

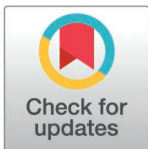
RESEARCH ARTICLE

Impact of swidden agriculture on palm populations in South-Central Guyana

Matthew J. Drouillard¹ , Anthony R. Cummings^{2*} , Persaud Moses³, Fabian Moses³, Catherine Auerbach²

1 Geospatial Information Sciences, School of Economic, Political and Policy Sciences, University of Texas at Dallas, 800 W Campbell Road, Richardson, Texas, United States of America, **2** Department of Earth and Environmental Sciences, Wesleyan University, Middletown, Connecticut, United States of America, **3** Wowetta Village, North Rupununi, Region 9, Guyana

* arcummings@wesleyan.edu



Abstract

Indigenous peoples across the tropics harvest fauna and flora from the local environments that they helped to shape. Among the flora that are harvested are palms that are distributed across swidden agriculture landscapes. Here we draw on imagery derived from unmanned aerial vehicles (UAVs) and convolutional neural network (CNN) object detection techniques to identify individual palms within a localized region of swidden agriculture in Guyana. A total of 10,194 palms were identified from six different species over 255 hectares. Land disturbed by swidden agriculture saw a 136% increase in palm density compared to undisturbed forest (53.3 versus 22.6). Local Moran's *I* cluster analysis showed that *Attalea maripa* was the dominant species in both undisturbed forest, representing 77.1% of palms, and swidden-disturbed land, representing 89.0% of palms. *Astrocaryum vulgare* declined in relative representation from 17.3% in undisturbed forest to 10.0% in disturbed forest, accompanied by reduced representation of other less abundant palms. These results demonstrate that swidden disturbance can increase total palm density while simplifying the palm assemblage and reducing the relative representation of less abundant species. This trade-off is important for informing more sustainable land-use pathways that maintain the livelihood and cultural functions of swidden agriculture while conserving palm-community diversity. Furthermore, 0.5-meter-resolution multispectral WorldView-2 imagery detected approximately 70% fewer palms than UAV imagery.

OPEN ACCESS

Citation: Drouillard MJ, Cummings AR, Moses P, Moses F, Auerbach C (2026) Impact of swidden agriculture on palm populations in South-Central Guyana. PLOS Sustain Transform 5(9): e0000275. <https://doi.org/10.1371/journal.pstr.0000275>

Editor: Prashant Sharma, ICAR-IISWC: ICAR Indian Institute of Soil and Water Conservation, INDIA

Received: May 22, 2025

Accepted: July 30, 2026

Published: September 18, 2026

Peer Review History: PLOS recognizes the benefits of transparency in the peer review process; therefore, we enable the publication of all of the content of peer review and author responses alongside final, published articles. The editorial history of this article is available here: <https://doi.org/10.1371/journal.pstr.0000275>

Copyright: This is an open access article, free of all copyright, and may be freely reproduced, distributed, transmitted, modified, built upon, or otherwise used by anyone for any lawful

Author summary

Indigenous communities throughout tropical regions often rely on traditional shifting cultivation, known as swidden farming, to grow staple crops and sustain livelihoods. They also commonly depend on local palm species for food, medicine, and building materials. While farming and palm use have been studied

purpose. The work is made available under the [Creative Commons CC0](#) public domain dedication.

Data availability statement: Data cannot be made publicly available because of agreements with the Indigenous community participating in this research. Under these agreements, data collected through the project may not be shared with third parties without permission from the participating community. Researchers interested in requesting access to the data may contact Anthony R. Cummings (arcummings@wesleyan.edu), Matthew J. Drouillard (mtdrouillard@gmail.com), or the designated Wowetta Village contact, Nowell Domingo (domingonowell07@gmail.com). Requests will be considered in consultation with the participating community and in accordance with the conditions under which the data were collected. The data will be retained securely by the research team to support long-term availability subject to these access restrictions.

Funding: This study was supported by the National Science Foundation under grant number 2047940, awarded to AC. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. No authors received salary support from the funder.

Competing interests: The authors have declared that no competing interests exist.

separately, the relationship between agricultural practices and palm species diversity remains less understood. Using drone imagery collected over forests and farming areas in Guyana, we found that shifting cultivation was associated with substantially greater overall palm abundance than tall-canopy forest. However, this increase was concentrated mainly in one dominant species, *Attalea maripa*, while other palms became less represented. Greater palm abundance therefore did not correspond to a more diverse palm community. Drone imagery also provided substantially more complete palm counts than satellite imagery. Recognizing the trade-off between overall abundance and community diversity can support land-use approaches that sustain Indigenous food production and culturally important resources while maintaining ecological diversity across swidden landscapes.

1. Introduction

Indigenous communities across the tropics have strong connections to their landscapes and local environments. Indigenous peoples harvest fauna and flora, including palms (e.g., Arecaceae) from within their homelands [1–4]. The traditional practices of indigenous peoples, including their swidden agriculture practices, facilitate the presence of the animals and plants found within indigenous peoples' landscapes [5]. Indigenous farming practices, known as swidden or shifting agriculture, involve clearing of forests to facilitate the cultivation of staple crops [5,6]. The procedures surrounding swidden agriculture, most of which have been employed by native people across the world for thousands of years, and their environmental impacts have received in-depth research and divided opinion for some time [5,7–10]. A typical swidden plot is cultivated for one to two growing seasons (2–3 years), followed by a multi-year fallow period that is often 2–15 years but may be longer [8–10]. Once the land is left to fallow, vegetation, typically of a non-agricultural nature, reclaims the land within as little as 1–2 years [11,12]. The soil chemistry and other conditions created by growing crops impact the diversity of vegetation species that emerge during fallow [10,13,14]. Other scholars have also noted that the diversity of vegetation that emerges is influenced by the original forest assemblage and the frequency and amount of human disturbance experienced on the land [10,12,15,16]. Repeated cycles of swidden agriculture can deplete soil phosphorus, leading to a millennium-scale timeline for full forest regeneration [17]. Furthermore, the intermediate disturbance hypothesis (IDH) [18], which postulates that the diversity of species following anthropogenic disturbance is a function of the frequency, quantity, and time gradient after disturbance, is a feature of swidden landscapes [19].

In the Neotropics, where palm diversity is high [20], swidden agriculture can reduce the local abundance of some palm species in the short term; however, after fields are left to fallow, secondary regrowth can favor a subset of disturbance-tolerant or broad-niche palms by relaxing competition with hardwood canopy trees and increasing light availability [21,22]. This successional pattern often results in higher

densities—and in some cases improved demographic performance—of pioneer or disturbance-adapted palms following primary canopy removal [23,24]. Comparable patterns have been documented across the Neotropics and Mesoamerica. In the Maya Lowlands, *Sabal yapa* persists across the milpa–fallow–mature forest cycle and exhibits habitat-specific demography and population growth shaped by both disturbance and management practices that retain palms during clearing [25,26]. In Mexican dry forests, traditional agroecosystem management and recurring burning are closely linked to the structure and expansion of *Brahea dulcis* stands, where slash-and-burn can facilitate recruitment and dominance during fallow periods [27,28]. In Amazonia, recruitment of large *Attalea* palms is strongly associated with canopy openness and disturbance, consistent with increases observed in secondary and human-modified forest mosaics [29,30]. Palms reported to regenerate following swidden include *Astrocaryum aculeatum*, *Astrocaryum vulgare*, and *Attalea maripa* [23], and anthropological work highlights long-term legacies of burning and cultivation in shaping palm-dominated landscapes [31]. Because successional trajectories and palm responses vary with local context (e.g., landscape structure and proximity to old-growth forest) [13,24], documenting the distribution of culturally important palms within swidden mosaics is critical for evaluating environmental impacts and supporting the sustainability of Indigenous livelihood practices.

Remote sensing can play an important role in examining the distribution and types of palms present within swidden agriculture landscapes. To date, most studies utilizing remotely sensed data for understanding swidden landscapes have been completed in Southeast Asia [32]. However, standard multispectral satellite imagery is not suitable for per-species discrimination of individual tree crowns in natural forest scenes [33], and hyperspectral imagery with high spatial resolution, multispectral imagery with short-wave infrared capability [34], or very high spatial resolution aerial imagery [35–39] provide better outcomes, but are typically expensive to acquire. Yet, fine-scale remotely sensed data derived from unmanned aerial vehicles (UAV) have been utilized to study vegetation dynamics within swidden agriculture landscapes [6].

Sustainable management of Indigenous swidden landscapes requires more than maintaining either agricultural production or forest cover in isolation. It requires understanding how repeated cycles of clearing and fallow affect both culturally important resources and the broader composition of ecological communities. Determining whether swidden disturbance benefits palms generally or instead favors a limited subset of species can therefore inform land-use approaches that support Indigenous livelihoods while maintaining biodiversity over time.

Here we build on past work completed within swidden landscapes using remotely sensed data derived from UAVs to examine the utility of such imagery coupled with convolutional neural network (CNN) object detection techniques to identify individual species and specimens (individual palms without reference to species) of palm within a swidden agriculture landscape. Our objective was to quantify palm distribution in the vicinity of indigenous swidden agriculture to address the following questions: (1) what are the identifiable species of palms and their abundance in the study area? (2) what physical characteristics of palms can be detected with UAV data? (3) what is the spatial pattern of the height of palms and their relationship to disturbed versus undisturbed forested areas within swidden landscapes? (4) how does the ability of satellite technology to resolve individual palm specimens compared to that of UAV imagery? Our work is among the first to examine the distribution of palms using UAV-derived data and provides evidence relevant to the sustainable management of Indigenous swidden landscapes, particularly the balance among palm abundance, community composition, and ongoing agricultural use.

