Ecography 000: 000–000, 2008
doi: 10.1111/j.2007.0906-7590.05151.x

Subject Editor: Jens-Christian Svenning. Accepted 15 October 2007

Large-scale spatial variation in palm fruit abundance across a tropical moist forest estimated from high-resolution aerial photographs

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Fruit abundance is a critical factor in ecological studies of tropical forest animals and plants, but difficult to measure at large spatial scales. We tried to estimate spatial variation in fruit abundance on a relatively large spatial scale using low altitude, high-resolution aerial photography. We measured fruit production for all 555 individuals of the arborescent palm *Astrocaryum standleyanum* across 25 ha of mapped tropical moist forest on Barro Colorado Island, Panama, by visually counting fruits from the ground. Simultaneously, we used high-resolution aerial photographs to map sun-exposed crowns of the palm across the same area, which were then linked to ground-mapped stems. First, we verified that the fruit crop size of individual trees was positively associated with both crown presence on aerial photos and crown area visible on aerial photos. Then, we determined how well spatial variation in *Astrocaryum* fruit density across the study area was predicted by spatial densities of photo-detected crowns and crown area compared to spatial densities of ground-mapped stems and stem diameters. We found a positive association of fruit crop size with crown visibility on aerial photographs. Although representing just one third of all individuals in the study area, photo-detected crowns represented 57% of all fruits produced. The spatial pattern of photo-detected crowns was strongly correlated with the spatial pattern of fruit abundance based on direct fruit counts, and correctly showed the areas with the highest and lowest fruit abundances. The spatial density of photo-detected crowns predicted spatial variation in fruit abundance equally well as did the spatial density of ground-mapped stems. Photo-detected crown area did not yield a better prediction. Our study indicates that remote sensing of crowns can be a reliable and cost-effective method for estimating spatial variation in fruit abundance across large areas for highly distinctive canopy species. Our study is also among the few to provide empirical evidence for a positive relationship between crown exposure of forest trees and fruit production.

Fruits and seeds play a central role in the ecology of tropical forests. For example, a large proportion of rainforest mammal and bird species consume fruits or seeds. Frugivores and granivores together can account for as much as three-quarters of forest bird and mammal biomass in tropical forests (Terborgh 1986a, Fleming et al. 1987). Fruit abundance strongly affects individual behaviour as well as population abundances and dynamics in these species. For example, frugivorous birds tend to be most abundant where fruits are most abundant (Moegenburg and Levey 2003). For this reason, fruit availability is often used as an index of habitat quality or productivity (Chapman et al. 1994, Basabose 2004, O'Driscoll Worman and Chapman 2006).

Local fruit and seed abundance is also important in the ecology of plant populations, as it may affect the probability of individual seeds surviving and establishing as seedlings. For example, effectiveness of seed dispersal by frugivorous or granivorous animals may depend, positively or negatively, on the local abundance of conspecific and/or heterospecific fruits (Howe and Vande Kerckhove 1981, Jansen et al. 2004). Furthermore, local fruit abundance may invoke greater incidence of frequency- or density-dependent seed predation and herbivory, ultimately decreasing the probability that seeds and seedlings survive (Clark and Clark 1984, Harms et al. 2000). Thus, the assessment of fruit abundance is critical to ecological studies of frugivores and animal-dispersed plants.

A variety of methods have been developed to estimate habitat-wide fruit abundance. These include fruit traps for sampling fruit fall and seed rain, phenological transects for monitoring the fruiting status of focal trees, or fruit counts of crown portions extrapolated to the entire crown (Chapman et al. 1994, Parrado-Rosselli et al. 2006). Because they are labour intensive, these methods are less suitable for estimating patterns of fruit abundance at larger spatial scales, which may be needed, for example, for selecting experimental areas of contrasting fruit abundance. An indirect approach is to infer spatial variation in fruit abundance from stem mapping, assuming that all individuals above a certain threshold diameter contribute fruits equally (Mangan and Adler 2002), or assuming that fruit crop size is a function of diameter or basal area (Chapman et al. 1992, Anderson et al. 2000, O'Driscoll Worman and Chapman 2006). But even these methods – which require field-mapping all stems over a certain diameter – easily become too laborious for large spatial scales, and will in practice remain largely limited to existing forest dynamics plots in which all trees have been mapped and tagged.

In this study we tried to estimate spatial variation in fruit abundance on large spatial scales using low altitude, high-resolution aerial photography. High-resolution remote sensing has been used in tropical forests, with varying success, to map individual species (Clark et al. 2005), logging damage (Asner et al. 2006), crown area (Brown et al. 2005) and tree mortality (Clark et al. 2004a), but we know of no attempt to quantify spatial patterns of fruit abundance. Many tree species providing keystone fruit resources in Neotropical forests are canopy trees (cf. Terborgh 1986b), and many important canopy trees have visually distinct individual crowns that are reliably detectable in remotely-sensed images (Myers and Benson 1981, Myers 1988, Bohlman and Lashlee 2005, Clark et al. 2005, Trichon and Julien 2006). We hypothesized that fruit abundance can be assessed via remotely sensed crowns because individual forest tree crowns that are sun-exposed and may thus detected on the photos ("photo-detected") tend to produce larger fruit crops than do shaded individuals (Ganzhorn 1995, Wright et al. 2005). Thus, photo-detected crowns may represent a major part of the fruit production for canopy tree species.

