Thermal sensitivity across forest vertical profiles: patterns, mechanisms, and ecological implications

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Title: Diverse anthropogenic disturbances shift Amazon forests along a structural spectrum

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Amazon forest, anthropogenic disturbance, land use change, forest structure, lidar, remote sensing, fire, drought, logging, fragmentation, secondary forests, degradation, forest transitions

Open Research statement

Data are archived on Github (https://github.com/m-n-smith/PCL-Am-disturbance-dataset). No novel code was used for this submission.

Abstract

Amazon forests are being degraded by myriad anthropogenic disturbances, altering ecosystem and climate function. We analyzed the effects of a range of land-use and climate change disturbances on fine-scale canopy structure using a large database of profiling canopy lidar collected from disturbed and mature Amazon forest plots. At most disturbed sites, surveys took place after 10-30 years, and many exhibited signs of recovery. Structural impacts differed more in magnitude than in character among disturbance types, producing a gradient of impacts. Structural changes were highly coordinated, in a manner consistent across disturbance types, indicating commonalities in regeneration pathways. The most severely affected site—burnt *igapó*—lacked signs of canopy regeneration, indicating a sustained alteration of microclimates and thus vulnerability to

transitioning to a more open-canopy, savanna-like state. Interestingly, disturbance rarely shifted forests outside of the natural background of structural variation within mature plots, highlighting the similarities between anthropogenic and natural disturbance regimes, and indicating a degree of resilience among Amazon forests. Studying diverse disturbance types within an integrated analytical framework builds capacity to predict the risk of degradation-driven forest transitions.

Introduction

Amazon forests are experiencing unprecedented rates of disturbance from anthropogenic land-use and climate change-related drivers. Degradation—including via selective logging, wildfire, and forest fragmentation—impacts existing forest, often leaving canopy cover but altering internal structure, microclimates, and critical ecosystem services, including biodiversity and carbon storage (Berenguer *et al.* 2014; Longo *et al.* 2016; Barlow *et al.* 2016). Degradation now outpaces deforestation as the major type of anthropogenic disturbance affecting Amazon primary forests (Matricardi *et al.* 2020). However, secondary forests naturally regenerating on abandoned agricultural land are also increasing in prevalence in tropical landscapes and provide an important mechanism of carbon sequestration capable of partially countering large carbon losses from degradation (Poorter *et al.* 2021). Predicting changes to Amazon ecosystem services requires an integrated understanding of forest responses to diverse anthropogenic disturbances and the likelihood of continued degradation versus recovery.

Disturbance alters structural properties of the forest canopy that are tightly linked to function. Forest canopy structure comprises the size, quantity, and spatial arrangement of trees and all above-ground vegetation in a forest. Metrics of canopy structure such as maximum and mean canopy height, surface rugosity, and gap fraction are strong predictors of aboveground biomass, biomass dynamics (e.g., tree growth and death) (Stark *et al.* 2012; Hardiman *et al.* 2013; Almeida *et al.* 2019a), and exchanges of energy, water, and carbon fluxes between forests and the atmosphere (Stark *et al.* 2020; de Oliveira *et al.* 2021). Degradation often acts to open the forest canopy and reduce canopy complexity, thereby increasing albedo and decreasing net radiation, while altering radiative fluxes to the ground (potentially leading to elevated surface radiation and within canopy temperatures) and the partitioning of sensible and latent heat (evapotranspiration) (Stark *et al.* 2020; de Oliveira *et al.* 2021). Altered (e.g., hotter) microenvironments can increase forest vulnerability to future disturbances (e.g. drought, fire; Brando *et al.* 2014; Aragão *et al.* 2018).