2. Materials and methods

2.1. Study area and UAV imagery for palm detection

This study was completed with data collected from the Makushi Amerindian village of Wowetta (Annai District), Upper Takutu-Upper Essequibo (Region 9), Guyana (4.017°N, 59.066°W) where the local population are active practitioners of swidden agriculture and where all the stages of the swidden agriculture process are easily observable (Fig 1). The region is defined by large amounts of tropical rainforest and has a tropical monsoon climate as per the Köppen-Geiger climate



Fig 1. Various stages of swidden agriculture in the area of interest: active clearing of land (top left), freshly planted *Manihot esculenta* (top right), established *Manihot esculenta* with emergent palm regeneration (bottom left), and mature *Manihot esculenta* (bottom right) with emergent palm at ground level in foreground. These images are of four separate fields within the study area, captured during the 2022–2023 fieldwork period; they represent a visual mosaic of typical *Manihot esculenta* growth and swidden stages. (Credit: M. Drouillard).

<https://doi.org/10.1371/journal.pstr.0000275.g001>

classification system. The area is a part of the Rupununi Savanna [40], and the terrain is of low relief. UAV imagery was obtained in August and December 2023 using a DJI Phantom Pro 4 V2.0 (Fig 2). True-color (RGB) imagery was collected using the Phantom's built-in 20-megapixel camera. The surveys were conducted using a linear transect pattern, orienting the flights to maximize the duration of the straight-line flight. The imagery was captured at Guyana's legal flight ceiling of 122 meters, with the front and side overlaps of the images varying from 50% in the southeast of the mapped area to 70% in the northwest. Ground control points were not utilized during the surveys.

Once the imagery obtained was sorted and cleaned, orthomosaics were created in Agisoft Metashape following the standard image processing workflows. Once the imagery was processed in Agisoft, the RGB orthomosaics and three-dimensional digital elevation model (DEM) of the area were generated at 0.033 m and 0.065 m resolution, respectively, in UTM 21N projected coordinate system. The orthomosaic surveyed in December 2023 (northwest portion of study area) was georeferenced manually as reasonably as possible to an available 0.5 meter (pan-sharpened) resolution WorldView-2 satellite image covering the study area [41]. The orthomosaic from August and December were subsequently



Fig 2. UAV survey being conducted in the study area. Vegetation in the scene is representative of a fallow swidden plot. The burned vegetation is due to a fire that encroached when an adjacent farm was cleared. (Credit: M. Drouillard).

<https://doi.org/10.1371/journal.pstr.0000275.g002>

georeferenced to one another by utilizing stable landmarks within the scenes, including farm buildings and tree stumps. Due to the specific interest in the relative height above the local ground level, a canopy height model (CHM), commonly known as a digital surface model, was created by manually selecting 568 bare-earth points between the two orthomosaic DEM scenes and generating a digital terrain model (DTM) through radial basis function interpolation from these points. The interpolated DTM layer was then subtracted from the DEM to derive the CHM, which is referenced to the local zero level of the bare earth.

Palm detection was performed using the Mask R-CNN deep learning algorithm [42] with a ResNet-50 backbone for transfer learning [43]. The Mask R-CNN algorithm was trained to perform both specimen detection and species classification simultaneously. Individual palm specimens were manually outlined to capture the precise shape of the visible crown and occlude background where possible. In total, 766 palms were selected for training and 72 for testing. The training dataset for species classification was manually generated based on a combination of *a priori* knowledge of species in the area [3], interpretation of selected images by field guides during data collection, and manual identification of palms during fieldwork in 2022. This manual verification ensured the accuracy of the six unique species labels assigned to the training specimens for the CNN. An image chip size of 448 x 448 pixels image chips (14.7-meter ground distance) was utilized for algorithm training, as this size allows for one full palm crown within the image tile. These were cumulatively produced by varying the x and y stride or overlapping of the search tiles as they pass through the training set zones. This had the net effect of multiplying the apparent training samples available for the Mask R-CNN. Using this method, 8,166 specimens on 4,825 image chips were available to train the algorithm from the original 766. Subsequently, these image chips were submitted for data augmentation [44], including variations in lighting, rotations, and a maximum zoom of 0.9 as they were processed through the training algorithm. Training occurred with batch sizes of 9 for 30 epochs [45] with a learning rate of $1.5e^{-4}$ and a one-cycle learning rate applied [46]. The trained algorithm was finally applied to the complete orthomosaic to identify instances of palms throughout the study area.

The circular crown diameter of each detected palm was calculated, and the height of each palm was sampled from the CHM as the mean height within the circle of crown diameter. The calculated crown diameters and heights rely solely

on the UAV-derived imagery and CHM data. Due to significant logistical and time constraints associated with the remote study location, field-based measurements (ground truth) of palm dimensions were not feasible to obtain for absolute validation and calibration of the image-derived measurements. Consequently, the geometric attributes presented (crown diameter and height) are relative estimates derived exclusively from the UAV orthomosaic and CHM. Palms with a crown diameter less than 1 square meter in area were removed as unreliable detections. The Intersection over Union (IoU) (equation 1.1) between the training or test features and the detected features was used to validate the detections. The F1 score (equation 1.4) was then optimized in the confidence range by locating where the difference between Precision (equation 1.2) and Recall (equation 1.3) is minimum.

$$J(A, B) = \frac{AB}{AB} \quad (1.1)$$

$$Precision = \frac{TruePositive}{TruePositive + FalsePositive} \quad (1.2)$$

$$Recall = \frac{TruePositive}{TruePositive + FalseNegative} \quad (1.3)$$

$$F1 = 2 * \frac{Precision * Recall}{Precision + Recall} \quad (1.4)$$

Palms less than 1.25 meters high were removed because they were difficult to reliably distinguish from other ground-level objects. The $\log(\frac{Area}{Height})$ The data from the palms was used to distinguish and remove outliers (a logarithm was applied to achieve a normal distribution), mainly due to atypically shaped crown detections that affected the estimation of the palm crown diameter. Palm species detected in low abundance were manually verified and corrected as needed.

2.2. Distribution analysis

The distribution of palms detected in the orthomosaics was focused on the height of the palm crown using the Local Moran's I algorithm [47], implemented by the Cluster and Outlier Analysis tool in ArcGIS Pro. This method identified local clustering of spatial associations considering a given attribute value (here, palm crown height) and adjacent values. There are five possible outcomes: (1) Outlier, where there are no local associations (2) Low-Low, clustering of low value surrounded by similarly low values (3) Low-High, attributes of low value surrounded by dissimilar high values (4) High-Low, attributes of high value surrounded by dissimilar low values, or (5) High-High, clustering of high value surrounded by similarly high values.

The radius of investigation, or scale of analysis, for Local Moran's I was determined by the Incremental Spatial Auto-correlation tool in ArcGIS Pro. The presence of spatial autocorrelation via the Global Moran's I [48] of the height attribute was investigated at 10-meter intervals to a maximum distance of 300 meters. At each interval, a z-score and p-value were computed, and the interval with the highest significant z-score was considered the optimal search radius, as this distance ideally represents the extent to which clustering of similar features was most notable. The spatial relationship between palm features was modeled through a zone of indifference, whereby all features within the search radius received the same weighting, and features outside the search radius received diminishing weight with distance. Row standardization of spatial weights was applied, and the algorithm was iterated 9,999 times.

3. Results

3.1. Palm Detection

The total area mapped after orthomosaic processing and image cleanup was 2.55 square kilometers (255 hectares; Fig 3). The area consisted of intermixed swidden farms (seen as bare earth patches in RGB and grey in the CHM), low forest (green in CHM image), and high forest (orange red in CHM image). Low forest was most prevalent surrounding the active swidden plots and has a high probability of human influence. The high forest, in contrast, is largely undisturbed by modern day human activity and remains the tallest, and thus the oldest, forest growth in the area surveyed. The CHM has a minimum height of 0.0 meters (bare earth), a mean of 10.0 meters, a maximum of 42.0 meters, and a standard deviation of 7.3 meters. Six unique species of palm were identified within the orthomosaic imagery: *Astrocaryum vulgare*, *Mauritia*

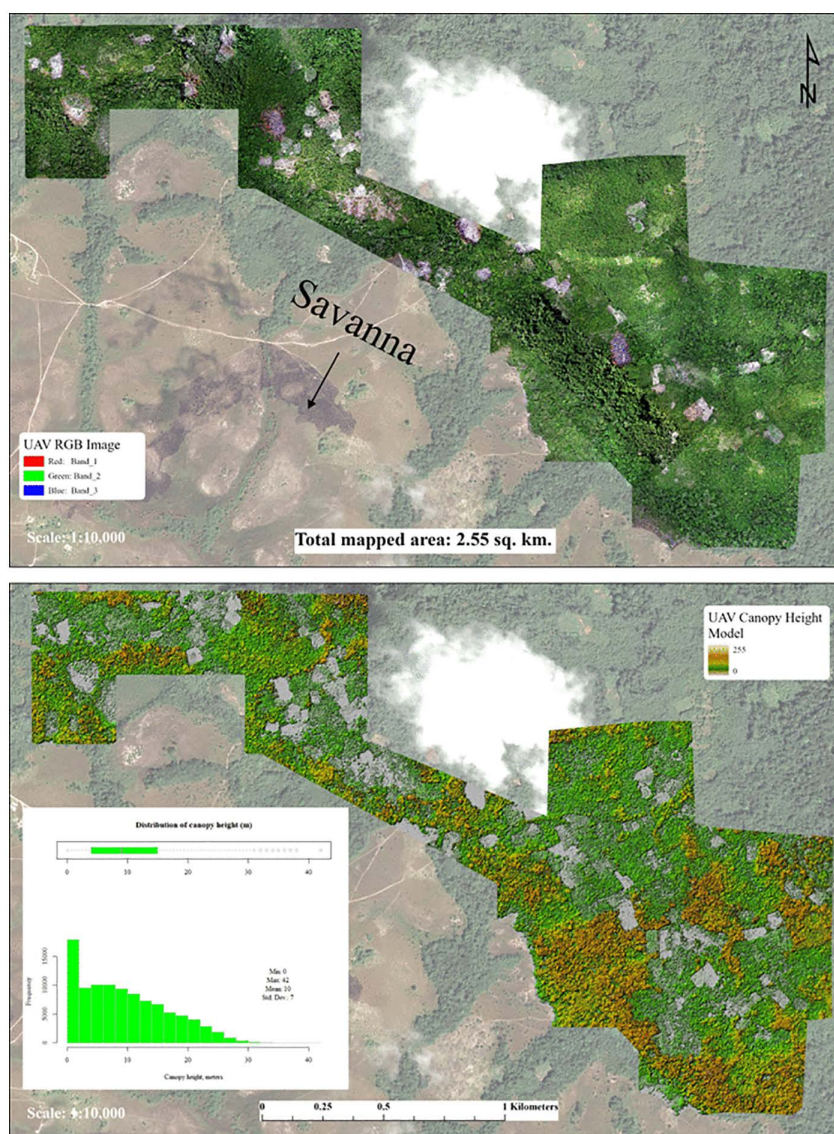


Fig 3. RGB mosaic (top) and canopy height model (CHM) (bottom) processed from UAV imagery collected in August and December 2023.