We studied individual-level fruit production and large-scale spatial variation in fruit abundance in the fleshy-fruited palm *Astrocaryum standleyanum* on Barro Colorado Island, Panama. Palm fruits are consumed by a wide diversity of vertebrates and are considered to be keystone food resources for Neotropical frugivores (Terborgh 1986a, Adler 1998). Our study species indeed is one of the most important fruit species for frugivorous and granivorous mammals at our study site (Glanz et al. 1982, Smythe 1986). We evaluated whether aerial mapping is a valid alternative for predicting spatial variation in this species' fruit abundance compared to ground-based stem mapping.

First, we tested whether photo-detected crowns for *A. standleyanum* do indeed produce more fruit than shaded crowns, and whether fruit production increases with photo-detected crown area. Second, we assessed whether predictions of spatial variation in fruit abundance based on locations and sizes of photo-detected crowns reflect the actual spatial pattern of fruit abundance, calculated from direct fruit counts, equally well as or better than do predictions of spatial variation based on stem maps or basal area.

Methods

Site and species

The study was conducted on Barro Colorado Island (BCI, 9°10′N, 79°51′W), Republic of Panama, a semi-deciduous moist tropical forest on a former hilltop that was isolated from the mainland by the formation of Gatun Lake to complete the Panama Canal. The climate is seasonal, with a distinct 4-month dry season (January–April) and 2600 mm average annual rainfall. Our study area was a 25-ha (500 × 500 m) plot located in secondary forest (estimated at 100–120 yr old) at the centre of BCI. In our 25-ha plot, all trees >20 cm diameter at breast height (dbh), as well as all reproductive individuals of tree species with seeds >1 g (which includes the study species), were mapped and identified to species (Wright and Jansen unpubl.). Diameters were measured in October–November 2004.

We chose the arborescent palm *Astrocaryum standleyanum* (Arecaceae, henceforth *Astrocaryum*) as our study species because of its importance as a food resource for frugivorous and granivorous mammals (Glanz et al. 1982, Smythe 1986, Hoch and Adler 1997); its conspicuous fruits, which can be easily counted from the ground; and its abundance: *Astrocaryum* is among the ten most abundant tree species in central Panama (Pyke et al. 2001). Adult palms produce up to eight pendulous infructescences, each up to 150 cm long with up to 500 fruits, which ripen during April and May, and occasionally outside that period. Fruits are ovoid and consist of one 20 × 15 mm seed (rarely two), surrounded by 1.5–3 mm of hard endocarp, 4–5 mm of sweet, fleshy mesocarp, and finally 0.5 mm of harder, orange exocarp.

Fruit crop size of individual palms

In March–April 2004, we estimated the crop size of individual palms by visiting all ground-mapped individuals in the study area and counting or estimating the number of infructescences and fruits per tree with the aid of binoculars. The organization of both leaves and fruits in discrete clusters in *Astrocaryum* makes it possible to reliably estimate crop size by visually counting fruits from the ground. This holds even for occasional late-fruiting individuals, which were already bearing green, developing fruits during the census. We also looked for old inflorescences and infructesences, which persist in the crown for up to one year before falling. The infructesences can then take up to one more year to decompose on the ground (Wright unpubl.). Based on the presence of fruits and old inflorescences and infructesences, we classified all individuals as 1) "reproductive and fruiting"; 2) "reproductive but not fruiting", or; 3) "non-reproductive".

Remote sensing of crowns

Aerial photographs were taken on 5 and 6 April 2005, and again on 5 April 2006, during flowering events of the canopy tree *Tabebuia guayacan* (Bignoniaceae). *Tabebuia guayacan* flowers when deciduous and the bright yellow blossoms are visible from both aircraft and high spatial resolution satellite images. We used a 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. We flew overlapping north-south swaths at an altitude of 400 m in 2005, when cloud cover precluded flying higher, and 700 m in 2006. Photographs were taken with the camera oriented parallel to the ground, as much as

