it contained 70% of the species. Diversity, standardized by stem count, for the canopy (≈135 species per 1000 trees) was higher than that of the forest as a whole (≈108 species per 1000 trees), and species composition was different between the two communities. Although only 50% of trees ≥10-cm DBH, the typical size range used in many forest inventories, were in the canopy, the species diversity and composition of the canopy and trees ≥10-cm DBH were nearly identical. The percentage of gap species in the canopy increased with tree size, providing evidence of the dynamic nature of the BCI forest. To the degree that tree function, such as carbon uptake and transpiration, vary among species, the rarified species richness of the canopy will generate high functional diversity at local-to-landscape scales.

Key words: species diversity; forest canopy; forest dynamics; crown layers; forest structure; stereophotographs; remote sensing; tropical forest.

INTRODUCTION

The forest canopy, the single layer of the sun-exposed trees that forms the forest's boundary with the atmosphere, is particularly important because of its contribution to ecosystem function. Canopy trees include the largest trees in the forest and thus contribute a large amount of the biomass in many forests (Chave and others 2003, 2008). By forming the outer envelope of the forest, the canopy plays a key role in the exchange of water and energy with the atmosphere (Calder 2001; Ozanne and others 2003). The proportion of total forest carbon uptake by the canopy layer is enhanced because canopy trees receive direct sunlight (Ellsworth and Reich

1993), and water and carbon uptake scales with tree size (Meinzer and others 2001). The canopy also supports a disproportionate amount of biodiversity of plants and animals (Ozanne and others 2003). To the degree that functions vary among canopy species (Ruiz-Jaen and Potvin 2010; Morin and others 2011; Schwendenmann and others 2014), species diversity of the canopy may have a greater impact on some ecosystem functions than overall forest diversity.

Although it is well known that tropical forests have high overall plant diversity, and the diversity of organisms that use the canopy, such as arthropods (Basset and others 2003) and epiphytes (Nieder and others 2001), are often reported, few studies have quantified species diversity of trees in the canopy (Broadbent and others 2008). Instead, tree diversity is usually reported for different diameter classes. Often trees over a certain diameter threshold (for example, 20 cm—Hubbell and Foster 1983, p. 30 cm—Ter Steege and others 2006, 40 cm—La Frankie and others 2006) are assumed to be in the canopy. In a number of global tropical forest inventory plots that measure trees ≥1-cm diameter at breast height (DBH), between 36% and 71% of the species were present in trees ≥30-cm DBH (Losos and Leigh 2004). However, using a single DBH as a canopy–understory threshold may not be accurate to describe the canopy layer because regenerating forest patches have small trees with sun-exposed crowns, whereas tall mature forest may have large trees that are completely shaded. For many tropical forest inventory plots, only trees ≥10-cm DBH are measured. Networks of these plots have been used to describe diversity, structure, and dynamics of tropical forests on local-to-regional scales (Phillips and others 2004; Lewis and others 2013; ter Steege and others 2013). It is unclear whether trees ≥10-cm DBH represent predominantly canopy trees or a more equal mix of canopy and understory trees.

How canopies compare to whole forests is applicable to remote sensing as well, which is now widely used for landscape-to-regional studies of forest structure and function (Chambers and others 2007). In dense tropical forests, the signal measured by remote-sensing devices is primarily determined by properties of the upper canopy, which reflects the most energy back to the sensor (Gastellu-Etchegorry and others 1999; Guillevic and Gastellu-Etchegorry 1999). There is a growing interest in using remote sensing to estimate biodiversity (Gillespie and others 2009; Baldeck and Asner 2013), but it is important to understand what portion of the forest's diversity is measured by different remote-sensing techniques.

How canopy and understory tree communities compare is highly relevant to studies of forest dynamic processes. Differences in species compositions between the canopy and understory may be an indicator of filtering processes, such as density dependence through multiple life stages, at work in the ecosystem. Density-dependent processes should reduce the conspecific clumps that form in seedlings and saplings as a result of dispersal limitations, and thus lead to a canopy that has greater species evenness than the understory (Condit and others 1996b; Gonzalez and others 2010; but see Baldeck and others 2013). The differences in canopy and understory functional group composition are also a product of gap dynamics and forest succession and thus may indicate the types of successional processes occurring in this forest. For example, the species composition of the canopy and understory should be similar, particularly in tall areas of forest versus recent gaps, if the forest has reached a late-successional equilibrium (Oliver and Larson 1996). Large differences may indicate non-equilibrium conditions, which may be characteristic even of old-growth tropical forests (Sheil and Burslem 2003; Baker and others 2005).