The impacts of disturbance vary widely depending on type, intensity, time since impact, and forest type (e.g., Longo *et al.* 2016). Structural alterations following degradation can be modest, for example under some logging practices (Longo *et al.* 2016). In these cases structural recovery can be fast (e.g., 10-30 years following fragmentation or drought; Almeida *et al.* 2019b; Stark *et al.* 2020). At the other extreme, severe structural degradation can lead to a persistent ecological state change. Forest degradation in concert with fire can induce a transition between alternative stable states, from closed canopy forest to open canopy savanna-like ecosystems, termed 'savannization' (Silvério *et al.* 2013; Oliveras and Malhi 2016). Understanding the mechanisms and probabilities of different forest structural transitions and state changes is key to resolving uncertainty in Amazon forest response to future climate (Malhi *et al.* 2009).

Research attention has focused on the structural impacts of disturbance intensity, while neglecting the impact of disturbance type (Atkins *et al.* 2020). Of studies that do investigate disturbance types, most address the structural outcomes of one or two agents (e.g., fragmentation: Almeida *et al.* 2019b; fire and logging: Longo *et al.* 2016 and Rappaport *et al.* 2018; all using lidar), rather than a range of disturbance types within an integrated analytical framework (but see Berenguer *et al.* 2014 who assessed multiple disturbance types in Amazon forests using forest inventories, and Atkins *et al.* 2020 in temperate forests using lidar). Lidar remote sensing is a powerful tool to investigate diverse disturbances because it is able to quantify multidimensional changes, an important feature of disturbance-induced changes in forest structure that may differentiate disturbance types (Fahey *et al.* 2019; Atkins *et al.* 2020).

Here, we quantify the consequences of a range of land-use and climate change-related disturbances for tropical-forest canopy structure using fine-scale biophysical information from a newly compiled database of ground-based profiling canopy lidar (PCL) data for Amazonia. This large dataset, collated from lidar surveys conducted for numerous projects over ~10 years, contains observations representing key disturbance types affecting Amazon forests: fragmentation, fire, drought, logging, and land clearing and subsequent forest regrowth. We analyze structural degradation against a backdrop of natural structural variation among undisturbed Amazon forests that span a spectrum of canopy openness, from tall closed-canopy forests to highly open savanna. We posit that the savanna state, as an endmember of canopy openness in natural forests, also represents a final state of severe structural degradation in anthropogenically altered forests. Indeed, the potential savannization of the Amazon represents a critical Earth System question influencing the likelihood of destructive climate change tipping points (Malhi *et al.* 2009; Steffen *et al.* 2018). Critically for predicting forest microclimates, ecosystem functioning, and the risk of long-term forest transitions, natural and derived savannas appear structurally similar (Stark *et al.* 2020), despite being floristically distinct (Veldman and Putz 2011).

We test the hypothesis (H1a) that the impacts of different disturbance types on forest structure can be distinguished because disturbance agents leave distinct structural signatures (Frolking *et al.* 2009; Fahey *et al.* 2019; Atkins *et al.* 2020). For example, drought tends to cause preferential mortality of large trees (Bennett *et al.* 2015), which should result in reductions in canopy height and upper canopy leaf area. Whereas, surface fires predominantly affect small trees (at least initially), likely reducing lower canopy leaf area (Barlow and Peres 2008). Further, we test whether anthropogenically disturbed forests are distinguishable from the natural background of forest structure across the Amazon.

Alternatively (H1b), different disturbance types will not leave distinct structural signatures, but will instead be distinguished by the magnitude of their structural impact. In this case, we expect to find a high degree of coordination among disturbance impacts (i.e., structural changes will be consistently correlated across disturbance types).

Methods

Deriving metrics of fine-scale canopy structure from lidar

We compiled a large database of PCL data collected across the Amazon (PCL-Am), comprising ground-based lidar data for 370 plots within 36 sites (see WebPanel 1 for lidar survey methods). Here, we focus on 79 disturbed and 62 mature-forest 'control' plots at 9 locations: Biological Dynamics of Forest Fragments Project (BDFFP), Alter do Chão, Universidade Federal do Amazonas (UFAM), Careiro Castanho, Caxiuanã National Forest Reserve, Tapajós National Forest (TNF) Seca Floresta, TNF K81, TNF K83, and Reserva Ducke (WebFigure 1; WebTables 1 and 2). BDFFP, Caxiuanã, and TNF Seca Floresta are sites of experimental manipulations (BDFFP for fragmentation and the other two for drought).