<https://doi.org/10.1371/journal.pstr.0000275.g003>

flexuosa, *Attalea maripa*, *Oenocarpus bataua*, *Euterpe oleracea*, and *Oenocarpus bacaba* (Fig 4) [see [23, 49] for details on each species and their associated importance to humans in the Amazon region].

Due to the minimal proportion of palm species other than *Astrocaryum vulgare* and *Attalea maripa* identified in the study area, the confidence threshold analysis was restricted to these two species. From this analysis, a confidence threshold of 80% was selected as the detection confidence threshold (i.e., detections with confidence less than 80% are discarded from further analysis) (S1 Table). The accuracy assessment metrics for the training set at confidence levels of 80% or higher demonstrate balanced Precision and Recall with a combined F1 score of 0.86 for all species (Table 1a). The test set exhibits a measured decrease in performance, particularly in Recall (Table 1b). The sizable proportion of false negatives in both the training and test sets is hypothesized to be caused in part by the irregularly shaped crown structures identified by the algorithm's detection capabilities and the challenges in aligning these with the training data using the standard intersection over union (IoU) method. This was tested by lowering the IoU threshold to 25% and rerunning the assessment metrics (S1 Table). With a lower threshold for overlap imposed on the complex palm outlines, combined false positive detection rates were reduced by 25 (-30%), and false negative detection rates were reduced by 29 (-24%) in the

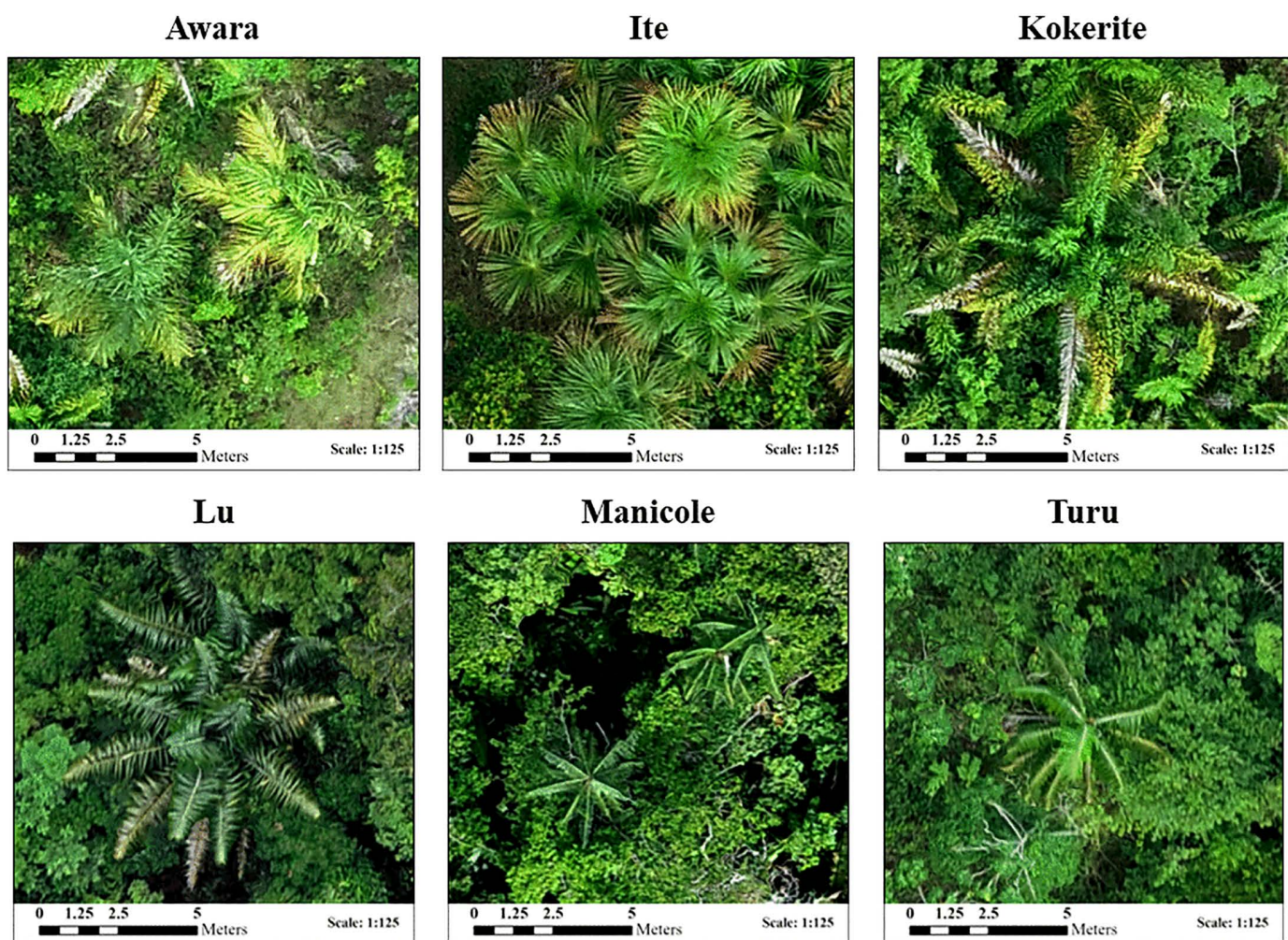


Fig 4. Identified palms within UAV imagery. Clockwise from top left: *Astrocaryum vulgare* (Awara), *Mauritia flexuosa* (Ite), *Attalea maripa* (Kokerite), *Oenocarpus bataua* (Turu), *Euterpe oleracea* (Manicole), *Oenocarpus bacaba* (Lu). (Credit: M. Drouillard).

<https://doi.org/10.1371/journal.pstr.0000275.g004>

Table 1. Assessment Metrics.

(a) Assessment metrics for the training data set.

Class	Precision	Recall	F1	TP	FP	FN
Combined	0.887	0.842	0.864	643	82	121
Kokerite	0.884	0.837	0.860	466	61	91
Awara	0.897	0.830	0.862	78	9	16
Manicole	0.887	0.922	0.904	47	6	4
Lu	0.926	0.862	0.893	25	2	4
Ite	0.889	0.889	0.889	16	2	2
Turu	0.846	0.733	0.786	11	2	4

(b) Assessment metrics for the test data set.

Class	Precision	Recall	F1	TP	FP	FN
Combined	0.790	0.625	0.698	45	12	27
Kokerite	0.800	0.645	0.714	40	10	22
Awara	0.833	0.500	0.625	5	1	5

Palms detection accuracy results from Mask-RCNN algorithm. All values at > 50% IoU and > 80% confidence detection.

<https://doi.org/10.1371/journal.pstr.0000275.t001>

training set. The test set saw an overall reduction of 4 false positives (-33%) and 4 false negatives (-15%). As a result, Precision, Recall, and F1 scores exhibited marginal improvements; however, for consistency with comparable literature, the accuracy metrics at an IoU of 50% are presented here. Following manual quality control of palm detections post-confidence threshold optimization, the final palm tally was 10,194 across the study area.

The diameter distribution of the palm crowns for Awara and Kokerite showed a positive skew distribution, with a mean diameter of 5.16 meters and maximum diameters ranging from 11 to 14 meters (Fig 5). Furthermore, the palm crown diameter was modeled as a function of palm height by second-order polynomial regression with $R^2=0.52$ (Fig 6). The regression curve approached linearity until palm heights of approximately 10 meters, where the curve inflected and began to flatten due to the influence of shorter palms with larger crown diameters.

3.1.1. Distribution analysis. Results of the Local Moran's I cluster analysis demonstrated four clear cluster patterns, along with boundary margin outliers. The Moran analysis shows a breakpoint between palms of low height and palms of high height at a value of 8.25 meters (Fig 7). The largest pattern of palms occurred in the Low-Low scenario, where palms of low height are surrounded by similarly low-height palms, and the second largest pattern is that of High-High, where high-height palms are surrounded by similarly high-height palms.

To efficiently display the Local Moran's I patterns in spatial map format, the CHM was classified into forest canopy (overall canopy, not solely palms) of less than and greater than 10 meters based on the mean canopy height value for the CHM. Active farming plots were defined as areas with substantial bare earth coverage that demonstrated signs of recent human activity, and are delineated accordingly on the map. Active cassava crops larger than 0.5 meters in height were also identified and marked. The paths for foot or vehicle traffic were manually interpreted and digitized (Fig 8) where sporadically intermixed Low-High palms as evidence of a fallow farm plot.