Here, I present the first detailed measurement of species diversity and composition of a tropical forest canopy compared to that of the understory and the whole forest to test the following hypotheses:

(1) The canopy has substantially *lower species richness* (total number of species) than the understory because guilds of short-statured, shade-tolerant tree species never reach the canopy. If only tall and mid-sized tree species reached the canopy, then the canopy would contain 64% of all tree species based on a classification of adult stature of at the study site (Condit and others 1996a).
(2) *Species evenness* is greater for the canopy than for the understory due to processes such as conspecific density-dependent mortality (Condit and others 1996b; Gonzalez and others 2010).
(3) The percentage of the canopy composed by gap species decreases as local forest height and maximum tree diameter increase, which is a proxy for time since disturbance (Hubbell and others 1999). The canopy of recently disturbed, short-statured forest will be dominated by fast-growing gap species. As stand development

proceeds, the gap species dominating the canopy will be replaced by shade-tolerant species in the canopy.

(4) Trees ≥10-cm DBH, which are the only trees measured in many tropical forest inventory plots and used to determine regional diversity estimates, contain both canopy and understory trees, and thus have an intermediate species diversity between these two groups.

I use a unique data set to quantify the species diversity of the canopy, understory, and whole forest of 8.6 ha of the 50-ha Forest Dynamics Plot of Barro Colorado Island (BCI), an old-growth tropical moist forest that has not had large-scale disturbance for about 500 years (Piperno 1990), and where stems ≥1-cm DBH have been mapped and identified to species. For this area, each sun-exposed tree crown was delineated from stereophotographs and linked, via ground-truthing, to a stem map of the 50-ha plot. I also used a canopy structure model that predicts which trees occupy the canopy versus understory (Bohlman and Pacala 2012) to extend the analysis to the whole 50-ha plot to test if the patterns observed in the 8.6-ha area are generalizable to a larger area.

MATERIALS AND METHODS

Site Description

The data for this study were collected on Barro Colorado Island (BCI) (9°09′N, 79°51′W), Republic of Panama, a 15-km^2 island covered with semi-deciduous lowland moist forest located in the Lake Gatun section of the Panama Canal. The old-growth forest on the island is believed to have been mostly free of agricultural clearing during the past 1500 years, and has a minimum age of 500 years (Piperno 1990). The island receives an average of 2650 mm year^{-1} of rainfall. Between 1980 and 1982, a 50-ha permanent plot was established in which every stem ≥1-cm DBH was mapped and identified to species level, and its DBH was measured. Every 5 years, the DBH values of all trees have been re-measured, and the tree mortality and recruitment into the 1-cm DBH class were recorded. Maximum canopy height averages approximately 30 m, and there are on average three canopy layers (Bohlman and Pacala 2012). Detailed descriptions of BCI and the 50-ha plot can be found in Hubbell and Foster (1983), Leigh (1999), and elsewhere.

Aerial Photos

In September 2000, high-resolution stereo aerial photographs were taken using a 70-mm Rolleiflex 6006 metric camera with an 80-mm planar lens stabilized by a Kenyon Gyro stabilizer and suspended from a Hughes 500 helicopter. A Collins dual-antennae radar altimeter was used to maintain the helicopter at a constant altitude. Adjacent photos had at least 60% overlap. Targets, which were 2 × 3 m^2 white sheets with black bull's eyes painted on them, were suspended 1–2 m above the ground in large tree fall gaps within the plot to serve as ground control points. Photos were taken at two different altitudes and thus at two different scales. Photos with 1:12,000 scale, in which three or more targets were visible, were used for aerial triangulation to the ground control points. Photos with 1:6000 scale were used for digitizing crown characteristics.

A standard bundle adjustment on the 1:12,000-scale photos was used to transform the coordinates of the photos to the coordinates of the plot (Wolf and Dewitt 2000). The ground control of the 1:12,000-scale photos was then bridged to the 1:6000-scale photos using five or more features, such as tree branches, which were clearly visible on both sets of photos. The deviations in the triangulation of 1:12,000-scale photos to the ground control targets averaged 0.278 m, 0.327 m, and 0.634 m in the X, Y, and Z coordinates, respectively. The deviations in bridging from the 1:12,000 scale to the 1:6000 scale averaged 0.41 m, 0.57 m, and 1.23 m in the X, Y, and Z coordinates, respectively. A contiguous 10.9-ha area of the plot with the best photograph quality was chosen for analysis.

Crown Map

Tree height and sun-exposed crown area (ECA) of individual trees crowns in the 10.9-ha area of the plot were digitized manually using an analytic stereo-plotter (AP190, Carto Instruments, Vashon, Washington, USA) in which the forest canopy can be viewed in three dimensions. Each crown's outer boundary, maximum height, and location of the maximum tree height were digitized. When multiple photo pairs were available for the same crown, the photo pair in which the crown was closest to the center of the photo pair was chosen to reduce distortions in crown shape due to off-nadir viewing angles at the edges of photos. Between 2002 and 2004, images of the 1:6000 photos with the digitized crown boundaries overlain were taken into

the field to determine which tagged tree stems linked to which digitized crowns. Each crown was checked at least twice to confirm the stem-to-crown association. Incorrectly digitized crown boundaries were re-mapped based on field observations. After all possible crowns were linked to tags, a crown map with each crown identified with a tag, species, and DBH taken from the stem database was generated (Figure 1).