From the lidar data, we generated fully vertically resolved leaf area density (LAD) profiles and identified a focal set of 11 ‘single value’ metrics that quantify different aspects of forest structure (WebTable 3; WebFigure 2): canopy height and variability (maximum and mean canopy height, canopy surface rugosity, and elevation-relief ratio - ERR), canopy openness and horizontal heterogeneity (gap fraction, and heterogeneity fraction), the quantity and density of vegetation (leaf area index – LAI and leaf area height volume - LAHV), and the vertical distribution of leaf area and light environments (leaf area weighted height - LAWH, height of 50% LAI, and height of 50% incident light). We compared sites and treatments based on metrics calculated from 20 m transect sections. This is an ecologically relevant scale that approximates the length scale of understory impacts of canopy gaps and tree crowns in tropical forests (Nicotra *et al.* 1999).

Analysis design

To equally weight disturbed versus undisturbed forests, and control for the influence of forest type, we analyzed 11 'treatment pairs' (WebTable 1). Each pair comprises a set of disturbed forest plots matched with a set of nearby control, undisturbed forest plots of the same forest type representing the associated 'pre-disturbance' state. Five disturbance types are included within our 11 treatment pairs: fragmentation, surface fire (in lowland "*terra firme*" and seasonally flooded "*igapó*" forests), experimental drought, reduced-impact logging, and regrowth following land clearing (including secondary forests dominated by tree genera *Vismia* and *Cecropia*); see WebTable 2 for details of disturbance histories. In addition, we include a naturally occurring savanna site as an outgroup representative of the extreme structural changes that can occur through savannization. Our database did not allow for even-weighting of samples by Amazon region or disturbance type. Additionally, we lacked the necessary information to control for disturbance intensity or time since disturbance (most are 10-30 years post-disturbance, though disturbance is on-going for a few; WebTable 2), and instead focus on disturbance impact at the time of the lidar survey. Control forests for fragmentation and the savanna outgroup at Alter do Chão have been somewhat disturbed by drought and anthropogenic factors, potentially underestimating structural impacts there.

We assessed anthropogenic disturbance impacts against the backdrop of natural structural variation among 229 undisturbed Amazon forest plots from the PCL-Am database using hierarchical clustering on principal components (HCPC with the 11 focal metrics; WebPanel 1). We summarized the magnitude of disturbance impacts among treatment pairs by calculating the mean rank order of the absolute differences between disturbed and control forests for all structural metrics; treatment pairs of the same disturbance type were combined where disturbance impacts were similar (WebFigures 3 and 4). Finally, we conducted bivariate regressions between changes in structural metrics (disturbed minus control forests) across treatment pairs to test for coordination of disturbance induced structural impacts. Outliers were first excluded using the Inter-Quartile Range method of outlier detection.

Results

The impacts of disturbance on the vertical leaf area profile ranged from moving the distribution of foliage upward (1 of 11 treatment profiles), no impact (4 of 11), to shifting towards a bottom-heavy distribution (6 of 11; Fig. 1 and WebFigure 3g). Following fire in *igapó*, the average height of a leaf (LAWH, a metric of vertical LAD distribution) did not change significantly, but leaf area was lost at all heights (Fig. 1k), representing the most severe disturbance impact to the LAD profile. The burnt *igapó* profile was most similar to that of the savanna outgroup, although the savanna differed from all disturbed forests in lacking an upper canopy (Fig. 1e). Average LAD profiles of disturbed forests differed significantly from undisturbed control forests, with disturbance decreasing leaf area in the upper and mid canopy (n=11 for each type; Fig. 1m). Disturbed forests differed significantly from control and the wider mature (natural background) forest database for many single-value metrics: mean canopy height, LAWH, LAHV, and heights of 50% LAI and incident light were lower in disturbed forests, while heterogeneity fraction was higher (according to 95% confidence intervals; Fig. 2a). ERR and LAI of disturbed forests were lower than mature forest plots (but not paired controls) and gap fraction was higher. Maximum canopy height decreased with respect to control plots (but not mature forests). Notably, structural metrics tended to be more variable among disturbed plots compared to controls and the wider mature forest PCL-Am database.

