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Mapping Tropical Forest Trees Using High-Resolution Aerial Digital Photographs

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ABSTRACT

The spatial arrangement of tree species is a key aspect of community ecology. Because tree species in tropical forests occur at low densities, it is logistically challenging to measure distributions across large areas. In this study, we evaluated the potential use of canopy tree crown maps, derived from high-resolution aerial digital photographs, as a relatively simple method for measuring large-scale tree distributions. At Barro Colorado Island, Panama, we used high-resolution aerial digital photographs (0.129 m/pixel) to identify tree species and map crown distributions of four target tree species. We determined crown mapping accuracy by comparing aerial and ground-mapped distributions and tested whether the spatial characteristics of the crown maps reflect those of the ground-mapped trees. Nearly a quarter (22%) of the common canopy species had sufficiently distinctive crowns to be good candidates for reliable mapping. The errors of commission (crowns misidentified as a target species) were relatively low, but the errors of omission (missed canopy trees of the target species) were high. Only 40 percent of canopy individuals were mapped on the air photographs. Despite failing to accurately predict exact abundances of canopy trees, crown distributions accurately reproduced the clumping patterns and spatial autocorrelation features of three of four tree species and predicted areas of high and low abundance. We discuss a range of ecological and forest management applications for which this method can be useful.

Abstract in Spanish is available in the online version of this article.

Key words: Barro Colorado Island; high-resolution aerial digital photography; remote sensing; spatial patterns; tropical forest.

THE SPATIAL ARRANGEMENT OF TREE SPECIES IS A KEY ASPECT OF COMMUNITY ECOLOGY AND CONSERVATION (Bolker *et al.* 2003, Condit *et al.* 2000, Hubbell 2001, Nathan & Muller-Landau 2000). Mapping species distributions is a prerequisite for determining relationships between species distribution and environment variables (Condit *et al.* 2000, 2002, Cottenie 2005), dispersal patterns (Augspurger 1984, Jansen *et al.* 2008), relationships with animal distributions (Etienne & Olff 2004, Wisz *et al.* 2008) and vulnerability to human impact (Asner *et al.* 2002, Cabeza & Moilanen 2001, Siren *et al.* 2004). Because tropical forests are characterized by a high diversity of species that often occur at low densities, a large survey area is usually required to ensure that both a sufficient number of individuals and enough spatial heterogeneity are sampled to address important ecological questions (Wu *et al.* 2002, Wheatley & Johnson 2009). The required area may exceed 50 ha, which is the size of the largest fully mapped tropical forest plots (Condit 1998, Hubbell *et al.* 2005), and thus would require tremendous effort to establish and survey plots. Coverage must be even larger if canopy trees need to be mapped because canopy-sized individuals occur with a density an order of magnitude lower than understory trees (Asner *et al.* 2002, Kobe & Vriesendorp 2009).

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Remote sensing techniques, particularly hyper-spectral and high-resolution satellite imaging, offer potential alternatives for mapping species distributions over large areas. Although remote sensing is a standard tool for assessing the spatial structure, complexity and dynamics of forests spanning large areas, especially in the temperate zone (Pouliot *et al.* 2002, Leckie *et al.* 2003, Gergel *et al.* 2007), few studies have successfully used satellite remote sensing to map the distribution of tree species in tropical forests (Clark *et al.* 2005, Asner *et al.* 2008). Even when hyperspectral and high-resolution satellite images are used, it is difficult to identify tree species, and these images are more expensive and therefore not affordable for most facilities that study tropical forests (Nagendra & Rocchini 2008).

A potentially simple and relatively inexpensive solution is high-resolution aerial photographs (Vooren & Offermans 1985, Herwitz *et al.* 2000, Trichon & Jullien 2006, Gonzâlez-Orozco *et al.* 2010, Morgan *et al.* 2010). Trichon and colleagues (Trichon 2001, Trichon & Jullien 2006, Gonzâlez-Orozco *et al.* 2010) have developed keys for identifying individual tree species from high resolution aerial photographs, and assessed the accuracy of these identifications in test locations, focusing on errors of commission, *i.e.*, the percent of crowns incorrectly identified as a target species. In order to map canopy tree densities from aerial photographs, errors of both commission and omission (the percent of canopy trees of the target species missed in the aerial mapping) are both important.

For many ecological and management purposes at large spatial scales, however, mapping relative species densities and spatial properties of species distributions is more important than mapping the exact number of individuals. Thus, even if the accuracy rates for individual tree detection are modest, the aerial mapping technique may provide a good quantification of the large-scale spatial properties of species distributions. Especially since such properties have become an important topic in ecology, not only as a descriptor but also as a key factor in the study of patterns and process. Properties like spatial distribution, patterns of aggregation and spatial dependency (*e.g.*, spatial autocorrelation) have been shown to influence significantly forest dynamics (Dale1999), hence the outcome of ecological studies (Perry *et al.* 2006).