All tree crowns visible in the photos and identified to a tag were considered to be in the canopy, that is, they are sun-exposed when the sun was directly above the tree. All the stems that were not linked to a crown in the crown map were assumed to be in the understory, that is, the crown had no sun exposure when the sun was directly overhead. Areas in which crown-to-stem assignment was difficult, typically areas containing many small crowns interconnected by lianas, were excluded from the analysis. These ''no identification'' areas covered 2.3 ha out of the total 10.9 ha, which resulted in 8.6-ha area that was used in this analysis.

Forest Structure Model

The digitized crown map covered less than 20% of the plot. To investigate the general applicability of the results from the area with stereo photos to the whole plot, the Perfect Plasticity Approximation (PPA) forest structure model (Bohlman and Pacala 2012) was applied to the 2000 census data to estimate which trees were in the canopy and understory for the whole 50-ha plot. The 50-ha plot was subdivided into 31.25 x 31.25 m subplots, which defines the area of competition among trees (Bohlman and Pacala 2012). In the PPA crown

structure model used here, each crown's shape is modeled as a flat disk with height and crown area determined by allometric relationships with the tree's DBH (Bohlman and Pacala 2012). The assignment of crowns to the canopy or understory is determined by first sorting all trees from a plot from the tallest to the shortest in each subplot. Starting from the tallest, the crown area of each successive tree is assigned to the canopy layer until the cumulative canopy crown area fills the whole plot, thus creating a single full layer. The last tree to ''enter'' the canopy layer, that is, the shortest tree in the canopy layer, defines the height above which all trees in the subplot are in the canopy and below which all trees are in the understory. Additional information about the model can be found in Bohlman and Pacala (2012).

Analysis

Species richness was compared for both the 8.6-ha area where crowns were determined to be in the canopy or understory directly from photos, and the whole 50-ha plot, where canopy versus understory occupancy was determined from the PPA model. For both the 8.6-ha area and the whole 50-ha plots, species richness was compared for several layers of the forest: the canopy, the understory, the whole forest (all trees ≥1-cm DBH), and trees ≥10-cm DBH. Total species richness was estimated using the non-parametric, abundance-based Chao1 estimator with log-linear 95% confidence intervals (Chao 1987) calculated using the program Estimate S (Colwell 2013). Species–abundance curves were calculated for the different canopy layers as well. The number of trees was calculated as a series of
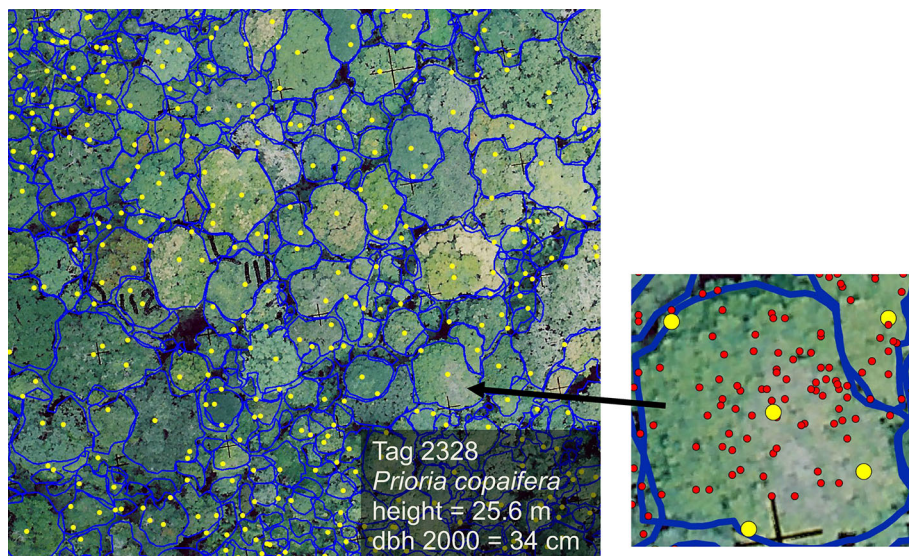

Figure 1. Stereo photos with crown boundaries in *blue*. The *yellow circles* are the locations of the trunks of canopy trees. The *red circles* are the locations of the trunks of understory trees. The information of one crown is highlighted in the *lower right corner* (Color figure online).