The clustering analysis (HCPC) grouped 72 disturbed plots within clusters that were dominated by mature forest plots (clusters 2 and 3), and the remainder into a cluster composed of 7 disturbed and 3 mature plots (cluster 1; Fig. 2b). Many disturbances did not shift the structural composition from one cluster to another. Burnt *igapó* exhibited the largest shift, moving from cluster 2 (mixed) to cluster 1 (degraded forest-dominated), similar to the differentiation of savanna plots from nearby forest plots at Alter do Chão (Fig. 2b).

Drought, fragmentation, and burning of *terra firme* forests led to the smallest structural impacts among our study sites (Fig. 3, and WebFigures 3 and 4). Forests regenerating after clearcutting and logging displayed medium-level structural impacts, and burnt *igapó* exhibited the largest structural differences relative to undisturbed forest. As expected, the savanna site was at the extreme end of structural differences (relative to nearby forest). Structural metrics tended to respond to disturbance in the same direction (increasing or decreasing) across most disturbance types, with the notable exception of surface rugosity (Fig. 3). Gap fraction showed very little change except for large increases in burnt *igapó* and, similarly, gap fraction was higher in the savanna as compared to nearby forest.

Structural changes induced by disturbance were highly correlated for many metrics (Fig. 4, WebFigure 5, WebTable 4). The strongest relationships included changes in canopy height and vertical structure variables (R^2 of up to 0.83, $P < 0.0001$). In contrast, metrics of canopy structural heterogeneity exhibited fewer and weaker (ERR and surface rugosity, R^2 up to 0.52, $P < 0.05$), and in some cases (gap and heterogeneity fractions) no significant correlations. Change in LAI (a metric of leaf quantity) also exhibited only weak correlations (R^2 up to 0.52, $P < 0.05$), though interestingly, correlations were higher for change in LAHV (a metric of canopy volume) (R^2 up to 0.83, $P < 0.0001$). For most bivariate relationships, the savanna outgroup and the most highly impacted site, burnt *igapó*, were in-line with the other treatments, albeit at the extreme ends, though in a couple of cases (ERR and LAI) they were identified as outliers.

Discussion

A gradient of structural impacts from anthropogenic disturbances

Overall, forest structural change did not differ in character between disturbance types so much as it differed in magnitude (Fig. 3, support for H1b). Most structural metrics changed significantly in response to disturbance, and changed in the same direction across disturbance types. Generally, disturbance was associated with a loss of leaf area in the upper canopy, reducing canopy height (mean and maximum) (Figs 1 and 2). Net changes in total leaf area (leaf area index, LAI) were small for most disturbances (Fig. 3 and WebFigure 3), with disturbance instead rearranging the distribution of leaf area, often increasing in the lower canopy (lower leaf area weighted height, LAWH), leading to a reduced height of leaf light interception. In contrast, surface rugosity was highly responsive to disturbance but variable in the direction of change among disturbance types. Two disturbance types did display distinct impacts: secondary forest regeneration ('clearing and regrowth') resulted in a more even-heighted canopy surface (increased elevation-relief ratio, ERR), and drought resulted in a more top-heavy leaf area profile (increased LAWH) (Fig. 3 and WebFigure 3; limited support for H1a); both impacts were opposite to the trends observed in the other disturbance types, indicating a limited ability to detect certain disturbance agents. In aggregate, disturbance and forest types fell along a gradient of structural impacts, from least impact (droughted, fragmented, and burnt *terra firme* forests), to more severe impact (secondary and reduced-impact logged forests), and greatest impact (burnt *igapó*) (Fig. 3).