In this study, we quantify the accuracy of using high-resolution aerial digital photographs to obtain spatial distributions of canopy tree species over 75 ha of diverse tropical forest at Barro Colorado Island, Panama. We mapped the distribution of canopy trees of four species and tested the rates of omission and commission based on fully mapped plots. We also determine how well the mapped crown density can replicate spatial properties of the stem maps, particularly relative tree density, spatial autocorrelation and spatial aggregation.

METHODS

STUDY AREA.—Barro Colorado Island (BCI), Panama (9°9′ N,79° 51′ W) is a 1560-ha island covered with tropical moist forest, which was isolated from the surrounding mainland between 1910 and 1914 when the Chagres river was dammed to form the central part of the Panama Canal. The island has an annual rainfall of 2623 mm with a 4-mon dry season between December and May (Leigh 1999). For all of BCI, 317 tree species have been recorded (Knight 1975) of which 115 are canopy species (average canopy height is 18–30 m). Fifty-nine of the canopy species are 'common' (Croat 1978).

We used two mapped forest plots for evaluation of the aerial photography method: a 50-ha (1000 × 500 m) of old-growth forest in which all trees ≥ 1 cm diameter at breast height (dbh) have been mapped (Condit 1998, Hubbell *et al.* 1999, 2005) and; (2) an adjacent 25-ha (500 × 500 m) plot of secondary forest in which all trees ≥ 0 cm dbh have been mapped (Wright & Jansen, unpubl. data). Also for the 25-ha plot, all reproductive individuals of the palm species *Attalea butyracea* (Mutis ex L.f.) Wess. Boer (Aracaceae), and *Astrocaryum standleyanum* Bailey (Aracaceae), and all trees ≥ 10 cm dbh for *Jacaranda copaia* Aubl. (Bignoniaceae) and *Dipteryx panamensis* (Pittier) Record & Mell (Fabaceae) were mapped. We used map data from 2005 for the 50-ha plot and 2004 for the 25-ha plot.

AERIAL PHOTOGRAPHY.—High-resolution digital aerial photographs were taken from a small plane (Cessna 172) that flew parallel transects over BCI. The door of the plane was removed and the photographer took the photographs with a digital camera (12.3-megapixel digital SLR camera -Fuji FinePix S3 Pro- with a 35 mm lens, f-stop 4.5–4.8, shutter speed 1/700–1/1000 s, and ISO speed 400) pointing straight down from the plane while sitting at the entrance and secured with a harness. We use the term digital aerial photographs (*sensu* Morgan *et al.* 2010), and just photographs for short, due to its common usage, although these images are technically images not photographs, which utilize film. A constant altitude was maintained. Transects were flown using the directions of a printed flying plan and tracked with a GPS receiver (Garmin 60CSx). Flights were flown in overlapping north-south swaths at an altitude of 400 m in 2005, 700 m in 2006 and 800 and 1000 m in 2007. In 2005, each photograph covered ≈8.6 ha with a spatial resolution of 0.085 m/pixel. In 2006, coverage and resolution averaged 15.9 ha and 0.114 m/pixel. In 2007, images were collected at two resolutions—0.122 m/pixel (10.2 ha coverage/photo) and 0.180 m/pixel (22.3 ha coverage/photo). The aerial photographs were registered to a geo-referenced March 2004 Quickbird satellite image of BCI (Digital-Globe, Longmont, CO, U.S.A.) using ERDAS IMAGINE v.8.7 software (Leica Geosystems, GA, U.S.A.). While Quickbird images allow discrimination of highly conspicuous trees, such as *Tabebuia guayacan* (Seem.) Hemsley (Bignoniacea) when it is flowering (Sánchez-Azofeifa *et al.* 2011), they cannot be used to map less-conspicuous species, including species and individuals whose crowns do not have highly conspicuous flowers, or species whose identification is based on fine scale shape, such as palms (Jansen *et al.* 2008 Fig. 1). We used features visible in both photographs and satellite image, such as flowering *T. guayacan,* edges of the island, telemetry towers and large tree crowns, as registration points for warping and geo-referencing the individual photographs in order to obtain an island-wide mosaic. For the 75-ha area used for ground-truthing (Fig. 1), we used 43, 19 and 7 georeferenced photographs in 2005, 2006 and 2007, respectively.