Tag 2328
Prioria copaifera
height = 25.6 m
dbh 2000 = 34 cm

exponentially increasing sets of trees. Trees were drawn from a circle surrounding randomly chosen points in the plot, with the circle's radius being large enough to exactly encompass the given set of trees, whose locations were recorded as a single point in the plot regardless of the trees' basal area. The number of samples drawn for each set of trees was determined by dividing the total number of trees in the whole plot by the number of trees in the sample. Mean and 95% confidence intervals were calculated for each layer.

As a measure of species diversity that takes evenness into account, the bias-corrected estimate of Shannon entropy of Chao and Shen (2003) was calculated for each layer and for 5-cm DBH classes to determine how species diversity compared between the canopy and understory, independent of tree size. The exponent of Shannon entropy generates the "effective number of species" (Jost 2006), which is the number of equally abundant species required to yield the species abundance profile of the sample. Given the same species richness, a community with less even abundances among species will have a lower effective number of species than a community with more even abundances. To eliminate differences in sample size for the 5-cm DBH classes, an equal number of trees were drawn randomly from both the canopy and the understory and the effective number of species computed. This was repeated 1000 times for each DBH class and canopy layer, and means and standard deviations were calculated. The R package 'entropy' was used.

To compare overlap in species composition between the canopy and understory, the Morisita-Horn similarity index, which is based on the probability that single individuals drawn from two communities are the exact same species, was used (Chao and others 2005). The canopy and understory layers had different numbers of individual trees, and the Morisita-Horn index is relatively robust to different sample sizes (Chao and others 2006). Mean and variance in similarity between the canopy and understory layers in 5-cm DBH classes were calculated in fifty 1-ha subplots of the 50-ha plot. The similarity between different layers was reported such that zero represented complete dissimilarity, and one represented complete similarity. The R package 'vegan' was used.

To compare how different functional groups of species (Poorter 2007) varied between the canopy and understory, species were classified according to adult stature (tall trees, mid-sized trees, treelets, and shrubs) and regeneration requirement (light-demanding, intermediate, and shade-tolerant trees) (Condit and others 1996a; Bohlman and O'Brien 2006). Functional group composition, based on the number of stems in each category, were also calculated in different 5-cm DBH classes. For canopy trees, this showed the functional group compositions at different forest successional stages, assuming that maximum DBH locally (represented by the canopy trees) increased with the successional stage.

RESULTS

Species Diversity

There were 35,507 trees and 246 species ≥1-cm DBH in the 8.6-ha area covered by the stereo photos. A small fraction of trees (5%), but a large majority of species (70%), were found in the canopy (Table 1). Estimated species richness was significantly different between the canopy versus understory and the canopy versus all trees, as their 95% confidence intervals did not overlap (Table 1). Estimated species richness was not statistically different between the understory and all trees. Sixty-four percent of all species were categorized as tall or mid-sized, and thus would be expected to have individuals in the canopy. However, while 87% of the tall and mid-sized species were found in the canopy, nearly half of the treelet species and a quarter of the shrub species also had at least one individual in the canopy (See Table S1 in the Supporting Information). For nearly all comparisons of species richness between different layers of the forest, similar results were found for the 8.6-h photo area and the whole 50-ha area where canopy status was determined by the canopy structure model (Table 1, Table S1).

The species–abundance curves showed 30% higher rarified species richness for the canopy compared with the whole forest or understory for the 8.6-ha area, and 15–20% more for the 50-ha plot (Figure 2, Figure S1). At all abundance levels, the canopy and understory 95% confidence intervals were non-overlapping. Finally, the number of effective species was nearly twice as large for the canopy (71.4) as that for the understory (38.9) or whole forest (42.7), indicating greater species diversity in the canopy when both species richness and evenness are taken into account (Table 1).

Greater diversity in the canopy than the understory was primarily because the canopy had more stems in the size category with the highest species diversity. For both the canopy and understory, the effective number of species peaked in the DBH range between 15 and 25 cm (Figure 3, Figure S2).

Table 1. Species and Stem Counts, Estimated Species Richness and Effective Species Number (Exponent of Shannon Entropy) in Different Forest Layers and Size Categories

	All	Canopy	Understory	≥10-cm DBH
8.6 ha				
Observed number of species	246	172	236	181
Number of stems	35,507	1803	33,704	3294
Estimated species richness	288.0	206.2	258.1	202.4
Estimated richness lower 95% CI	262.1	187.7	242.8	189.6
Estimated richness upper 95% CI	355.6	246.1	297.3	234.0
Effective number of species	42.7	71.4	38.9	68.7
50 ha				
Observed number of species	302	226	297	228
Number of stems	213,791	13,151	200,640	21,204
Estimated species richness	330.9	245.3	316.5	233.5
Estimated richness lower 95% CI	312.1	232.9	304.1	229.6
Estimated richness upper 95% CI	384.8	280.0	350.5	247.6
Effective number of species	50.9	74.2	47.0	71.2