The two ends of our gradient of structural impact correspond to two distinct, intensity-based categories of disturbance described in the literature: (i) non-stand replacing disturbances with minimal impacts to soil, from which forests can regenerate readily, and (ii) disturbances that involve stand-replacement or substantial mortality of canopy trees, as well as severe soil damage, which slows forest recovery (Chazdon 2003; Frolking *et al.* 2009). Drought, fragmentation, and fire in *terra firme* fit within the first category, with low excess mortality rates (~1-5% per year) often differentially affecting large trees (Laurance *et al.* 2006; Costa *et al.* 2010), though fire impacts are highly variable and can be extreme (Brando *et al.* 2014). Correspondingly, we observed low overall structural impacts and often reduced upper canopy leaf area for these disturbances (Figs 1 and 3; previously documented by Almeida *et al.* 2016, 2019b). We note that our lidar measurements of the Caxiuanã drought experiment did not match this trend, apparently capturing the documented elevated mortality of small- and medium-sized trees (reduced lower canopy leaf area), but not the greater excess mortality of large trees (Fig. 1; da Costa *et al.* 2010), perhaps due to our limited sample size. Regrowth following land clearing, reduced-impact logging, and fire in *igapó* forests are examples of the second disturbance category, involving soil degradation and complete (land clearing) or substantial (11-15% of aboveground biomass removed due to logging at TNF K83, Miller *et al.* 2011; ~60% loss of trees following fire at the *igapó* site, Resende *et al.* 2014) removal of forest. Consequently, we observed pronounced reductions in canopy volume (LAHV) and canopy height, and for logged and secondary forests, significant reorganization of vertical leaf area ~30 years post-disturbance (Figs 1, 3, and WebFigure 3).

Burnt *igapó* experienced the greatest structural impacts, including large changes in most metrics, increased canopy openness, and a loss rather than simply a rearrangement of LAI (first reported by Almeida *et al.* 2016). These changes were closely aligned with the savanna outgroup vs. mature forest contrast, and consistent with an intermediate forest state that may be at risk of a savanna-state transition (from closed canopy to a persistently open canopy state; savannization). Seasonally inundated forests are highly vulnerable to savanna state transitions because slow regrowth following fire maintains an open canopy structure and promotes future fire incidence (Almeida *et al.* 2016; Flores *et al.* 2017). Impacts were nearly as severe in logged and secondary forests (Fig. 3), yet they did not exhibit canopy opening or large losses in LAI. Instead, lower canopy leaf area increased relative to control forests, consistent with forest recovery that may indicate resilience to disturbance.

Coordination of disturbance-induced structural changes

Overall, we did not observe distinct structural impacts associated with different disturbance agents in our dataset. Rather, structural impacts were aligned along a gradient, and as we predicted, were highly coordinated across disturbance treatments (strong correlations between the changes in many metrics; Fig. 4). The only exceptions were the burnt *igapó* and natural savanna sites, which were consistently at the extreme ends of bivariate relationships, or classed as outliers. In contrast, a similar study using lidar in temperate forests did find distinct signatures of different disturbance types (Atkins *et al.* 2020). It is possible that disturbance intensity at our sites was too low to leave distinct structural signatures, though this seems unlikely given our observations of significant structural impacts (disturbed vs. control plots). Alternatively, the coordinated structural changes that we observe may be a product of forest recovery. Most of our sites were surveyed 10-30 years post-disturbance, and previous studies of two of them documented substantial recovery of forest structure within this timeframe (TNF Seca Floresta drought experiment, Stark *et al.* 2020; BDFFP forest fragments, Almeida *et al.* 2019b). All but one of the lidar surveys in Atkins et al. (2020) were made immediately after disturbance or during on-going chronic disturbances. We posit that the disturbance types studied here may have elicited distinct, uncoordinated impacts on canopy structure, but these were relatively transient; subsequently, structural changes became coordinated, indicating fundamental commonalities to structural regeneration trajectories. For example, many of our sites exhibited growth of the lower canopy, a regeneration response (gap infilling) stimulated by elevated light levels following the removal or death of canopy trees (Miller *et al.* 2011; Almeida *et al.* 2019b) that may indicate forest resilience to disturbance.