SPECIES EVALUATION.—We overlaid the photomosaic with a diameter-scaled stem map of the 50-ha plot to determine which of the 59 common canopy tree species could be reliably identified and

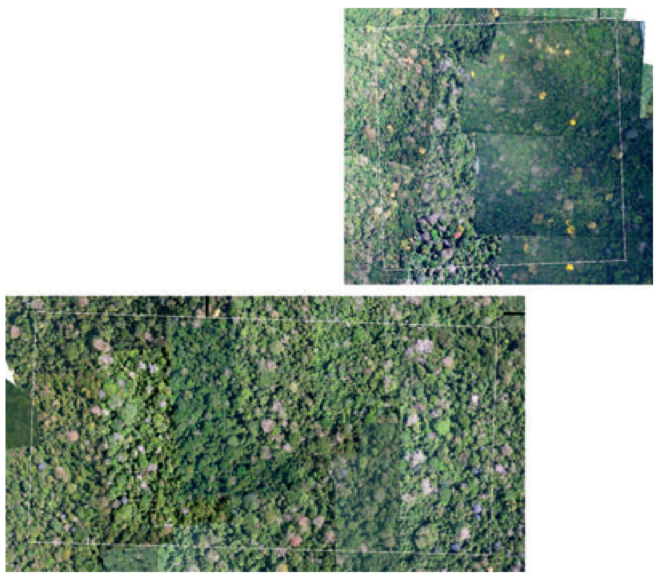

FIGURE 1. Aerial photographs mosaic of the study area (75-ha) at BCI.

mapped from aerial photographs. We divided the 50-ha plot into two equal sections, a training section and a test section. Nine species with less than five individuals in the training section were excluded from analysis because there was low intraspecific variation captured. In the training section, we develop an identification key (Fig. 2) based on the crown typology, specifically conspicuous crown contour, architecture, foliage cover and texture, color and phenology (Trichon 2001). Species with non-distinct or highly variable crowns were not included. After a training session, the test section was surveyed to map individuals of each of the species and the resulting maps were compared to the stem map to determine the percentages of correct identifications (Fig. 2). Given that the accuracy in the estimation of species spatial patterns might rely on the ability to capture both flowering and non-flowering crowns, the target species in this study where selected based on the high detection percentage of all crowns.

Crown mapping and accuracy assessment.—Using ArcGIS v.9.3 (ESRI 2011), two analysts separately surveyed the 2005, 2006 and 2007 photographs for crowns of the four study species (Table 1) for the 50-ha and 25-ha plots. These species were selected because they had the most distinctive crowns of all species (Fig. 2). This survey was done by placing a 50 × 50 m grid over the 75 ha and identifying all tree crowns per grid square. By drawing polygons that traced the contours of each crown, we produced a map of the distribution of sun-exposed individuals and their crown sizes for the entire 75 ha, from which average crown size and canopy stem density were determined.

TABLE 1. *Characteristics of the four species selected for crown mapping from the aerial photographs in this study.*

Species	Attalea butyracea	Astrocaryum standleyanum	Jacaranda copaia	Dipteryx panamensis
Dispersal mode	Animal	Animal	Wind	Animal
Height (m)	30	20	30	50
Characteristics	palm tree	palm tree	Tree	Tree
Shade tolerance	Low	Medium	Low	Low
Individuals mapped	3121	2456	977	412
Phenology	Evergreen	Evergreen	Deciduous	Deciduous
Flowers	Inconspicuous	Inconspicuous	Conspicuous (purple)	Conspicuous (red-violet)
Flowering period	April to September	May to September	February to May	May to August
Blooming	–	–	Clusters	Mass (July)
Crown diameter (m)	8.9	6.4	15.1	24.8
Density (ha^{-1})	2.05	1.73	0.67	0.25