The 8.6-ha area coverewith high-resolution aerial photographs where trees were observed directly to be in the canopy or understory (canopy status). The 50-ha area covered the whole forest dynamics plot, and the canopy status was determined from the PPA model. Percentages show the percent values of all stems or species (trees ≥ 1-cm DBH) found in each layer or size category. Non-overlapping 95% confidence intervals for estimated species richness (using Chao1 estimator) between different layers/size categories indicate a conservative interpretation of significant differences in estimated species richness (Gotelli and Colwell 2011).
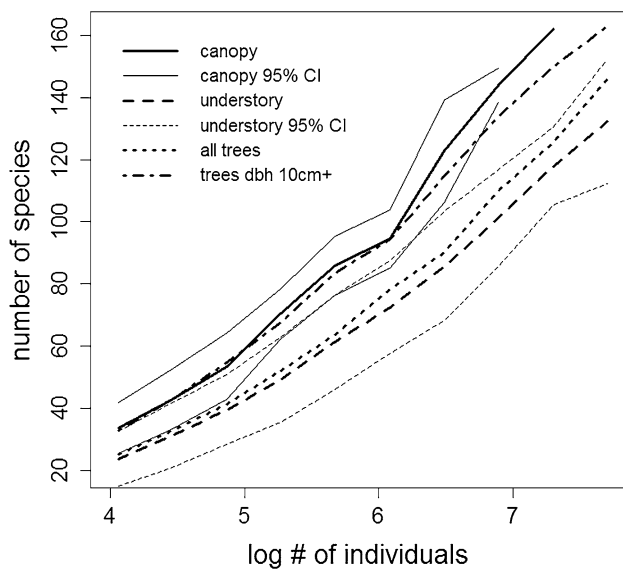

Figure 2. Species–individual curves for different layers and size categories for the 8.6-ha area mapped with high resolution aerial photographs where trees were observed directly to be in the canopy or understory.

Less than 2% of the understory stems are in this DBH range of maximum diversity, but 25% of the canopy stems are 15–25-cm DBH.

Species Composition

As measured by the Morisita-Horn index, the figures for similarity in species composition between the canopy and understory were 0.41 for the 8.6-ha area and 0.52 for the whole 50-ha plot (mean ± SD; 0.67 ± 0.14 for 50 1-ha subplots; Table S2). Four species were among the 10 most abundant in both the canopy and the understory. These species were *Alsies blackiana*, *Faramea occidentalis*, *Tetragastris panamensis*, and *Trichilia tuberculata* for the 8.6-ha area, and *A. blackiana*, *F. occidentalis*, *Hirtella trianda*, and *T. tuberculata* for the 50-ha area (Table S3). Within narrow DBH classes, similarity peaked above 0.70 for trees 5–15-cm DBH, then decreased steadily for those above 15-cm DBH (Figure 4). *A. blackiana* and *T. tuberculata* were among the 10 most abundant species for nearly every DBH size class in both the canopy and understory (Table S3).

Functional Group Composition

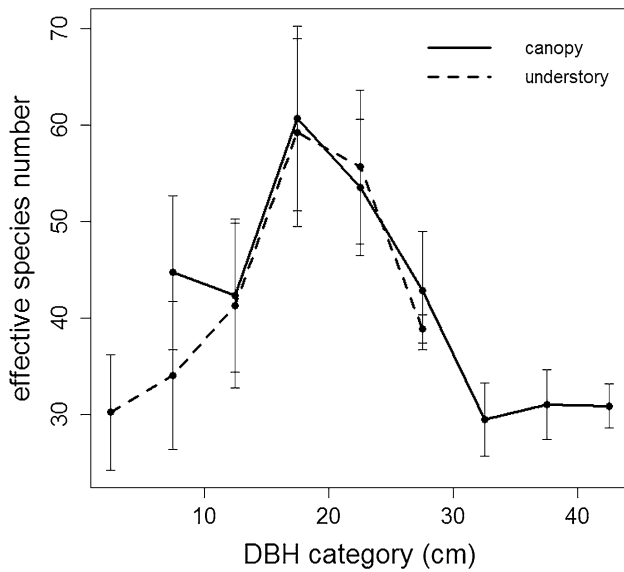There were pronounced differences in functional compositions between canopy and understory.