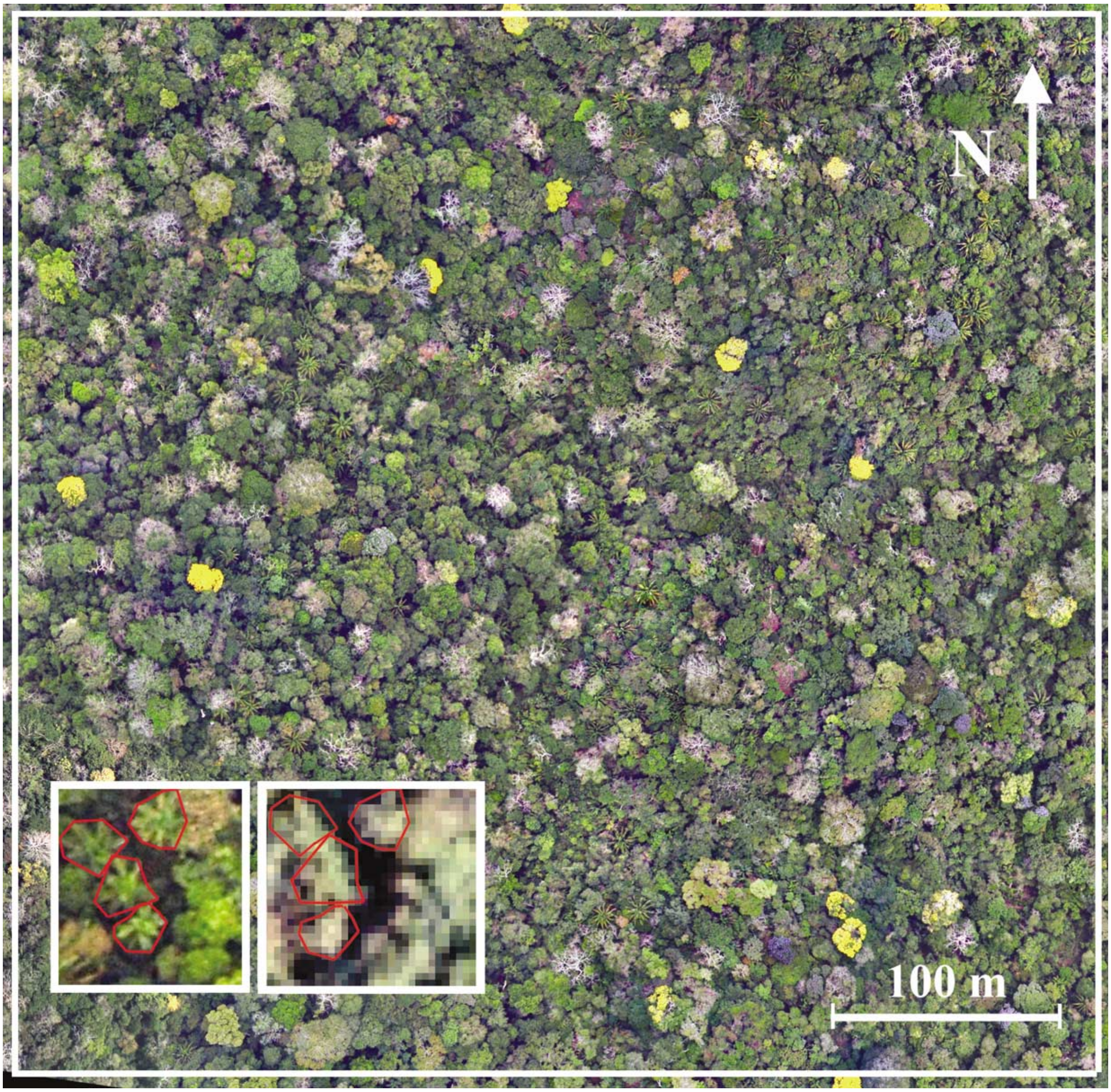

Fig. 1. Mosaic of geo-referenced aerial photographs for 25 ha of tropical moist forest at Barro Colorado Island, Panama. Left inset shows a detail with four *Astrocaryum standleyanum* palm crowns with the contours drawn to estimate the sunlit area. Right inset shows the same contours applied to the Quickbird satellite image, from which the palms cannot be recognized.

possible, and with some overlap between adjacent photographs to enable mosaicking of the images. In 2005, each photo on average covered 8.6 ha (358 × 241 m) with a spatial resolution of 0.085 m/pixel. In 2006, coverage and resolution averaged 15.9 ha (483 × 329 m) and 0.114 m/pixel.

The aerial photographs were registered to a geo-referenced Quickbird satellite image of BCI (DigitalGlobe, Longmont, CO, USA), taken in March 2004 during the flowering of *T. guayacan*. Quickbird images have a resolution of 2.5 m/pixel, which allows discrimination of large canopy trees (Read et al. 2003, Clark et al. 2004a, b). Registration points included flowering *T. guayacan* and other large crowns with distinct shapes and colours that were clearly visible on both types of images. For each aerial photo, we obtained 15 ± 4 (mean + SD) ground control points from the Quickbird image that were approximately uniformly distributed over the photo. We used the ERDAS IMAGINE v8.7 software (Leica Geosystems, GA, USA) for registering, resizing, rotating and warping the aerial photographs to fit them to the Quickbird image and its associated geographical coordinate system. We used ten overlapping aerial photographs from 2005 supplemented with one photo from 2006 to create a geo-referenced 11-photo mosaic of the 25-ha study area (Fig. 1).

The geo-referenced aerial photographs were individually loaded into ARCMAP v9.1 (ESRI) and carefully visually surveyed for locations of palm crowns, which were then identified to species by two different analysts. One analyst had prior training in this type of analysis, one did not. For areas with overlapping photos, all photos that covered the area were used to identify the palms. The photo-detected crown area of each tree was determined by drawing polygons bounded by the frond tips visible in the image.

For crowns that appeared to be partially covered by another crown, only the part of the crown visible in the photographs was included. Note, however, that the photo-detected crown area need not precisely match the amount of crown exposed at a nadir sun angle, as the viewing angle of the camera was not always straight down due to parallax as well as tilt of the camera and the plane. Each polygon was labelled as *Astrocaryum*, *Attalea butyracea*, *Oenocarpus mapora*, or *Socratea exorrhiza*. This procedure was followed independently by the two analysts, without knowledge of the mapped location of palm stems. The results of these ''naïve'' censuses were combined to create a preliminary crown map that we used for accuracy assessment. Then, the same two analysts performed a second search for palm crowns with the ground-based palm stem map superimposed on the images, hence with knowledge of where palms were located, i.e. where sun-exposed crowns were potentially present and to what species they belonged. The results of these ''knowledgeable'' censuses were combined to create a final crown map that was used for testing our hypotheses.

Analyses

We tested how well one ground- and two photo-based parameters predicted the presence/absence of fruit (binary variable) and fruit crop size (continuous variable) of individual trees. The ground-based, continuous parameter was basal area (calculated from stem diameter at breast height). The two photo-based parameters were presence/absence of palm crowns in the photo (binary), and photo-detected crown area (continuous). We used logistic regression for the binary response variable (presence/absence of fruit). We used generalized linear modelling (GLM) with Poisson or quasi Poisson errors and a log-link function (also called Poisson regression) for the continuous response variable (fruit crop size). For these tests, we used the final crown map, i.e. the best available knowledge of crown exposure. We cannot rule out that the crown area of individual palms had changed over the year since diameter measurement and fruit census, but assumed that these time lags did not affect the relationships.