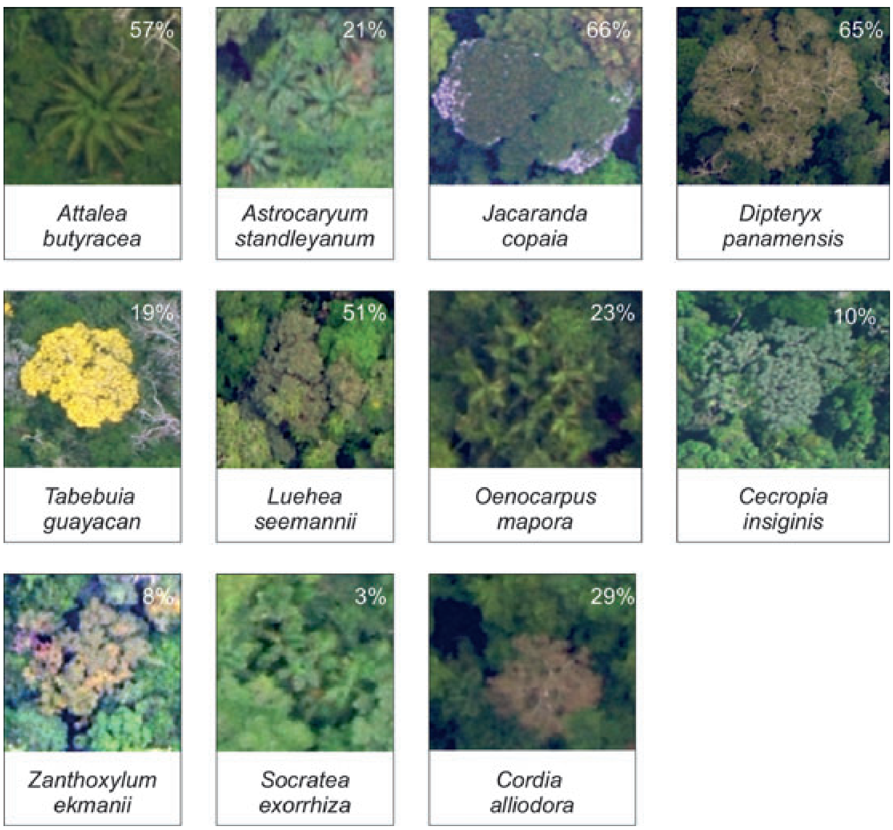

FIGURE 2. Aerial photographs of crowns for 11 tree species on Barro Colorado Island that may be suitable for aerial mapping. Numbers are the percentage of correct identifications in a blind survey for the 25 ha training area.

The accuracy of these maps was evaluated by comparing the photo-derived crown maps to the stem maps. We attempted to link all aerially mapped crowns to ground-mapped stems using the GPS locations and overlaying both maps. Crowns identified in the aerial photographs that could not be linked to a stem were considered false positives. Errors due to commission (false positives) and omission (false negatives) were assessed for each analyst using a modified version of the error matrix described by Congalton (1991). To perform these tests, we established a minimum dbh threshold above which all trees could be assumed to be in the canopy: ≥ 10 cm dbh for palms and ≥ 30 cm dbh for non-palms. The combined effort of both analysts' identifications resulted in a final distribution map that was used in the analyses of spatial patterns described below. For *D. panamensis*, we only used the crown map from just the analyst with the lowest errors.

To do determine if the crown map could estimate the relative abundance and clumping patterns of these species, we compared ground and aerial photo-based maps using three methods: Ripley's K, Morans I, and spatial regression. Ripley's K function (*K(d)*), calculated from individual stem and crown locations, quantifies the spatial aggregation of tree stems at various inter-tree distances and determines if the amount of clumping deviates significantly from a random distribution (Ripley 1976). The *K(d)* function was transformed to $L(d) = \sqrt{K(d)/\pi}\text{-}d$, and plotted as $L(d)/d$, to illustrate how the observed spatial pattern of each species deviates from a random distribution at various distances (Besag & Diggle 1977). For each species, we compared separate L(d)/d functions determined from the stem map and the crown map.

We then compared the patterns of spatial autocorrelation between the stem and crown maps with the Moran's I test, using different grid sizes to determine how the spatial resolution of the study might affect the results. We estimated the average density of individual trees in several square grids (grid sides of 25, 50, 100 and 200 m) for both the crown and stem maps. We used Moran's I test to measure the spatial autocorrelation at each resolution, and generated spatial correlograms that show Moran's I coefficients for various grid sizes. We tested for global significance between the correlograms generated by the stem map and aerial photographs using the Bonferroni criterion, which accounts for the dependence among coefficients at different spatial scales (Fortin 1999). Global significance between the stem and photo correlograms indicates that the crown and ground maps generated similar strengths and distances of spatial autocorrelation.

Finally, we performed spatial regressions to ascertain whether the crown maps could determine the areas of relatively high and low abundance while taking into account the spatial autocorrelation of the data. Using the stem map as the predictor variable and the crown map as the response variable, we determined the accuracy (coefficient) and strength (r^2) of the relationship between the crown and stem maps for different grid sizes for each species. The Moran's I and spatial regression analyses were performed using the software package OpenGeoDa for Mac OS X v. 0.9.9.12 (Anselin *et al.* 2006). The linear regressions and Ripley's K analyses were done in R using the packages splancs (Ripleys K) and stats (regressions) packages.

RESULTS

Of the 50 common canopy tree species, eleven (22%) were potentially suitable for aerial crown mapping based on evaluation in the 25-ha training area (Fig. 2). We choose four of the species with percentage of correct identification above 20 percent. For the 4 target species, 1290 canopy individuals were mapped on the ground in the 50- and 25-ha plots, but just 531 (41%) of the canopy-sized stems of these species were detected in the aerial photographs. Analyst 1 detected 480 individuals on the photographs (37%) while analyst 2 detected 390 individuals (30%). Crowns of *J. copaia* were most accurately identified on the photographs (76%) while those of *A. standleyanum* were the least accurately identified (19%). The two analysts had very similar accuracy rates for the two palms, but different accuracy rates for the non-palms, including a high error of commission rate for *D. panamensis* for analyst 1 (Table 2).