Low-Low clustered palms occur exclusively within areas of canopy less than 10 meters in height, and generally adjacent to pathways and/or active farms. High-High cluster palms are limited to a canopy greater than 10 meters in height. Low-High and High-Low clustered palms are either sporadically intermixed, or act somewhat as transition zones between canopy less than and greater than 10 meters. An example of Low-High clusters suggests older incursion of farm plots into high forests that have subsequently been left to fallow (Fig 9).

A summary count of palm features within each canopy height subclassification showed that Kokerite was the dominant species in either canopy height grouping, representing 89% of palms in a canopy less than 10 meters high and 77% of

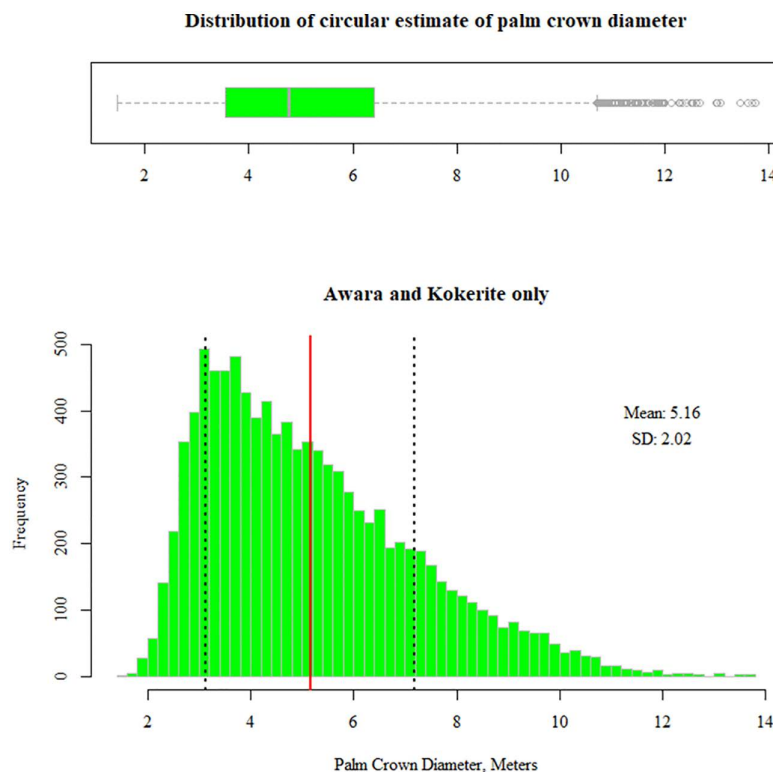


Fig 5. Distribution of estimated circular palm crown diameter, Awara and Kokerite palm only.

<https://doi.org/10.1371/journal.pstr.0000275.g005>

palms in a canopy greater than 10 meters high. Awara was the second largest species by representative count, comprising 10% and 17% in a canopy less than and greater than 10 meters, respectively. Continuing this pattern, Kokerite, followed by Awara, are the largest representatives in any of the four Local Moran's I cluster groupings (Fig 10). Based solely on the raw count of palms in each subclassification, Kokerite palms are the largest increase in low canopy conditions, increasing from 1,916 in canopies greater than 10 meters to 6,898 in canopies less than 10 meters. Moreover, out of the 4,182 palms categorized as Low-Low (Fig 9), 3,791 (or 91%) are Kokerite (Fig 10).

3.1.2. Satellite versus UAV detected palms. The subject of detection of palms from satellite imagery in the same study area was described elsewhere [50]. A consideration when discussing remotely sensed data, particularly when comparing satellite and UAV-based imagery, is understanding what can be detected and studied in the two imagery datasets. UAV imagery typically provides greater spatial resolution [51], and while there are general rules that one may apply to predict resolvable features [52], the highly variable nature of Earth's landscapes makes detection of objects questionable. To quantify the differential in detection between remote sensing of palms, we analyzed the difference between palm detections from WorldView-2 using the Mask R-CNN algorithm [50] and those detected from UAV imagery. The satellite-derived and UAV-derived palms were accumulated into a single group, and the count summarized in both forests for palms less than and greater than 10 meters high. Since there was a 13-year gap between the acquisition of the satellite image (2010) and the UAV imagery (2023), the comparison was completed with caution. The primary goal of this comparative analysis was not to track temporal land-cover change, but rather to quantify the differential in palm detection capability resulting from the vast difference in spatial resolution between the two remote sensing platforms, WorldView-2 (0.5 m) and UAV (0.033 m). The forest currently classified as less than 10 meters may not have been in that state during the satellite imagery data collection and any palms that may have regenerated in the subsequent decade would not have

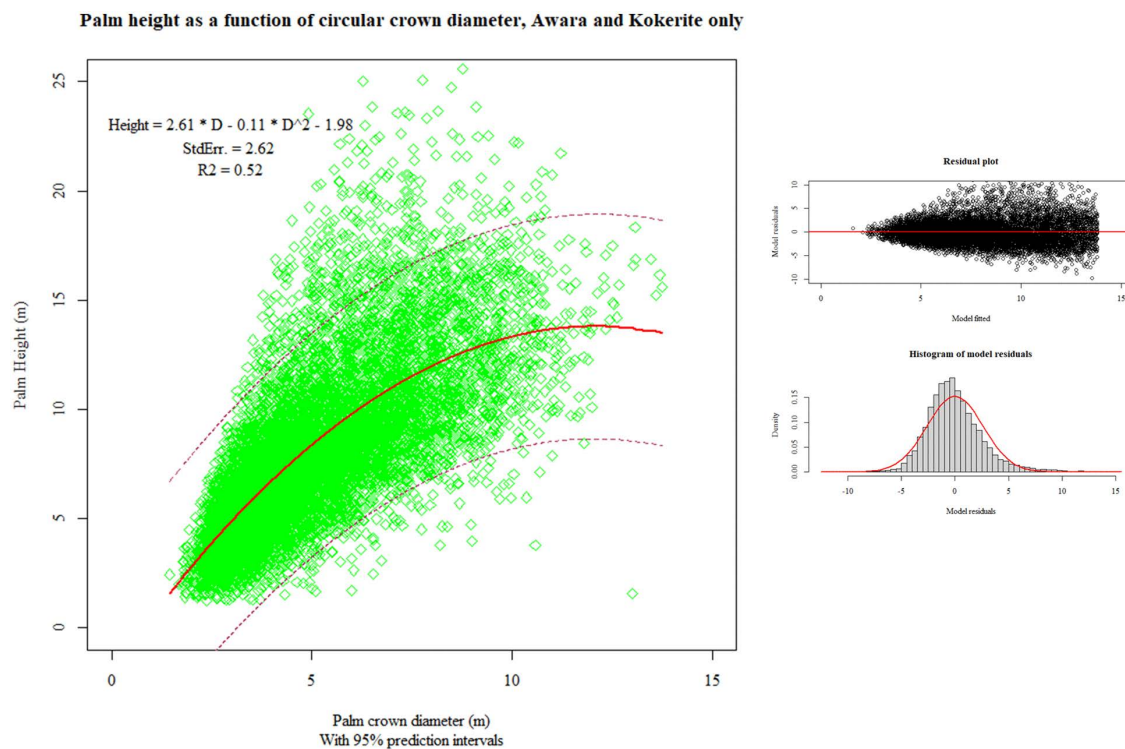


Fig 6. Polynomial model of palm height against canopy circular diameter (left) and residuals diagnostic plot (right).

<https://doi.org/10.1371/journal.pstr.0000275.g006>

been present in 2010. It is much more likely that the forest currently classified as greater than 10 meters in height was and remains reasonably undisturbed during the time interval, and thus the overall palm count should be reasonably stable.

The result of this comparative analysis showed that the palm features detected by satellite were highly disproportionate to those detected in UAV imagery (Fig 11). Palms detected by satellite in high forest (higher than 10 meters in height) represented only 31% of the palms detected by UAV. The number of satellite palms detected in low forest (less than 10 meters height) was approximately equal to those detected in high forest (750 versus 780); however, only represented 9.7% of the UAV detections. While the location comparison of low forest classification satellite palms could be used to make inferences on major land clearing in the intervening 13 years, the summary count comparison is likely highly misleading due to the regeneration of new palms since 2010. Therefore, the primary measure of sensor underestimation is derived from the high forest (>10m) classification, where the palm population is assumed to be relatively stable due to minimal disturbance over the 13-year interval. The summary suggests that the satellite palm survey underestimated the UAV survey by 70%.