The effectiveness of the two analysts in detecting and identifying *Astrocaryum* crowns on the aerial photos was assessed by comparing the preliminary crown map with the final crown map. We calculated the proportion of individual trees on the final crown map that the analysts detected in the first and second censuses, the proportion of false-negative identifications (*Astrocaryum* that were incorrectly identified as other palm species), and the proportion of false-positive identifications (other species that were incorrectly identified as *Astrocaryum*).

Then, we tested how well the ground- and photo-based parameters could predict the spatial patterns of fruit abundance of *Astrocaryum* palms. To do this, we mapped the spatial pattern of fruit abundance by subdividing the study area into 625 20 × 20 m square cells, and calculating the actual fruit density for each cell based on the direct fruit counts. We used the density kernel function in ArcGIS 9.1 Spatial Analyst with a 40 m ''search'' radius. This function, which is based on the quadratic kernel function described in Silverman (1986), fits a smoothly curved surface over each palm, with the value of the surface diminishing with increasing distance from the palm, reaching 0 at the circular search radius. The density at each output raster cell is then calculated by adding the values of all the kernel surfaces where they overlay the raster cell centre. Using the kernel density function, we also generated four additional cell-based ''predictor'' maps based on 1) the density of stems and 2) stem basal area 3) the density of photo-detected crowns and 4) the crown area of the detected crowns. The photo-based measures were based on the final crown map. The relationship between the predictor maps and the fruit abundance map were based on the following assumptions. The stem density map assumed that all mapped *Astrocaryum* contributed to fruit abundance equally. The basal area map assumed that fruit abundance is proportional to basal area. The crown density map assumed that all each photo-detected crown contributed to fruit abundance equally, and that non-detected individuals contributed nothing. The crown area map assumed that fruit abundance is proportional to the digitized crown area of photo-detected trees, and also that non-detected individuals contributed nothing.

To determine how strongly actual fruit abundance per cell was associated with each of the four other density estimates, we used ordinary linear regression. Our test statistic was the square of the correlation coefficient (r^2), i.e. the proportion of variation in fruit abundance that was explained by the estimates. Additionally, we used Spearman's rank correlation test to determine how well the fruit densities were predicted in relative terms. Because there was spatial dependence in the predictor and observed variables, the degrees of freedom in the correlations may be inflated, although the correlation estimates should not be biased (Hawkins et al. 2007). To determine the effective degrees of freedom, we used the method of Duttileul (1993) as implemented by Legendre (2000). Finally, to determine how much performance of the remotely sensed estimates degraded if analyst error was incorporated, we assessed the performance of predictor maps based on the preliminary crown map, including misidentifications and other error. All statistical analyses were done in R 2.4.0 (R Development Core Team 2006; available at <http://www.r-project.org>).

Results

Based on complete ground-based stem mapping, the study area included 555 adult and subadult *Astrocaryum* palms, or 22.2 individuals per ha. Of these, 91% were reproductive and 66% carried fruits during the 2004 fruiting season. The number of fruits per fruiting palm averaged 215 (±218, SD). We detected 188 *Astrocaryum* crowns on the aerial photographs (after combining the final censuses of the two analysts, with knowledge of the stem map) which could all be linked to ground-mapped individuals.

Crop size and crown exposure

There was a clear positive association between crown visibility in the aerial photos and crop size. Forty-three percent of all fruiting individuals were visible in the photographs, compared to 19% of the reproductive individuals that did not carry fruit, and 8% of the non-reproductive individuals. Photo-detected individuals were more likely to have fruit than individuals that were not visible on the photographs (chi-square test: $\chi_1^2 = 39.5$, $p < 10^{-9}$). Photo-detected trees had larger fruit crops (mean 240 ± SD 263 fruits, $n = 188$) than did undetected trees (92 ± 142, $n = 367$; ANOVA: $F_{1,553} = 74.6$, $p < 10^{-15}$). This was also true if only fruiting individuals were considered ($F_{1,365} = 32.1$, $p < 10^{-7}$). Thus, although representing just 34% of all ground-mapped *Astrocaryum* stems, photo-detected individuals accounted for 57% of all fruit production by the species. The probability of palms fruiting also increased with the crown area digitized from aerial photographs (Fig. 2a; logistic regression: $n = 555$, $z = 5.6$, $p < 10^{-7}$). Likewise, crop size increased with photo-detected crown area, both among all fruiting individuals (quasi Poisson regression: $n = 367$, $z = 133.0$, $p < 10^{-15}$) and among just the fruiting palms that were photo-detected (Fig. 2b; $n = 158$, $t = 3.5$, $p < 0.001$). These results validate the basic ecological relationship underlying our remote sensing approach: fruit production increases with sun-exposure of tree crowns. The probability of palms fruiting also increased with ground-mapped basal area (Fig. 3a; logistic regression: $z = 4.0$, $p < 0.0001$), but crop size of fruiting individuals was independent of basal area (Fig. 3b; quasi Poisson regression: $t = 0.89$, $p = 0.37$).