Despite identifying less than 50 percent of the canopy individuals, the crown maps accurately captured the spatial patterns of three of the four species. The spatial aggregation, which is measured as Ripley's K function, was very similar for stem and crown maps for *A. butyracea, A. standleyanum* and *J. copaia* (Fig. 3). Ripley's K functions for *D. panamensis*, however, showed high clumping at short distances for the crown map but not for the stem map.

The correlograms of the Moran's I values for different plot sizes were globally significant for three (*A. butyracea, A. standleyanum* and *J. copaia*) of the four species, indicating crown and stem maps produced similar spatial autocorrelation patterns across all grid sizes (Fig. 4). Thus for *A.butyracea, A. standleyanum* and *J. copaia*

TABLE 2. *Accuracy assessment of 75-ha crown maps derived from aerial photographs for four tree species on Barro Colorado Island.*

	Commision (%)		Ommision (%)		Accuracy (%)		Total accuracy per species (%)
	Analyst 1	Analyst 2	Analyst 1	Analyst 2	Analyst 1	Analyst 2	
Attalea butyracea	5.3	0.8	43.0	42.6	57.0	57.4	64.8
Astrocaryum standleyanum	3.4	0.6	83. 9	89.3	16.1	10.6	18.8
Jacaranda copaia	5.0	4.7	29.0	44.5	70.9	55.4	76.0
Dipteryx panamensis	60.3	1.6	34.9	52.4	65.1	47.6	65.1
Total accuracy per analyst (%)	18.5	1.9	47.7	57.2	37.2	30.2	41.2

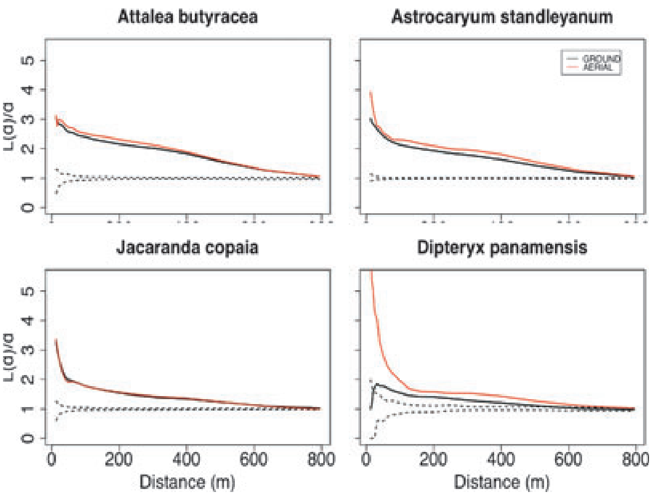

FIGURE 3. Ripley's K functions of clumping compared between (aerial) crown maps and ground-based stem maps over 75 ha, for four canopy tree species on Barro Colorado Island. Values of L(d)/d above 1 indicate greater clumping, and below 1 indicate even distributions. Solid lines represent observed L(d)/d relations, while dashed lines represent the 95% envelope for a random (not spatially clustered) pattern of the same number of individuals, generated through 99 Monte Carlo simulations assuming complete spatial randomness.