4. Discussion and conclusions

4.1. Discussion

Total palm density was higher in disturbed/low-canopy forest than in tall-canopy forest ($53.3 \frac{\text{palms}}{\text{Ha}}$ in low forest and $22.6 \frac{\text{palms}}{\text{Ha}}$ in high forest; a 136% increase); however, this pattern should not be generalized to all palm taxa. Palms span contrasting ecological strategies ranging from shade-obligate understory species to gap-dependent and light-demanding arborescent species whose recruitment and/or stem-elongation phases often require higher light availability [53,54]. Accordingly, secondary forests and swidden fallows often show increases driven by a subset of disturbance-adapted or

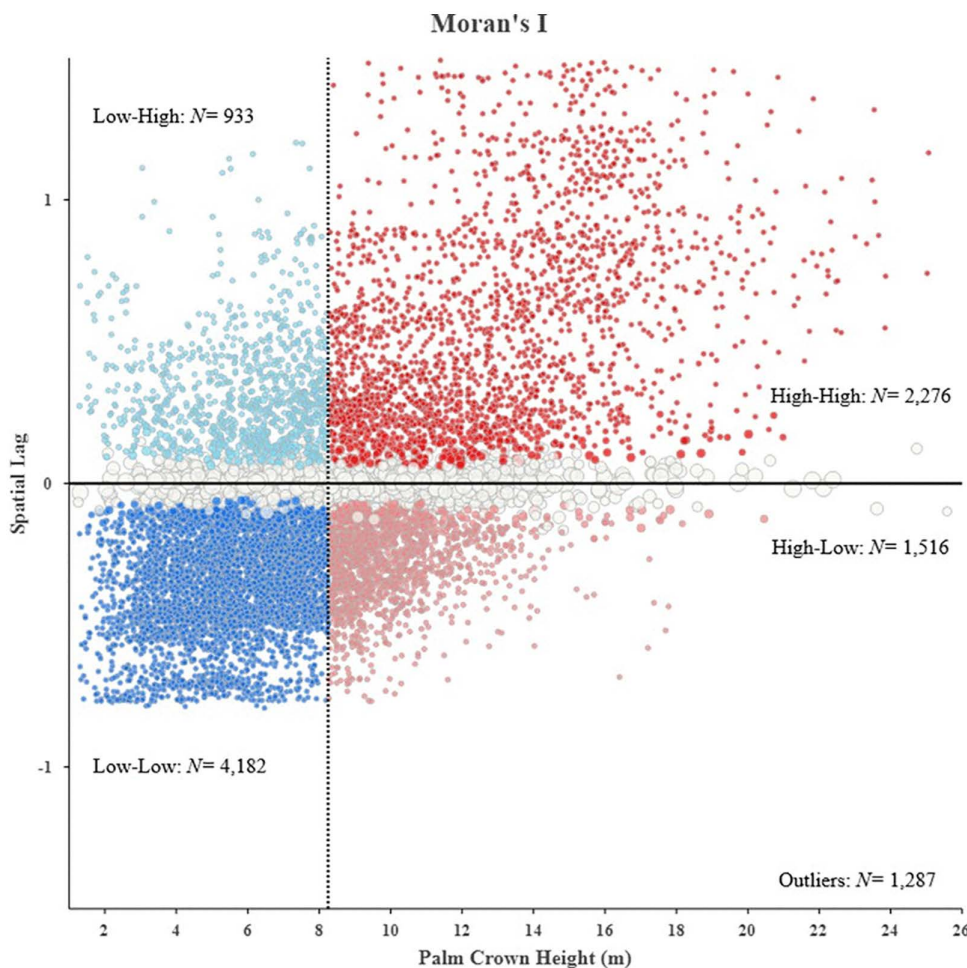


Fig 7. Graphical results of Local Moran's I analysis. Point size is proportional to pseudo p-value from 9,999 iterations, with smaller point size indicating lower p-value.

<https://doi.org/10.1371/journal.pstr.0000275.g007>

broad-niche palms, while shade specialists and habitat specialists may remain stable or decline in relative or absolute terms. In our study, the density increase is explained primarily by a shift in composition toward Kokerite, which dominates disturbed/low-canopy areas, consistent with disturbance-linked recruitment in *Attalea* [29] and with swidden landscapes where increases are reported mainly for disturbance-tolerant or managed taxa such as *Sabal* and *Brahea* under milpa slash-and-burn regimes [26,28]. Here, Kokerite increases from 77.1% of total palms in high forest to 89.4% in low forest, while Awara declines from 17.3% to 10.0%; infrequent palms (Manicole, Lu, Ite, and Turu) also lose relative representation, each comprising <1.0% of individuals in low forest (Table 2). This composition shift- higher total density but lower evenness and diversity- is also reflected in the Local Moran's I results, which show spatial clustering patterns consistent with our 10 m forest-height threshold separating low vs. high forest (Fig 10).

These findings reveal an important sustainability trade-off that would be obscured by considering total palm abundance alone. The greater density of palms in low-canopy forest may increase the abundance of some culturally important resources, but the concurrent increase in Kokerite dominance indicates a simplification of the palm community. More sustainable stewardship of these landscapes should therefore account for both livelihood benefits and changes in species composition, rather than treating agricultural use and biodiversity conservation as mutually exclusive objectives.

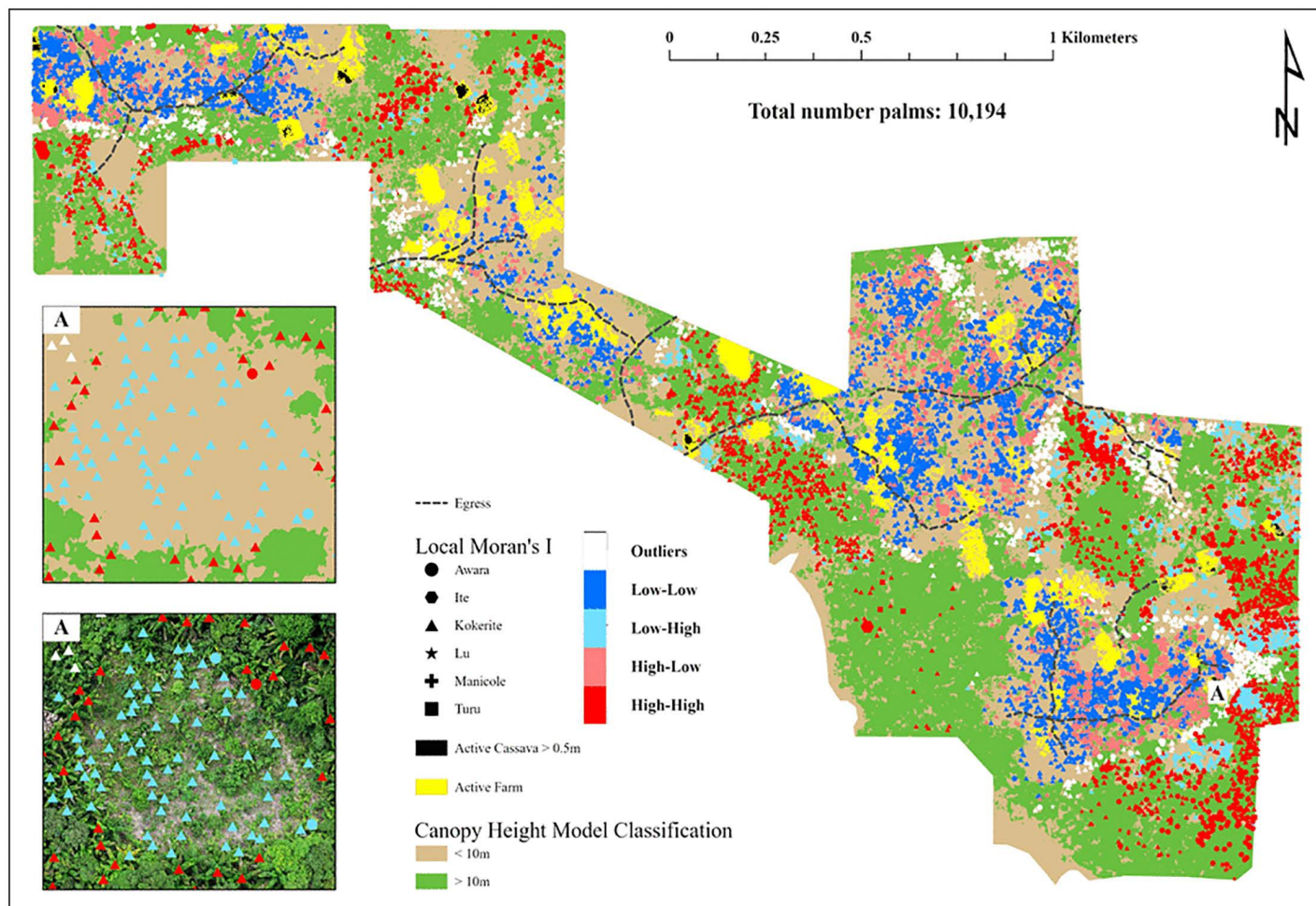


Fig 8. Spatial results of Local Moran's I analysis. The total area of low forest (< 10 meters) is 144.8 hectares, and 109.9 hectares for high forest (> 10 meters).

<https://doi.org/10.1371/journal.pstr.0000275.g008>

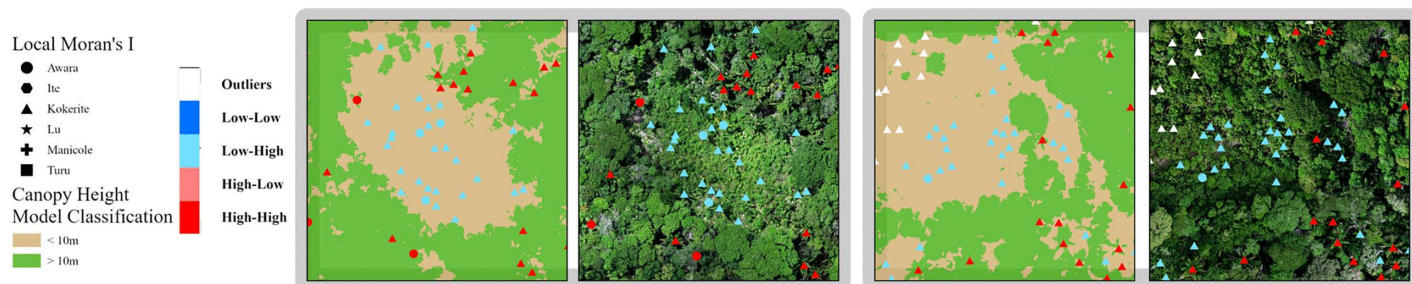


Fig 9. Examples of Low-High palm clustering suggestive of older fallow swidden farm plots.