Photograph analysis accuracy

Although 188 *Astrocaryum* palm crowns were visible on the photographs, only a fraction of these were photo-detected by each of the individual analysts in the first census, without knowledge of palm stem locations. Analyst 1 saw 90 (48%) *Astrocaryum*, of which she misidentified three (3%) as other palm species, while an additional 15 palms were false positive identifications. Analyst 2 saw 97 (52%) *Astrocaryum*, of which he misidentified 22 (23%) as other species, while another 14 palms were false positive identifications. After combining these two "naïve" censuses, the number of *Astrocaryum* crowns photo-detected increased to 128 (68%), with 22 (17%) false-negative identifications, while the number of false-positive identifications decreased to 12.

In the second census, with knowledge of mapped palm stem locations, the proportion of the 188 photo-detected *Astrocaryum* increased to 66% and 84% for analyst 1 and 2, respectively. Only 40% of the crowns were detected by both analysts, while the majority (60%) were detected by only a single analyst. These low scores are due to differences in prior training of the photo analysts, blurriness in some of the photographs due to shaking of the camera in the plane, and distortions at the edges of the photos due to parallax. Moreover, small, partially obscured or shadowed crown were difficult to detect in the photographs and tended to be seen by only one analyst.

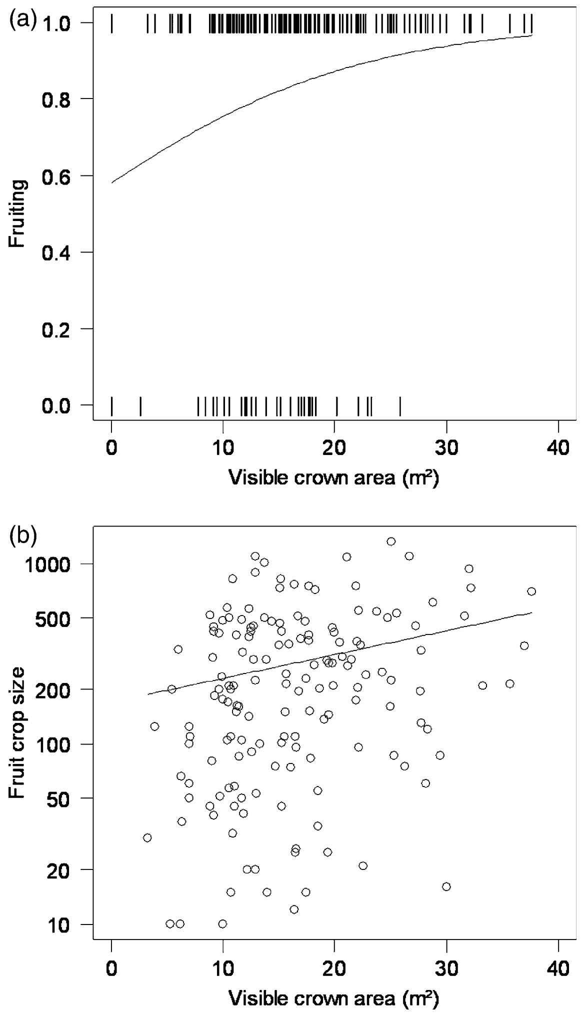

Fig. 2. Crown area visible on aerial photos a as predictor of (a) fruiting and (b) fruit crop per individual in the palm *Astrocaryum standleyanum*. Symbols (ticks) in (a) are all 555 ground-mapped palms, which are either fruiting (1) or not (0). Ticks may represent single or multiple individuals; the symbols at crown area = 0 m^2 include 209 fruiting and 158 non-fruiting individuals that were not visible on the aerial photos. Lines are logistic regression fits. Symbols in (b) are all 158 fruiting individuals that were visible in the photos. Lines are logistic regression (a) quasi Poisson regression (b) fits.

Spatial patterns of fruit abundance

The spatial pattern of actual fruit density, calculated from direct fruit counts, showed clear differences in fruit abundance across the study area, with relatively high densities in the topleft (northeast) quarter of the plot and relatively low densities along the lower (southern) edge (Fig. 4A). All four predictors of fruit abundance showed strongly positive correlations with the patterns of fruit abundance based on actual fruit counts (Fig. 4B–D), and correctly identified the parts of the study area with the highest and the lowest fruit abundance. Correlations with the "true" fruit abundance were comparable between estimates based on ground-mapped stem locations (Spearman's rank correlation with adjusted degrees of freedom: $\rho = 0.74$, DF = 46.5, $F = 56.4$, $p < 0.001$) and those based on photo-detected crown