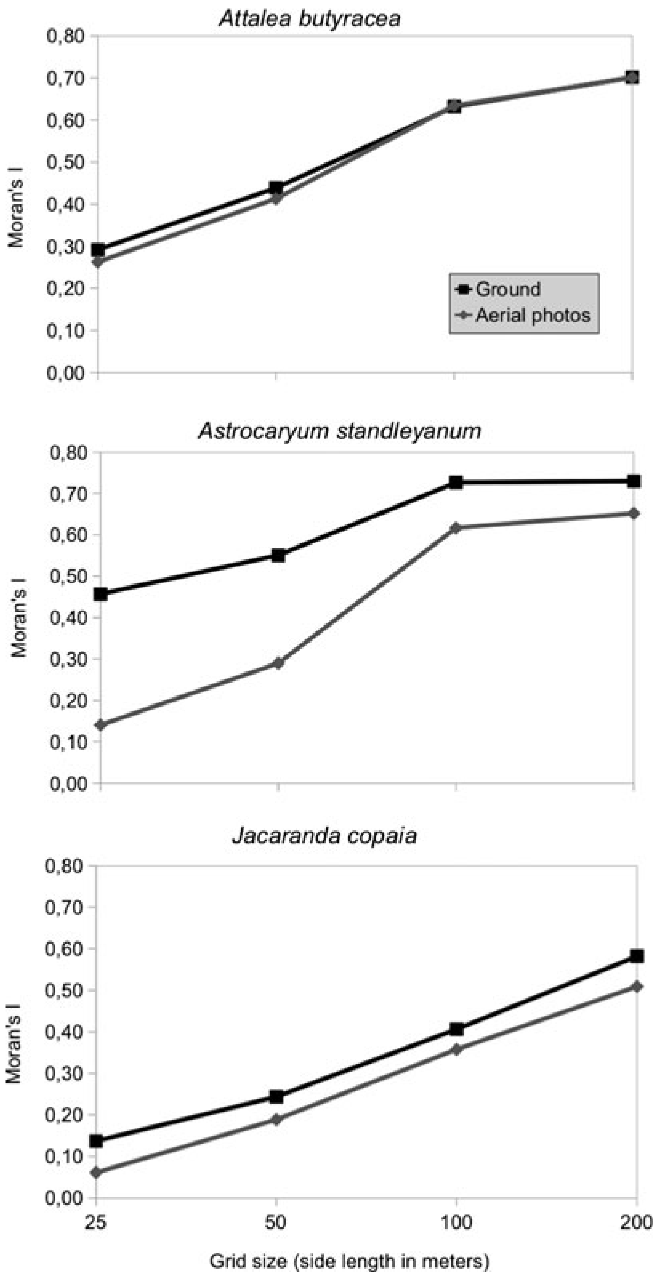

FIGURE 4. Correlograms of Moran's I test with stem maps and crown maps for four canopy tree species on Barro Colorado Island.

the spatial autocorrelation increased with grid size. In the case of *D. panamensis*, the Moran's I test was not significant globally or for any of the resolutions between the stem or crown maps. The correlograms showed a nearly identical magnitude of spatial autocorrelation for *A. butyracea* at all grid sizes, and a similar pattern but slightly lower magnitude of spatial autocorrelation for *J. copaia*. The crown map produced substantially lower Moran's I values for *A. standleyanum* than the stem map, especially at smaller grid (Fig. 5).

Visual inspection of the crown and stem maps indicated that areas of high and low tree densities on large scales were similar (Fig. 5; Appendix S1). This was confirmed by the spatial regression, which showed a significant correlation between the stem and crown maps for all grid sizes and species (Table 3). The regression coefficient did not change with grid size for three of the four species but decreased with grid size for *D. panamensis* (Table 3).

DISCUSSION

High-resolution aerial photographs potentially offer a solution for mapping trees over large areas at a relatively low cost (Morgan *et al.* 2010). This would enable ecological and management issues related to canopy tree distributions on a large scale to be addressed. The successful use of aerial photographs to identify various species of trees (*e.g.*, Read *et al.* 2003, Trichon 2001, Trichon & Jullien 2006) makes the use of this methodology especially promising.

Mapping spatial patterns.—This study indicated that high resolution aerial photographs may be a useful tool for determining overall spatial patterns of canopy tree species distributions, but not providing exact estimates of canopy tree species abundance. We found that in most cases, tree crowns identified to species were accurately identified, *i.e.* there are low rates of commission errors, which is consistent with other studies in tropical forests (Trichon 2001, Myers 1982). One exception was for analyst 1 in mapping *D. panamensis*, which had a commission rate of error of 60 percent (Table 2). This method, however, missed many individuals of the target canopy species, *i.e.* it had high rates of omission errors (≈40%). Trichon and Jullien (2006) report a similar low percentage (≈45%) of canopy trees that could be identified

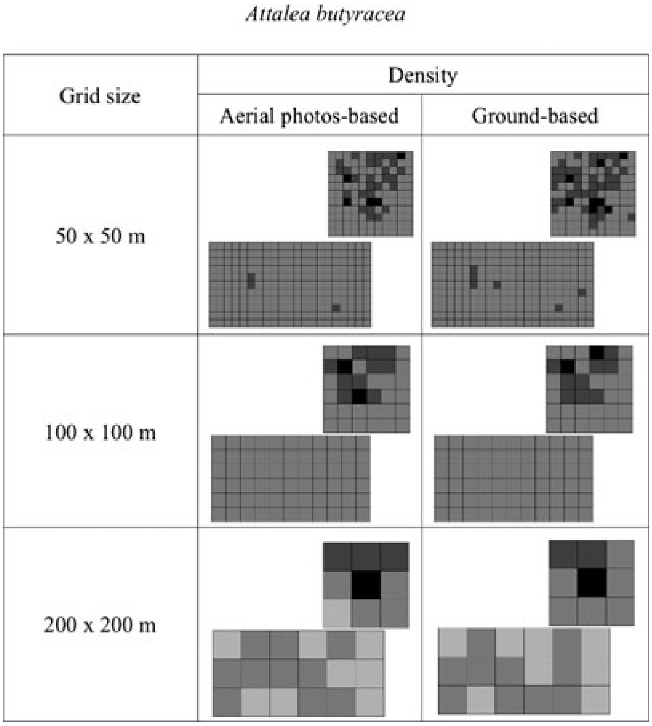

FIGURE 5. Density maps of the 50-ha (rectangle) and 25-ha (square) plots using various grid sizes for the palm *Attalea butyracea*. Tree density is represented by a gradient of 4 densities in proportions of the total number of individuals (*i.e.*, 25, 50, 75, 100), from low-density areas (light) to high tree density areas (dark).

in high resolution aerial photographs, although this was not evaluated for individual species.