<https://doi.org/10.1371/journal.pstr.0000275.g009>

Local Moran's I palm count by cluster

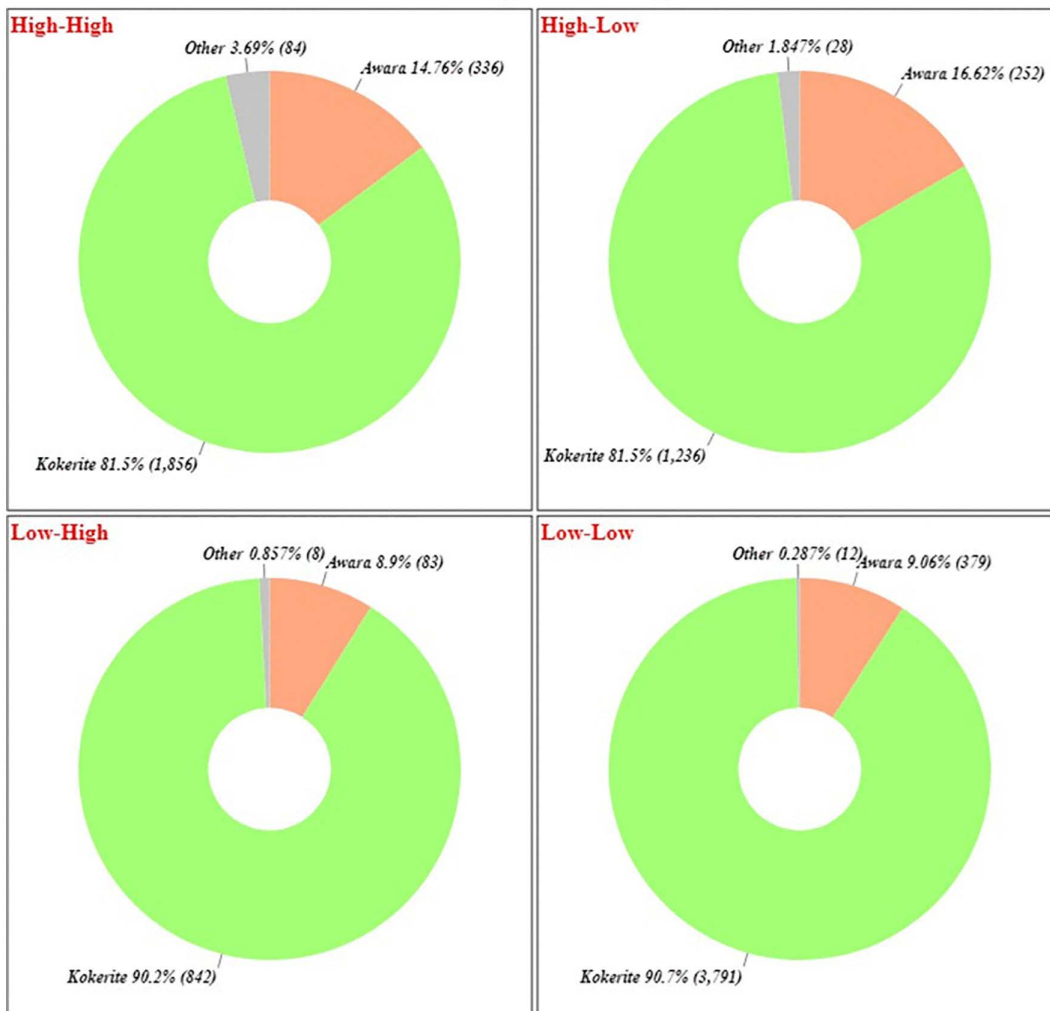


Fig 10. Division of palms in each significant cluster (outliers not included) identified by Local Moran's I analysis.

<https://doi.org/10.1371/journal.pstr.0000275.g010>

The UAV-derived relationship between palm height and crown diameter (Fig 6) shows a positive association with clear nonlinearity at larger sizes, broadly consistent with published height–DBH allometry for Amazonian palms modeled with nonparametric (LOESS) fits (e.g., *Euterpe precatoria* [55]). Because our size proxy is crown diameter (not DBH) and our dataset excludes very small individuals, differences in the lower tail are expected, but the overall form supports the plausibility of the image-derived size–height relationship.

However, these geometric results should be interpreted with appropriate caution because our analysis relied exclusively on UAV-derived measurements without field-based ground truth. This limits absolute calibration of crown diameter and height estimates and prevents direct validation of CHM-derived height values. Although the observed height–crown diameter relationship ($R^2=0.52$) and its general consistency in form with field-based palm analysis suggest that relative patterns and statistical relationships are meaningful, absolute dimensions should be interpreted as approximate. Future work should prioritize field campaigns to collect ground measurements (e.g., measured height and crown diameter, and DBH where applicable) to refine and calibrate UAV-derived estimates and strengthen biophysical interpretation.

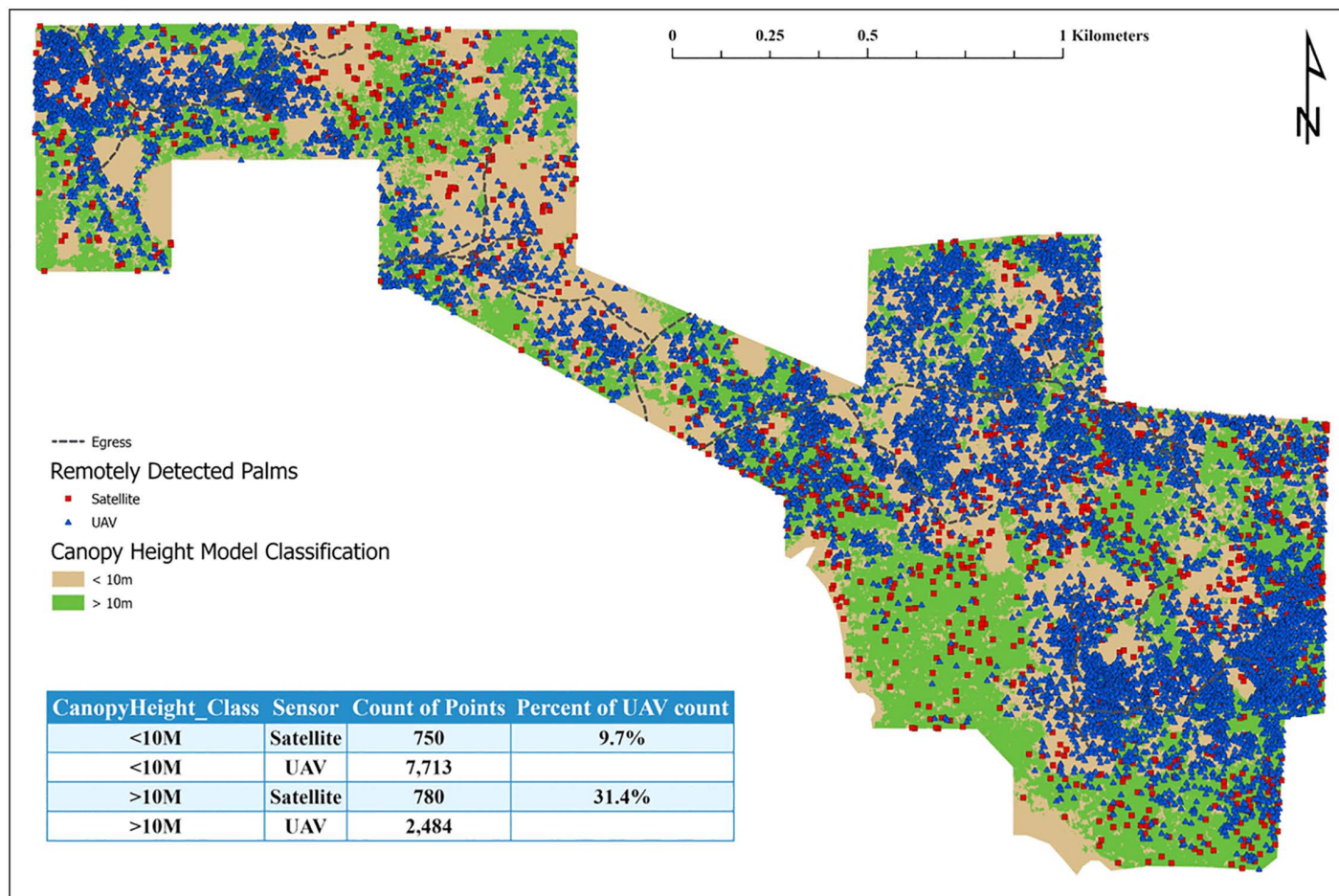


Fig 11. Statistical comparison between palms detected by UAV imagery and satellite imagery.

<https://doi.org/10.1371/journal.pstr.0000275.g011>

Table 2. Canopy and Palm Crown Characteristics.

Canopy Height	Palm	Mean Crown Height	Palm Count	Percent Palm Count
<10 meters	Kokerite	6.5	6,898	89.4%
	Awara	6.8	774	10.0%
	Turu	6.3	22	0.3%
	Ite	7.4	9	0.1%
	Lu	9.0	6	0.1%
	Manicole	8.2	4	0.1%
>10 meters	Kokerite	13.3	1,916	77.1%
	Awara	13.9	430	17.3%
	Manicole	16.0	72	2.9%
	Lu	14.8	41	1.7%
	Ite	12.2	14	0.6%
	Turu	15.3	11	0.4%

Summary statistics of per species palms between forest canopy height less than 10 meters and greater than 10 meters.

<https://doi.org/10.1371/journal.pstr.0000275.t002>

The Intermediate Disturbance Hypothesis (IDH) would predict that shifts in disturbance regime can influence diversity patterns [18]. However, we avoid drawing strong conclusions about the mechanisms underlying the reduction in palm diversity observed in low forest because palm recruitment and persistence are also shaped by factors not measured here, including light environment [56,57], soil conditions [13,14,57], the original forest assemblage and the intensity of land use [12,15,16,57], and seed source/parentage effects [24]. In addition, applying IDH in practice presents well-known challenges [58], and evaluating diversity responses to swidden disturbance would require explicit temporal replication across multiple successional stages.