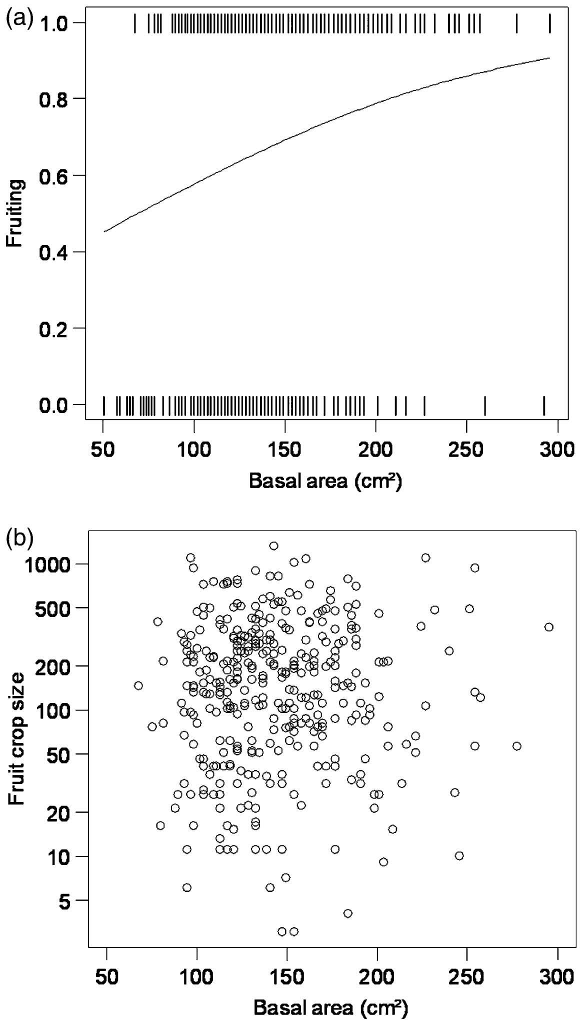

Fig. 3. Basal area as predictor of (a) fruiting and (b) individual tree fruit crop in the palm *Astrocaryum standleyanum*. Symbols in (a) are all 555 ground-mapped individuals (as in Fig. 2). Symbols in (b) are all 367 fruiting individuals. See Fig. 2 for further details. The probability a palm is fruiting increases with its basal area, but crop size does not.

locations ($\rho = 0.74$, DF = 46.5, F = 55.2, $p < 0.001$). Density estimates based on basal area gave only a slightly higher correlation ($\rho = 0.75$, DF = 44.2, F = 57.0, $p < 0.001$) than density estimates based on stem locations. Density estimates based on photo-detected crown area gave a lower correlation ($\rho = 0.62$, DF = 57.9, F = 36.2, $p < 0.001$) than density estimates based on photo-detected crown locations. Hence, the density of photo-detected crowns predicted spatial variation in fruit abundance as well as did the density of ground-mapped stems.

Effects of measurement error

To assess how photograph analysis error degraded the predictive value of photo-detected crowns, we also calculated density estimates based on photo-detected crowns and crown areas from the preliminary (naïve) map, which did not include all visible *Astrocaryum* crowns, and did include false-negative identifications (Fig. 6). The density estimates were still positively correlated with actual fruit densities in 20 × 20 m plots, both for photo-detected crown locations (Fig. 5A; $\rho = 0.61$, DF = 66.6, F = 39.4, $p < 0.001$) and photo-detected crown area (Fig. 5B; $\rho = 0.57$, DF = 73.7, F = 35.5, $p < 0.001$). Estimates based on photo-detected crowns still correctly identified the parts of the study area with the highest fruit abundance.

Discussion

This study shows that spatial variation in a palm species' fruit abundance on a landscape level may be derived from basic and relatively easy to acquire remotely sensed data. First, the reproductive status and fruit crop size of individuals was clearly correlated with the presence and crown area of *Astrocaryum* trees on the aerial photographs, validating the basic ecological relationship underlying the remote sensing approach explored in this study: fruit production in forest trees increases with sun-exposure of tree crowns. Few studies so far have empirically shown that sun-exposed forest trees produce larger fruit crops than do shaded individuals (Ganzhorn 1995, Wright et al. 2005). Thus, although crowns detected on aerial photographs represented just one third of all individuals across the study area, they represented a major part (57%) of the fruit production.

Second, the pattern of relative fruit abundance across 25 ha predicted from photo-detected crown locations was strongly correlated with the actual pattern of fruit abundance. Despite detecting many fewer individual palms than were found on the stem map, the photo-detection method performed as well as did predictors based on ground-based stem mapping. However, photo-detected crown area did not yield a better prediction than photo-detected crown locations, presumably because the relationship between crop size and photo-detected crown area was relatively weak (Fig. 2b). We conclude that mapping crowns from aerial photographs is a suitable method for assessing relative fruit abundance on large spatial scales for *Astrocaryum* and potentially for other species that can be easily discriminated on aerial photographs. As far as tree species producing so-called keystone fruits and seeds for frugivorous vertebrates (cf. Terborgh 1986a, b) are canopy trees with visually distinct crowns, which is the case at our study site, remote sensing can potentially be a way to evaluate which areas have high and low abundance of fruit resources and thus high and low habitat value for frugivores, depending on the level of clumping of adult trees.

Even our crown map based on "naïve" censuses without knowledge of the stem locations (Fig. 5) reflected the spatial patterns of fruit abundance, suggesting this result was robust to photograph analysis error due to imperfect analyst and photograph quality. This may be due partly to the clumping of trees and fruit production in our study species. In a species where fruiting individuals is more uniformly distributed, missing an individual tree could lead to greater errors in the map of fruit abundance. Given the clumped distribution of most tropical tree species (Condit et al. 2000), however, photo-derived crown maps at the relevant spatial scale should prove sufficient for other species as well.