Despite the low accuracy of quantifying exact species abundances across the 75-ha, the crown maps generated from the aerial photographs accurately described the spatial characteristics of the canopy-sized individuals for three of the four target species. The crown maps reproduced the clumping characteristics and spatial autocorrelation patterns of these three species. Finally, the spatial regressions showed that the crown maps were good predictors of the relative densities derived from the stem map. This confirms the study by Jansen *et al.* (2008), which using different methods showed the density of *A. standleyanum* in the 25-ha plot of BCI was highly correlated with stem-based densities. In this analysis, we extend this analysis to include the 50-ha plot, as well as showing the strong correlation for two other species, *A. butyracea* and *J. copaia*.

The aerial mapping method was least successful in reproducing the spatial abundance of *D. panamensis*. While ground-based spatial clumping and spatial autocorrelation patterns were not reproduced by the crown map, spatial regressions between the crown and ground map were significant at all scales for this species, although the coefficients were not consistent among spatial scales (Table 3). A better approximation of tree densities using the air photographs may be provided by more advanced techniques, such as those described by Caillaud *et al.* (2010), which used dbh-calibrated probability and smoothing functions to predict tree density from the crown map.

It is interesting to compare the results of *A. standleyanum*, which had the highest rates of omission, and *D. panamensis*, which had the highest rates of commission. As mentioned above, the crown map of *D. panamensis* did a poor job of reproducing the spatial characteristics of the ground-based stem map. However, even though only 20 percent of the canopy individuals of *A. standleyanum* were identified over 75-ha in the photographs, the crown map performed reasonably well in predicting the spatial patterns of canopy stems. Clumping patterns were well reproduced. The pattern of spatial autocorrelation was reproduced, although the magnitude of spatial autocorrelation from the photographs was too low at all grid sizes. Finally, densities of crown significantly predicted densities of canopy stems, and the amount of variation explained increased with grid size, indicating this method was most reliable for predicting landscape scale trends in this species. This suggests that the key to correctly describing the spatial pattern of a species from aerial photographs is to have low rates of commission rather than low rates of omission. This suggests that species in other studies with low rates of commission but not reported rates of omission (Trichon 2001, Trichon & Jullien 2006), would be good candidates for mapping spatial characteristics of the species over landscape scales.

D. panamensis had a low rate of commission errors for analyst 2 but a high rate of commission errors of analyst 1 (Table 2). In most cases, there was good agreement between the two analysts, indicating the repeatability of this method. Additional training, iterative consultation between analysts or, the recently tested,

TABLE 3. *Spatial regression coefficients and* R^2 *of the correlation between the ground-based maps and the aerial photo-based map.* $P < 0.0005$ *in all cases.*

	Attalea butyracea		Astrocaryum standleyanum		Jacaranda copaia		Dipteryx panamensis	
Grid size (m)	Coefficient	R^2	Coefficient	R^2	Coefficient	R^2	Coefficient	R^2
25 × 25	0.66	0.75	0.17	0.25	0.52	0.62	00.75	0.43
50 × 50	0.67	0.86	0.16	0.43	0.52	0.69	0.75	0.46
100 × 100	0.65	0.93	0.13	0.64	0.50	0.76	0.77	0.51
200 × 200	0.65	0.96	0.18	0.86	0.49	0.91	0.57	0.64

dichotomous identification keys and computer base interfaces (Gonzâlez-Orozco *et al.* 2010), however, may be important to make consistent identification for all species and to lower error rates.

It is important to note that we used a diameter threshold to generate stem maps of all potential canopy trees, which is likely to misrepresent which trees are actually sun-exposed and thus potentially visible from aerial photographs. The two non-palms species (*D. panamensis* and *J. copaia*) are both light-demanding, which would indicate that trees of these species would be found in the canopy even below 30 cm dbh. Because the palms do not have radial growth, it is even more difficult to use a diameter threshold to indicate canopy or understory species. However, even without a precise map of only trees that have reached the canopy, our results indicate the crown map reliably reproduces the large-scale spatial patterns of large trees of three of the four study species.