Figure 3. Effective number of species at different diameters (5-cm DBH classes) for the 8.6-ha area covered by the high-resolution aerial photographs. Trees were observed directly to be in the canopy or understory. Effective species are the number of equally abundant species required to yield the species-abundance profile of the sample. Standard deviations are based on 1000 draws of equally sizes from the canopy and understory layers.
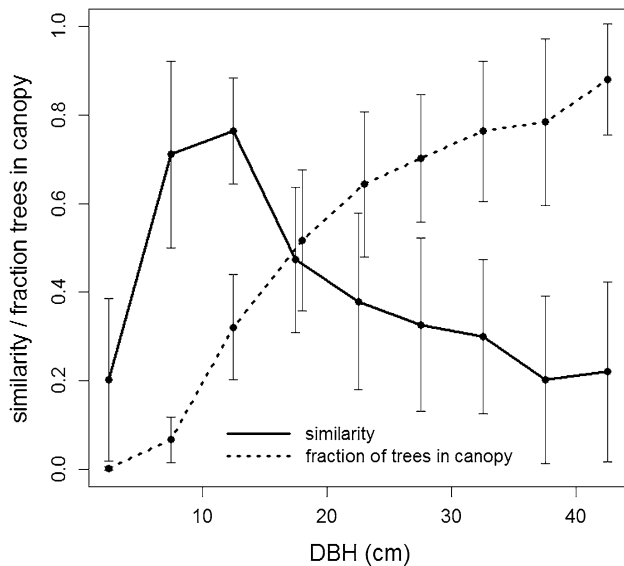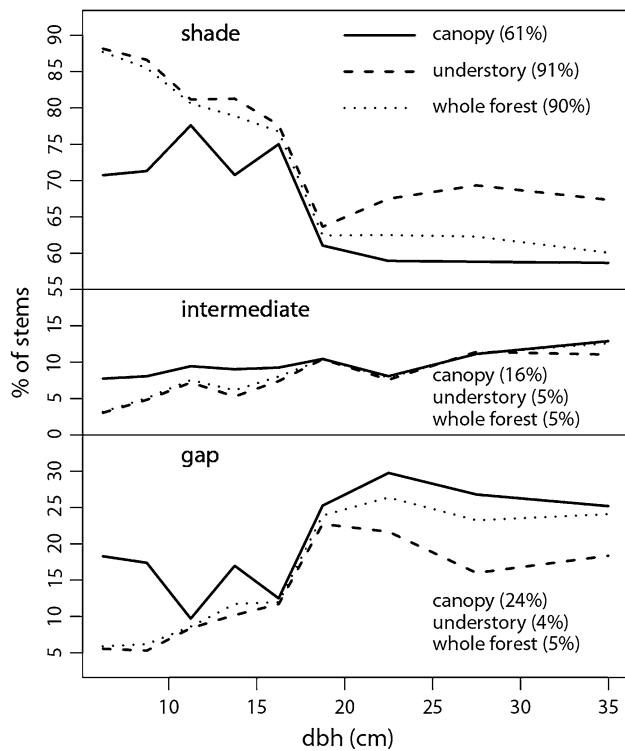

Figure 4. Fractions of trees in the canopy and similarity in species composition between the canopy and understory layers in 5-cm DBH classes calculated in fifty 1-ha subplots of the 50-ha plot. Species similarity was determined using the Morisita-Horn Index in which increasing values indicate increasing similarity. *Error bars* show the standard deviation.

Compared with the understory, gap-dependent and intermediate shade-tolerant species were overrepresented in the canopy, whereas shade-tolerant species were underrepresented (Figure 5, Table S4). Tall-statured species numerically dominated the canopy, whereas all adult-stature categories were fairly evenly represented in the understory (Table S4). For all 5-cm DBH classes, the canopy had larger percentage of gap trees, and the understory had more shade-tolerant trees, except between 15 and 20 cm where the shade tolerance compositions of the canopy and understory were very similar (Figure 5; Figure S3). Contrary to the expectation, the percentage of canopy stems composed of gap and intermediate light-demanding species increased with DBH (Figure 5; Figure S3).

Conversely, the largest understory trees, which presumably form the mid-story that will replace some fallen canopy trees in the future, has a much higher percentage of shade-tolerant trees than the canopy trees at the same height.

Trees 10-cm DBH and Larger

About 50% of the trees ≥10-cm DBH had sun-exposed crowns and thus were in the canopy layer (Table 1). Nevertheless, trees ≥10-cm DBH and canopy trees had similar species richness (Table 1) and functional group composition (Table S4), had a high Morisita-Horn index of similarity (>0.90; Table S2), and shared most of the top 10 species, in

Figure 5. Species' regeneration requirement for different size categories of trees in the 8.6-ha area of the BCI 50-ha forest dynamics plot where high-resolution aerial photographs allowed direct observation of which trees were in the canopy and understory. In parentheses are the percentages of stems in each functional group over all diameters. For all stems ≥10-cm DBH, the percentage values of trees in each functional group were 17% gap, 13% intermediate, and 70% shade.

terms of both number of stems and basal area (Table S3). The species richness values between trees ≥10-cm DBH and the understory, and between trees ≥10-cm DBH and the all trees, were significantly different (Table 1). The species–abundance curves for trees ≥10-cm DBH and canopy trees were nearly identical, but trees ≥10-cm DBH had greater species richness per standardized stem number than the understory or whole forest (Figure 2, Figure S2). About a quarter (27.5%) of the trees ≥10-cm DBH that were not in the canopy (thus in the understory) belonged to just two species: *Trichilia tuberculata* and *Alseis blackiana*.