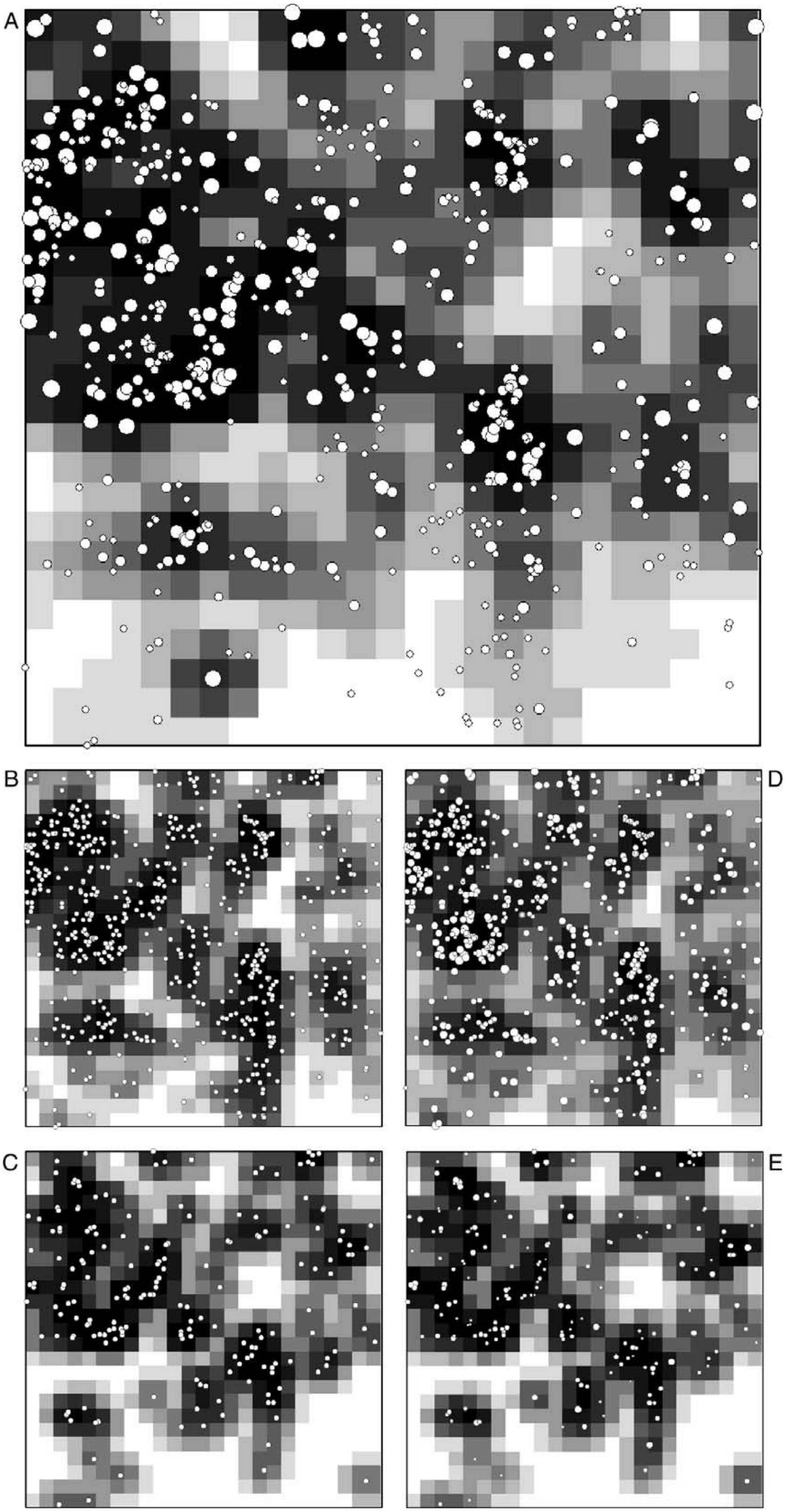

Fig. 4. (Continued)

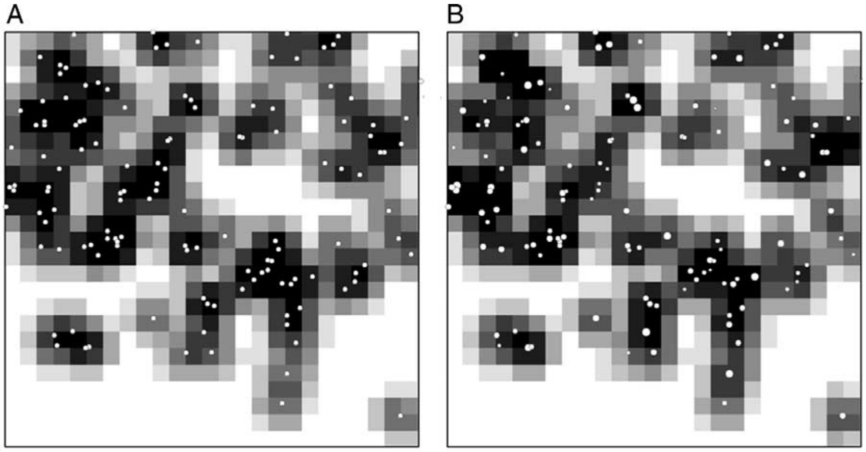

Fig. 5. Spatial density of photo-detected *Astrocaryum standleyanum* crowns (A) and crown area (B) across 25 ha of forest on Barro Colarado Island, Panama, based on aerial photo analysis without knowledge of the stem map and that includes errors due to misidentifications and missed crowns. See Fig. 4 for further explanation of symbols.

Basal area was a poor predictor of fruit crop size, and therefore did not improve the estimate of relative fruit abundance based on stem locations. This is in line with palms lacking secondary vascular cambium and therefore having little capacity for secondary growth (Tomlinson 1979, Rich et al. 1986). In contrast, crown size in dicot and conifer species, is positively correlated with stem diameter (Aiba and Kohyama 1997, Anderson et al. 2000, Wyckoff and Clark 2005, Bohlman and O'Brien 2006) and there is some evidence that stem diameter is positively correlated with fruit production (Hubbell 1980, Stevens 1987, Chapman et al. 1992). However, we did find a significant positive correlation of *Astrocaryum* basal area with the presence of exposed crowns on aerial photographs, suggesting that individuals with thick stems were more likely to have reached the canopy than were individuals with thin stems. Plausible explanations for this bias against small diameters in canopy-statured individuals are that the likelihood of mortality increases with stem slenderness due to reduced mechanical stability (Chazdon 1986), that thin-stemmed individuals do not grow as tall as thick-stemmed individuals, or that *Astrocaryum* does have significant secondary diameter growth.