Ite, Lu, Manicole, and Turu (grouped as “Other” in Fig 10) occur most frequently in the High-High and High-Low clusters. Beyond their low overall abundance, two interpretations are plausible. First, their concentration in High-High clusters may indicate that these species occupy habitats that are less suitable for farming (e.g., Manicole is associated with swampy areas [23]) or that sites containing these less common palms are avoided for clearing because of their perceived value. Second, their presence in High-Low clusters may suggest selective retention when encountered during clearing because of utilitarian importance. Indigenous management of culturally important flora near settlements and activity areas has been documented in comparable contexts [1,23,59]. Outlier palms form relatively sharp transitions along the same boundary zone, especially in the southeastern portion of the map. At present, we interpret these outliers as transitional features that do not consistently match the four dominant clustering classes, and we cannot provide a stronger explanation without additional site-level data.

Future work should include extended spatial point pattern analysis to test whether juveniles are clustered around large adults and to quantify neighborhood-scale recruitment structure, which may help identify candidate seed-source adults [60,61]. In addition, long-term repeat surveys using permanent plots across known times-since-abandonment would better resolve recruitment, growth, and diversity trajectories in swidden landscapes. A prototype for a locally participatory monitoring program has been outlined previously and could be adapted here to enable sustained data collection [6].

4.2. Conclusion

Swidden-disturbed, low-canopy forest in the study area supported substantially higher palm density than tall-canopy forest (53.3 vs. 22.6 $\frac{\text{palms}}{\text{Ha}}$; a 136% increase). Using UAV imagery and CNN-based detection across 255 ha, we identified 10,194 palms across six species, enabling both community-level and species-level comparisons between CHM canopy-height classes. This increase does not reflect a uniform rise across taxa; instead, it is driven by a pronounced compositional shift toward Kokerite (*Attalea maripa*). Kokerite dominated both forest types and increased from 77.1% of individuals in high forest to 89.4% in low forest, while Awara (*Astrocaryum vulgare*) declined from 17.3% to 10.0% and infrequent palms (Manicole, Lu, Ite, and Turu) fell to <1.0% each in low forest. Together, these results indicate that swidden disturbance can increase overall palm abundance while simplifying the palm assemblage (lower evenness and diversity), with dominance concentrated in a small subset of disturbance-tolerant taxa. Local Moran's I identified four dominant palm-height clustering patterns with a breakpoint at 8.25 meters, and these clusters were spatially consistent with the 10-meter canopy-height threshold used to compare low- and high-canopy forest.

Comparison of WorldView-2 (0.5-meter resolution) results with UAV imagery indicates that satellite-based detection underestimates palm abundance by ~70% and cannot reliably differentiate species. While this may be acceptable for broad regional mapping, it is insufficient for localized studies requiring accurate counts and species-level information. These results indicate that UAV-based approaches are better suited for fine-scale studies requiring accurate counts and species-level information. Although hyperspectral or SWIR-capable multispectral imagery can improve species discrimination, spatial resolution remains a limiting factor for detecting smaller individuals; prior satellite-based work typically resolves crowns on the order of approximately 5 meters, whereas the UAV imagery used here supports detection to approximately 2 meters.

The principal sustainability implication of this study is that greater palm abundance following swidden disturbance does not necessarily indicate maintenance of palm-community diversity. In the study area, the increase was concentrated

primarily in *Attalea maripa* and was accompanied by reduced representation of other species. These findings provide a quantitative basis for evaluating future land-use and monitoring approaches aimed at preserving the livelihood and cultural functions of swidden agriculture while maintaining the ecological heterogeneity of palm communities.

Supporting information

S1 Fig. Confidence threshold optimization graphs for Awara and Kokerite palms.
(TIF)

S1 Table. Palms detection accuracy results from Mask-RCNN algorithm. All values at > 25% IoU and > 80% confidence detection.
(DOCX)

Author contributions

Conceptualization: Matthew J. Drouillard.

Data curation: Matthew J. Drouillard, Anthony R. Cummings, Persaud Moses, Fabian Moses.

Formal analysis: Matthew J. Drouillard.

Funding acquisition: Anthony R. Cummings.

Investigation: Matthew J. Drouillard.

Methodology: Matthew J. Drouillard.

Project administration: Anthony R. Cummings.

Resources: Anthony R. Cummings, Persaud Moses, Fabian Moses.

Software: Anthony R. Cummings.

Supervision: Anthony R. Cummings.

Validation: Persaud Moses, Fabian Moses.

Writing – original draft: Matthew J. Drouillard.

Writing – review & editing: Matthew J. Drouillard, Anthony R. Cummings, Catherine Auerbach.

References

1. Ozanne CMP, Cabral C, Shaw PJ. Variation in indigenous forest resource use in central Guyana. *PLoS One*. 2014;9(7):e102952. <https://doi.org/10.1371/journal.pone.0102952> PMID: 25068801
2. Pulido MT, Coronel-Ortega M. Ethnoecology of the palm *Brahea dulcis* (Kunth) Mart. in central Mexico. *J Ethnobiol Ethnomed*. 2015;11:1. <https://doi.org/10.1186/1746-4269-11-1>
3. Cummings AR, Read JM. Drawing on traditional knowledge to identify and describe ecosystem services associated with Northern Amazon's multiple-use plants. *International Journal of Biodiversity Science, Ecosystem Services & Management*. 2016;12(1–2):39–56. <https://doi.org/10.1080/21513732.2015.1136841>
4. Read JM, Fragoso JMV, Silvius KM, Luzar J, Overman H, Cummings A, et al. Space, Place, and Hunting Patterns among Indigenous Peoples of the Guyanese Rupununi Region. *Iag*. 2010;9(3):213–43. <https://doi.org/10.1353/lag.2010.0030>
5. Conklin HC. The Study of Shifting Cultivation. *Current Anthropology*. 1961;2(1):27–61.
6. Cummings AR, Karale Y, Cummings GR, Hamer E, Moses P, Norman Z, et al. UAV-derived data for mapping change on a swidden agriculture plot: preliminary results from a pilot study. *International Journal of Remote Sensing*. 2017;38(8–10):2066–82. <https://doi.org/10.1080/01431161.2017.1295487>
7. Cairns M. Shifting cultivation and environmental change: indigenous people, agriculture and forest conservation. London; New York: Earthscan, Routledge. 2015.
8. Li P, Feng Z, Jiang L, Liao C, Zhang J. A Review of Swidden Agriculture in Southeast Asia. *Remote Sensing*. 2014;6(2):1654–83. <https://doi.org/10.3390/rs6021654>