DISCUSSION

How do the species diversity and composition of tropical forest canopy relate to those of understory and the whole forest is an important yet unanswered question, relevant to many aspects of ecosystem structure and function. Species richness in the forest canopy was slightly higher than that hypothesized from functional group composition alone (70% actual versus 64% for just tall and mid-sized species). As expected, species evenness was higher in relation to the understory and the whole forest. Trees ≥10-cm DBH, which is a standard size for tropical forest inventories, had nearly identical species diversity to the canopy layer despite including twice as many stems as those of the canopy

layer. The canopy had a higher percentage of gap- and tall-statured species than the understory as expected, but surprisingly, the percentage of gap species increased with tree size, providing evidence of the dynamic nature of the old-growth BCI forest as discussed below.

Canopy Species Diversity and Function

The canopy layer of the BCI 50-ha plot has extraordinary diversity by multiple measures. It contains less than 5% of the stems in the 50-ha plot but includes 75% of the species. When standardized for the number of stems, species richness is greater for the canopy than the understory or whole forest. Indeed, the higher diversity in the canopy versus the understory mirrors the diversity patterns found in some other life forms, such as arthropods (Basset and others 2003) and epiphytes (Nieder and others 2001), for which the canopy layer provides habitat. The high species diversity of the canopy has numerous implications for ecosystem structure and functioning because canopy trees can contribute toward the majority of carbon uptake, biomass, rainfall interception, and transpiration, among other functions in tropical forests. To the degree that these functions vary among species, the high diversity of the canopy will generate high functional diversity at local to landscape scales. For example, variations in allometry and wood density

among canopy species will contribute to spatial variation in biomass (Chave and others 2003). The species diversity in the canopy may provide spatially heterogeneous responses to perturbations, such as drought and wind (Zimmerman and others 1994; Condit and others 2013). High canopy species diversity will also create heterogeneity in microhabitats used by forest animals and plants (August 1983; Andrade and Nobel 1997).

Why is the Canopy Diverse?

The greater species diversity in the canopy than the understory is consistent with the increasing species diversity during the transition from sapling-to-adult tree stages found by Condit and others (1996a, b) and Gonzalez and others (2010) for BCI and French Guiana, respectively. The proximate reason for the greater diversity in the canopy layer is that the canopy has a larger percentage of stems than the understory in the most diverse size class of the forest (15–25-cm DBH). What causes species diversity to peak between 15 and 25-cm DBH? In seedlings, species richness is high because all species recruiting to the forest are present, but species evenness is low (Comita and others 2007) due to differential seed production among species (Wright and others 1999, 2005) and clumped dispersal (Seidler and Plotkin 2006). Negative density dependence and storage effects increase species evenness with size, whereas habitat filtering and competition may decrease species richness and evenness with size (Gonzalez and others 2010). These mechanisms are undoubtedly operating simultaneously, but may have different strengths at different sizes.

Negative density dependence, reported to be the strongest at small sizes (Wills and Condit 1999), causes decreased within-species clumping between the sapling and adult stages (Condit and others 2000; Bagchi and others 2011) and is likely to be contributing to the increase in species evenness up to 15–25-cm DBH. Baldeck and others (2013) found no evidence of differences in habitat associations among size classes, and thus no evidence of habitat filtering, above 1-cm DBH. However, habitat associations may still contribute to the observed differences between the canopy and understory in species richness, standardized for stem density, due to differences in stem density between the forest layers. Compared with the understory, the same number of trees in the canopy covers a much larger area and potentially wider array of habitats than those in the understory. To encounter 100 species requires 2 ha of canopy versus 0.2 ha of understory on BCI. Thus, the canopy's lower stem density, along with habitat heterogeneity, may elevate stand- to landscape-level species diversity of the canopy compared with the understory.

The decline of species diversity for trees ≥25-cm DBH may be partly due to loss of short-statured species at larger diameter sizes (Condit and others 1995). In addition, for the understory, there may be a limited number of species that can survive in the shade of the understory at large sizes. Only two species, *Trichilia* and *Alseis*, compose a significant percentage of large trees (20–30% of trees ≥10-cm DBH) that occurred in the understory.