IDENTIFICATION OF SPECIES.—In this study, aerial photography allowed us to map the distribution of canopy individuals for 22 percent of the common canopy tree species for a 75 ha study area, which is considerably higher than 9.2 percent of species reported by Trichon and Jullien (2006) for 15 ha of tropical forest in French Guiana. The higher percentage of identifications may be due to the larger area, which included a stem map for all canopy trees, covered in this study. The large study area allows closer examination of the intra- and inter-specific variation in crown typology, which is critical to generate a higher number of reliable tree identifications. We only performed careful analysis of four of the 11 species with relatively distinguishable crown typology. For the other seven species, it would be worthwhile to determine the rates of commission errors to generate good candidates for large-scale mapping. This leaves 80 percent of the common canopy-statured species that are poor candidates for mapping from aerial photographs. Other techniques, especially high resolution, airborne hyperspectral imagery, holds the most promise for large scale mapping of these species (Bohlman & Lashlee 2005, Clark *et al.* 2005, Asner *et al.* 2008). These images are very expensive and rarely available, however, thus the aerial photography method is a good choice for species where there is cause to believe that their crowns are distinct.

The species that were distinguishable in the study had particular characteristics that may be relevant for choosing target species to map in other areas of tropical forest. First, our study, as well as that of Gonzâlez-Orozco *et al.* (2010), indicates palm species are good candidates for aerial mapping. Two of the four most distinguishable species, and four of the 11 possible species, were palms that are not only distinctive from non-palms, but also are distinctive from each other. Second, *D. panamensis, L. seemanii, Z. ekmanii* and *T. guayacan* were all distinctive in large part because of the phenological state of the species when the images were taken in the dry season. *D. panamensis, L. seemanii,* and *Z. ekmanii* had senescing leaves. *T. guayacan,* and to a lesser extent *J. copaia*, had crowns covered in flowers. To identify a species that is good candidate for aerial mapping based on phenology requires that the phenological state be visually striking when viewed from above, distinct from other species, and fairly synchronous across a population. In some cases, this is fairly easy to judge, such as *T. guayacan* trees, which are extremely noticeable even on the ground when they flower synchronously across central Panama. In other cases, such as *L. seemanii* and *Z. ekmanii*, it would be more difficult to determine on the ground that these tall canopy tree species would be distinct, and their detectability can only be assessed after viewing them in the aerial photographs.

ECOLOGICAL APPLICATIONS.—The species that were reliably identified in aerial photographs included several ecologically important species occurring on BCI. For example, *A. butyracea* is host to the triatomine insect *Rhodnius prolixus* Stal, an important vector of Chagas disease (Sanchez-Martin *et al.* 2006). The potential distribution of the Chagas disease could be refined by mapping palms from digital aerial photographs, which has not been possible with satellite images (Guhl 2010). In addition, indigenous communities in Panama and Colombia use *A. standleyanum* leaves to build the walls of houses and weave traditional baskets (Dalle *et al.* 2002, Potvin *et al.* 2003). However, *A.standleyanum* does not germinate easily, and the seedling takes a long time to emerge and grow to an appropriate size for harvesting (Potvin *et al.* 2003). Knowledge of the spatial distribution of *A. standleyanum* in relation to human densities would help determine possible impacts of human populations on *A. standleyanum*. Also, better management of the species would be enabled by determining where reproductive adult trees are concentrated, thus facilitating seed collection. Additionally, the fruits of *D. panamensis, A. butyracea* and *A. standleyanum* are key resources for the terrestrial mammals on BCI (Smythe 1986). Mapping these tree species allows the habitat quality for vertebrates to be assessed and the interactions between vertebrates and their food plants to be evaluated, as shown in previous studies (*e.g.*, Caillaud *et al.* 2010, Galvez *et al.* 2009, Jansen *et al.* 2008).

Finally, the technique described here offers flexibility in terms of time and costs. Over flights can be timed at specific flowering events and take advantage of favourable cloud conditions, which can be limited in the tropics, on short notice. This technique can be less costly than satellite imagery or airborne images from commercial sensors with high enough spatial or spectral resolution for species identification. Although we mounted the readily available digital cameras on a small aircraft in their study, it can also be potentially used from helicopters, and unmanned aerial vehicles (UAV), which are becoming more widely available and inexpensive (Getzin *et al.* 2012).

CONCLUSION

Visual analysis of high-resolution aerial photography is suitable for the mapping of specific tropical forest canopy tree species across large spatial scales. For several species, conclusions on spatial distributions and patterns inferred from ground-surveyed and aerial photo-surveyed trees are similar. The proposed method is a relatively low-cost and low-tech alternative to large-scale ground surveys and hyper-spectral remote sensing, with various promising potential applications.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

APPENDIX S1. Density maps of the 50-ha and 25-ha plots using various grid sizes for Astrocaryum standleyanum, Dipteryx panamenisis and Jacaranda copaia.

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