9. Li P, Nath AJ. The history and revival of swidden agriculture research in the tropics. *CABI Agric Biosci*. 2024;5(1):84. <https://doi.org/10.1186/s43170-024-00298-z>
10. Schmidt-Vogt D. Secondary forests in swidden agriculture in the highlands of Thailand. *Journals of Tropical Forest Science*. 2001;13(4):748–67.
11. Eden MJ, Andrade A. Ecological aspects of swidden cultivation among the Andoke and Witoto Indians of the Colombian Amazon. *Human Ecology*. 1987;15(3):339–59. <https://doi.org/10.1007/BF00888030>
12. Jakovac CC, Peña-Claros M, Kuyper TW, Bongers F. Loss of secondary-forest resilience by land-use intensification in the Amazon. *Journal of Ecology*. 2015;103(1):67–77. <https://doi.org/10.1111/1365-2745.12298>
13. Boukili VK, Chazdon RL. Environmental filtering, local site factors and landscape context drive changes in functional trait composition during tropical forest succession. *Perspectives in Plant Ecology, Evolution and Systematics*. 2017;24:37–47. <https://doi.org/10.1016/j.ppees.2016.11.003>
14. de Pinho RC, Pequeno PACL, Alfaia SS, Barbosa RI, Lincoln NK. Soil fertility in indigenous swidden fields and fallows in northern Amazonia, Brazil. *Soil Use and Management*. 2023;39(4):1517–31. <https://doi.org/10.1111/sum.12886>
15. Karp DS, Rominger AJ, Zook J, Ranganathan J, Ehrlich PR, Daily GC. Intensive agriculture erodes β -diversity at large scales. *Ecol Lett*. 2012;15(9):963–70. <https://doi.org/10.1111/j.1461-0248.2012.01815.x> PMID: 22727063
16. Araia MG, Chirwa PW, Assédé ESP. Contrasting the effect of forest landscape condition to the resilience of species diversity in a human modified landscape: implications for the conservation of tree species. *Land*. 2020;9(1):1. <https://doi.org/10.3390/land9010004>
17. Runyan CW, D'Ondorio P, Lawrence D. Effect of repeated deforestation on vegetation dynamics for phosphorus-limited tropical forests. *J Geophys Res*. 2012;117(G1). <https://doi.org/10.1029/2011jg001841>
18. Connell JH. Diversity in tropical rain forests and coral reefs: High diversity of trees and corals is maintained only in a nonequilibrium state. *Science*. 1978;199(4335):1302–10. <https://doi.org/10.1126/science.199.4335.1302>
19. Downey SS, Walker M, Moschler J, Penados F, Peterman W, Pop J. An intermediate level of disturbance with customary agricultural practices increases species diversity in Maya community forests in Belize. *Commun Earth Environ*. 2023;4(1):428. <https://doi.org/10.1038/s43247-023-01089-6>
20. Eiserhardt WL, Svenning J-C, Kissling WD, Balslev H. Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. *Ann Bot*. 2011;108(8):1391–416. <https://doi.org/10.1093/aob/mcr146> PMID: 21712297
21. Kahn F, Granville JJ. *Palms in Forest Ecosystems of Amazonia*. 1st ed. Springer Berlin, Heidelberg. 1992.
22. Normand S, Vormisto J, Svenning J-C, Grández C, Balslev H. Geographical and environmental controls of palm beta diversity in paleo-riverine terrace forests in Amazonian Peru. *Plant Ecol*. 2006;186(2):161–76. <https://doi.org/10.1007/s11258-006-9120-9>
23. Smith N. *Palms and people in the Amazon*. Cham: Springer International Publishing. 2015. <https://doi.org/10.1007/978-3-319-05509-1>
24. Sezen UU, Chazdon RL, Holsinger KE. Multigenerational genetic analysis of tropical secondary regeneration in a canopy palm. *Ecology*. 2007;88(12):3065–75. <https://doi.org/10.1890/06-1084.1> PMID: 18229841
25. Pulido MT, Caballero J. The impact of shifting agriculture on the availability of non-timber forest products: the example of Sabal yapa in the Maya lowlands of Mexico. *Forest Ecology and Management*. 2006;222(1–3):399–409. <https://doi.org/10.1016/j.foreco.2005.10.043>
26. Pulido MT, Valverde T, Caballero J. Variation in the population dynamics of the palm Sabal yapa in a landscape shaped by shifting cultivation in the Yucatan Peninsula, Mexico. *J Trop Ecol*. 2007;23(2):139–49. <https://doi.org/10.1017/s0266467406003877>
27. Ramírez-Rodríguez R, Mussali-Galante P, Quero H, Tovar-Sánchez E. Management and its relation to hybridization, clonality and genetic structure of the Mexican palm *Brahea dulcis*. *Forest Ecology and Management*. 2012;285:92–100. <https://doi.org/10.1016/j.foreco.2012.07.055>
28. Pérez-Valladares CX, Moreno-Calles AI, Casas A, Rangel-Landa S, Blancas J, Caballero J. Ecological, Cultural, and Geographical Implications of *Brahea dulcis* (Kunth) Mart. Insights for Sustainable Management in Mexico. *Sustainability*. 2020;12(1):412. <https://doi.org/10.3390/su12010412>
29. Salm R. The importance of forest disturbance for the recruitment of the large arborescent palm *Attalea maripa* in a seasonally-dry Amazonian forest. *Biota Neotrop*. 2005;5(1):35–41. <https://doi.org/10.1590/s1676-06032005000100004>
30. Gehring C, Zelarayán MLC, Almeida RB, Moraes FHR. Allometria da palmeira babaçu em um agroecossistema de derruba-e-queima na periferia este da Amazônia. *Acta Amaz*. 2011;41(1):127–34. <https://doi.org/10.1590/s0044-59672011000100015>
31. Maezumi SY, Elliott S, Robinson M, Betancourt CJ, Gregorio De Souza J, Alves D. Legacies of Indigenous land use and cultural burning in the Bolivian Amazon rainforest ecotone. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 2022;377(1849):20200499. <https://doi.org/10.1098/rstb.2020.0499>
32. Jiang N, Li P, Feng Z. Remote sensing of swidden agriculture in the tropics: A review. *International Journal of Applied Earth Observation and Geoinformation*. 2022;112:102876. <https://doi.org/10.1016/j.jag.2022.102876>
33. Wagner FH, Dalagnol R, Tagle Casapia X, Streher AS, Phillips OL, Gloor E, et al. Regional Mapping and Spatial Distribution Analysis of Canopy Palms in an Amazon Forest Using Deep Learning and VHR Images. *Remote Sensing*. 2020;12(14):2225. <https://doi.org/10.3390/rs12142225>
34. Ferreira MP, Zortea M, Zanotta DC, Shimabukuro YE, de Souza Filho CR. Mapping tree species in tropical seasonal semi-deciduous forests with hyperspectral and multispectral data. *Remote Sensing of Environment*. 2016;179:66–78. <https://doi.org/10.1016/j.rse.2016.03.021>
35. Mulley M, Kooistra L, Bierens L. High-Resolution Multisensor Remote Sensing to Support Date Palm Farm Management. *Agriculture*. 2019;9(2):26. <https://doi.org/10.3390/agriculture9020026>

36. Culman M, Delalieux S, Van Tricht K. Individual Palm Tree Detection Using Deep Learning on RGB Imagery to Support Tree Inventory. *Remote Sensing*. 2020;12(21):3476. <https://doi.org/10.3390/rs12213476>
37. Ferreira MP, Almeida DRAd, Papa D de A, Minervino JBS, Veras HFP, Formighieri A, et al. Individual tree detection and species classification of Amazonian palms using UAV images and deep learning. *Forest Ecology and Management*. 2020;475:118397. <https://doi.org/10.1016/j.foreco.2020.118397>
38. Arce LSD, Osco LP, Arruda M dos S de, Furuya DEG, Ramos APM, Aoki C, et al. *Mauritia flexuosa* palm trees airborne mapping with deep convolutional neural network. *Sci Rep*. 2021;11(1):19619. <https://doi.org/10.1038/s41598-021-98522-7>
39. Yarak K, Witayangkurn A, Kritiyutanont K, Arunplod C, Shibasaki R. Oil Palm Tree Detection and Health Classification on High-Resolution Imagery Using Deep Learning. *Agriculture*. 2021;11(2):183. <https://doi.org/10.3390/agriculture11020183>
40. Eden MJ. The savanna ecosystem: an analysis of plant, soil and water relations in the northern Rupununi savannas of British Guiana as an aid to understanding their nature and origin. McGill University. 1964. <https://escholarship.mcgill.ca/concern/theses/th83m3519>
41. Drouillard MJ, Cummings AR. Regional-Scale Detection of Palms Using VHR Satellite Imagery and Deep Learning in the Guyanese Rainforest. *Remote Sensing*. 2024;16(24):4642. <https://doi.org/10.3390/rs16244642>
42. He K, Gkioxari G, Dollár P, Girshick R. Mask R-CNN. *arXiv*. 2018. <https://doi.org/10.48550/arXiv.1703.06870>
43. He K, Zhang X, Ren S, Sun J. Deep Residual Learning for Image Recognition. <https://arxiv.org/abs/1512.03385v1> 2015. Accessed 2023 October 10.
44. Shorten C, Khoshgoftaar TM. A survey on Image Data Augmentation for Deep Learning. *J Big Data*. 2019;6(1). <https://doi.org/10.1186/s40537-019-0197-0>
45. Bengio Y. Practical recommendations for gradient-based training of deep architectures. *arXiv*. <http://arxiv.org/abs/1206.5533> 2012. Accessed 2024 March 21.
46. Smith LN. A disciplined approach to neural network hyper-parameters: Part 1 -- learning rate, batch size, momentum, and weight decay. *arXiv*. 2018. <https://doi.org/10.48550/arXiv.1803.09820>
47. Anselin L. Local Indicators of Spatial Association—LISA. *Geographical Analysis*. 1995;27(2):93–115. <https://doi.org/10.1111/j.1538-4632.1995.tb00338.x>
48. Griffith DA. Spatial autocorrelation: a primer. Washington, D.C.: Association of American Geographers. 1987.
49. Macía MJ, Armesilla PJ, Cámara-Leret R, Paniagua-Zambrana N, Villalba S, Balslev H. Palm Uses in Northwestern South America: A Quantitative Review. *Bot Rev*. 2011;77(4):462–570. <https://doi.org/10.1007/s12229-011-9086-8>
50. Drouillard MJ, Cummings AR. A Big Data Approach for the Regional-Scale Spatial Pattern Analysis of Amazonian Palm Locations. *Remote Sensing*. 2025;17(5):784. <https://doi.org/10.3390/rs17050784>
51. Jensen JR. *Remote Sensing of the Environment: An Earth Resource Perspective*. Second ed. Pearson Education Inc. 2007.
52. Tobler W. Measuring spatial resolution. In: *Proceedings, Land Resources Information Systems Conference*, 1987. 12–6.
53. Chazdon RL. Physiological and morphological basis of shade tolerance in rain forest understory palms. *Principes*. 1986;30(3):92–9.
54. Svenning J-C. Recruitment of tall arborescent palms in the Yasuní National Park, Amazonian Ecuador: are large treefall gaps important?. *J Trop Ecol*. 1999;15(3):355–66. <https://doi.org/10.1017/s0266467499000875>
55. Brum HD, Souza AF. Flood disturbance and shade stress shape the population structure of açai palm *Euterpe precatoria*, the most abundant Amazon species. *Botany*. 2020;98(3):147–60. <https://doi.org/10.1139/cjb-2019-0090>
56. Denslow JS, Guzman G. S. Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. *J Vegetation Science*. 2000;11(2):201–12. <https://doi.org/10.2307/3236800>
57. Guariguata MR, Ostertag R. Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management*. 2001;148(1–3):185–206. [https://doi.org/10.1016/s0378-1127\(00\)00535-1](https://doi.org/10.1016/s0378-1127(00)00535-1)
58. Li J, Loneragan WA, Duggin JA, Grant CD. Issues affecting the measurement of disturbance response patterns in herbaceous vegetation – A test of the intermediate disturbance hypothesis. *Plant Ecology*. 2004;172(1):11–26. <https://doi.org/10.1023/b:vege.0000026028.58317.17>
59. Sivasailam A, Cummings AR. Does the Location of Amerindian Communities Provide Signals About the Spatial Distribution of Tree and Palm Species?. *Advances in Geographic Information Science*. Springer International Publishing. 2017. p. 169–79. https://doi.org/10.1007/978-3-319-22786-3_16
60. Baddeley AJ, Møller J, Waagepetersen R. Non- and semi-parametric estimation of interaction in inhomogeneous point patterns. *Statistica Neerlandica*. 2000;54(3):329–50. <https://doi.org/10.1111/1467-9574.00144>
61. Velázquez E, Martínez I, Getzin S, Moloney KA, Wiegand T. An evaluation of the state of spatial point pattern analysis in ecology. *Ecography*. 2016;39(11):1042–55. <https://doi.org/10.1111/ecog.01579>