Species Similarity

Similarity in species composition between the canopy and understory was low, which was consistent with the dominance of shade-tolerant, short-statured species in the understory; and gap, intermediate-light demanding, and tall-statured species in the canopy. Within just narrow DBH classes, the similarity between the canopy and understory was much higher and peaked in the 5–15-cm range. High similarity between the canopy and understory below 15-cm DBH may be related to gap formation processes. In the newly created gaps, understory trees that grew under the fallen canopy crowns often survive with crowns intact, or re-sprout new crowns (Paciorek and others 2000; Dietze and Clark 2008). Thus, a new canopy of sun-exposed short-statured trees may be created with a species composition resembling the understory of mature forest. As time passes after gap formation, the released trees and new recruits of light-demanding species will outgrow shade-tolerant species (Davies 2001; Gilbert and others 2006), thus stratifying the former gap into gap and understory, and likely decreasing species similarity between the canopy and understory layers at larger tree sizes.

Forest Inventory Plots and Remote Sensing

Because of difficulty in measuring all trees in tropical forests, alternative methods are often used to assess diversity, such as censusing just trees above a certain size threshold or using remote-sensing techniques. The results here suggest that forest inventory plots where only samples of trees ≥10-cm DBH are considered accurately represent the species diversity of the canopy, but not the understory nor the whole forest, which is dominated in terms of stem density by the understory in mature, moist tropical forests. The species richness and diversity,

and species and functional-group compositions, of canopy trees and trees ≥10-cm DBH had similar overall properties, even though only half the individuals ≥10-cm DBH were found in the canopy. The results here suggest that plots with trees ≥10-cm DBH also sample the DBH range (15–25-cm DBH) with the greatest number of effective species (the number of equally abundant species required to yield the species abundance profile of the sample). However, because the statures and size distributions of different forests vary, the link between trees ≥10-cm DBH trees and canopy diversity, as well as the DBH range of greatest tree diversity, may also differ among tropical forests.

Remote sensing is increasingly used to measure and model species diversity (Gillespie and others 2009). Our study suggests that species diversity measured by remote-sensing devices, particularly optical remote-sensing platforms that detect primarily the canopy layer, would include a majority of the species in the whole forest, have equal or greater per stem diversity as the whole forest, and match up well with diversity estimates from forest inventories of trees ≥10-cm DBH.

Implications for Forest Succession

The canopy of the forest in this study, often considered old growth, was dominated by gap and intermediate light-demanding species (50% of exposed crown area), and the percentage of gap species in the canopy *increased* with the canopy height. This is not expected in a mature-phase forest according to forest successional theory, which posits that shade-tolerant species should dominate the canopy of old-growth forests (Oliver and Larson 1996). There may be multiple mechanisms to explain this pattern. A small number of light-demanding, long-lived species on BCI have large individuals in the canopy but few recruits in the forest (Knight 1975; Condit and others 1998). As there is no evidence of human disturbance in this forest for at least 500 years (Piperno 1990; Sheil and Burslem 2003), these large trees probably recruited to the forest during a large-scale human disturbance centuries ago or during rare, large wind blowdown events that are sufficiently large for recruitment of these species. These tree species with few recruits make up 17% of the 50-ha plot sun-exposed crown area and will likely be replaced by other species when they die, which suggests that this forest is still transitioning to an old-growth successional phase (Oliver and Larson 1996; Wirth and others 2009). Ongoing gap phase dynamics also likely play a role in maintaining the

dominance in the canopy of gap and intermediate light-demanding species which are recruiting in significant numbers. The return time for gap disturbance on BCI is estimated to be 114–160 years (Brokaw 1982; Pagnutti and others 2011). Although gap and intermediate-light demanding species tend to be short-lived, the life-spans of many light-demanding species on BCI are estimated to be greater than 160 years (Condit and others 1995; Metcalf and others 2009). Because the mean return time for gap disturbance is shorter than the life span of many gap species, gap species can dominate the forest canopy both in terms of number of stems as well as canopy area. Gap and intermediate-light demanding species might also increase in abundance in tall parts of the forest if there were increased mortality of shade-tolerant canopy trees during disturbance events such as El Niño droughts. However, the 1982-3 El Niño drought affected species with different regeneration niches equally (Condit and others 1995).

Relevance to Other Tropical Forests

Similar studies in other tropical forests are required to determine the generalizability of the conclusions of this study. The similarity of the canopy and understory should differ in forests of different successional stages, or undergoing other directional change. The diversity of trees ≥10-cm DBH and the diversity of the whole forest may be more similar in forests with sparser mid- and under-stories. However, because an increase in species diversity with size has been observed in other tropical forests (Gonzalez and others 2010), high diversity in the canopy may be widespread among tropical forests. An interesting exception is mono-dominant tropical forests, in which one species can compose the majority of canopy trees, even though the entire forest may be quite diverse (Makana and others 2004). A low exogenous disturbance rate is a common property of mono-dominant stands and a proposed mechanism contributing to canopy mono-dominance (Peh and others 2011). For BCI and probably many other tropical forests, disturbance likely contributes to species and functional group diversity in the canopy (Connell 1978; Denslow 1987; Uriarte and others 2011).

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