Advantages and prospects

The advantages of the method outlined in this study are the ability to get information about fruit abundance over large areas at a relatively small time cost, even for inaccessible forest locations. Also, aerial photographs have the advantage of providing a permanent record of the forest canopy at one point in time, which can be compared to future photographs. Aerial photography offers a potentially economical alternative to time- and cost-intensive ground surveys. The main costs in our study were purchasing a satellite image, obtaining aerial photographs and photo processing, given that the required software was already available to us. The most time-intensive steps were registering the aerial photographs onto the satellite image (60 min per 8.6-ha photo) and mapping the crowns from the photographs (30 min ha^{-1} $\mathrm{analyst}^{-1}$). These time investments represent just a fraction of the time investment to get equal data through ground-based field work.

If the spatial resolution of satellite images increases in future instruments, mapping of small crowns in the canopy, such as palms, may be possible directly from satellite images. Using a single satellite image versus many aerial photos would greatly reduce the time needed to map tree crowns from images. With current high resolution satellite images, we can already map and track individual tree crowns from satellite images for species with large emergent crowns (Clark et al. 2004a, b, cf. Read et al. 2003) or with very conspicuous flower loads (for example *T. guayacan* as mentioned in the methods). However, mapping crowns from satellite images in the visible and infrared wavelengths will always suffer from lack of data due to cloud cover, whereas aerial photos can be collected even whenever the cloud ceiling is high enough for the airplane to be flown beneath it.

Mapping accuracy

Although the preliminary map predicted areas of high and low density of *Astrocaryum* fruit fairly well, the correlation with actual fruit abundance increased substantially between the preliminary map and the final map. There is a clear benefit of having a training location where individual stems are mapped that analysts can use to learn to detect and properly identify crowns of species of interest. Also, our

Fig. 4. Actual and predicted spatial distribution of *Astrocaryum standleyanum* fruits across 25 ha of forest on Barro Colarado Island, Panama. Maps show (A) the actual spatial density of fruits, based on direct visual fruit counts; (B–D) are predicted fruit densities based on (B) stem locations; (C) stem basal area; (D) locations of photo-detected crowns; and (E) photo-detected crown area. Cell colours correspond with ten equally-sized classes of Kernel-smoothed density, with black representing the 10% highest values and white including the 10% lowest values. Symbols show the location of individual trees used for determining the cell densities. For (A), (C), and (E), the symbols are scaled to crop size, basal area and crown area, respectively.

results demonstrate that multiple analysts can yield better results than a single analyst.

Measurement error can also be minimized by improving the quality of the photographs. The photographs used for this study were taken by a photographer hanging out the side of a small airplane using a medium-resolution camera without stabilizers. Professional aerial photographs made from specialized survey airplanes with stabilized high-resolution cameras are sharper and have a more uniform, nadir viewing angle of the canopy than the photos used in this study. On high quality photographs, potentially viewed in stereo, crowns would be more distinguishable and more easily identified to species. Also, the sunlit crown area measurements would be more controlled, as the camera would always be looking down straight on the canopy. Finer resolution images could also be achieved by flying at a lower altitude with the drawbacks that there will be greater parallax and each image covers a smaller area, requiring processing of a greater number of images to cover the same area on the ground.

Conclusions

We have combined a simple ecological relationship – fruit production in tropical forest trees increases with sun-exposure of tree crowns – and available technology to demonstrate that remote sensing of crowns can reliably estimate spatial variation in fruit abundance across large areas. This method identified areas of relatively high and low fruit abundance, and performed as well as did the more expensive ground-based stem-mapping methods. The potential of using remote sensing for estimating spatial variation in fruit abundance seems high where tree species that are important at the community level and/or represent keystone resources to frugivorous wildlife are canopy trees with distinct crowns.

Possible applications of the remote sensing technique outlined in this study are various. For example, areas can be selected with contrasting abundances of a tree species, for example for experimental studies of frequency- or density-dependence of reproductive success (Alvarez Buylla 1994, Wright 2002). Likewise, areas with contrasting fruit abundances can be identified for experimental studies of resource abundance effects on animal behaviour, abundance and population dynamics (Mangan and Adler 2002, Moegenburg and Levey 2003). A possible application in wildlife conservation is the selection of high-resource areas, which can support a larger biomass of wildlife per unit area than random areas, and may therefore yield a relatively large return for conservation efforts.

Acknowledgements – We thank Andres Hernandez and his crew for stem mapping, Marcos Guerra for taking the aerial photographs, Carlos Diaz for piloting the flights, Andrew Hida, Pablo Ramos and Marisha Futer for assistance with photo processing, Steve Paton, Arturo Sanchez, Jim Kellner, and Bob Stallard for data support, David Clark and four anonymous reviewers for valuable comments, and the Smithsonian Tropical Research Inst. for logistical support. This study was supported by the Netherlands Organization for the Advancement of Tropical Research (grant W84-584, P.A.J.), the research grant program of the Center for Tropical Forest Science at STRI (S.A.B.), and the Univ. of Minnesota (H.C.M.).

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