In contrast, we did not observe a similar recovery response in the fire affected *igapó*. The persistent lack of canopy regeneration may indicate a sustained alteration of microclimates, which contributes to a tendency to remain in a degraded, savanna-like state (Resende *et al.* 2014; Almeida *et al.* 2016; Flores *et al.* 2017). The spectrum of forest responses that we observe can be interpreted within the theory of alternative stable states, exemplified by forest-savanna transitions (Oliveras and Malhi 2016; Flores *et al.* 2017). This describes how certain ecosystems can exist in alternative states and can transition from one to the other in the presence of a large enough perturbation, relative to the resilience of the ecosystem. We hypothesize that the observation of similar coordination of structural changes among forests indicates a tendency to revert to their original, closed-canopy forest state, while sustained discoordination of structural change indicates a potential to remain in a new stable state.

Detection of disturbance-induced structural impacts via lidar

Our results show that lidar can distinguish magnitudes of response to anthropogenic disturbance, and has the potential to distinguish forests on recovery pathways from those at risk of continued degradation (Figs 3 and 4). However, we are limited in our ability to generalize about the impacts of specific disturbance types, since our database contains only 1-3 examples per disturbance type and did not enable us to control for disturbance intensity or time since disturbance. In all but the most severely impacted forests, metrics of vertical structure, but not LAI, were predictive of multiple disturbance effects (Fig. 4), indicating the greater ability of lidar over optical remote sensing platforms (e.g., MODIS derived LAI) to monitor moderate disturbance (Atkins *et al.* 2020). Integrating the analysis of diverse disturbance types and natural forests in a single analytical framework showed structural similarities between anthropogenically and naturally disturbed forests, at least where some recovery has occurred (Fig. 2b, support for H1b; Franklin *et al.* 2002). Their similarity could simplify the representation of disturbance and recovery processes in ecosystem models, though we note that structural similarity does not necessarily imply floristic and functional similarity (Poorter *et al.* 2021). However, anthropogenic disturbances may be better distinguished from natural disturbances based on spatial uniformity and extent, factors not analyzed here but which should be more detectable with larger scale (e.g., satellite-based) remote sensing. While we were not able to distinguish between anthropogenic disturbance types when structural changes were moderate, it may be possible to identify structural indicators of particular disturbance types through time-series studies that capture pre-, during, and post-disturbance states.

Implications for the future of Amazon forests

Understanding forest structural feedbacks is critical for predicting when degradation can lead to a persistent state change. Loss of upper canopy leaf area and increased light penetration following disturbance likely create more stressful microclimates in the lower canopy, such as higher temperatures, light, and vapor pressure deficit (Smith *et al.* 2019; Zellweger *et al.* 2020). Particularly in fire-affected *igapó*, these conditions may inhibit tree recruitment and growth directly, and also indirectly by facilitating the recurrence of fire or exacerbating drought, providing mechanisms for forest transitions to degraded savanna-like states (Resende *et al.* 2014; Almeida *et al.* 2016; Flores *et al.* 2017). The interactivity of disturbance types means that transition risks can increase non-linearly, giving rise to potential threshold-like tipping points (Brando *et al.* 2014). Additionally, some ecosystem function changes may exhibit independent nonlinear or thresholdtype responses to land cover changes, which may contribute to forest change feedbacks that must be accounted for in predictive frameworks (Stark *et al.* 2020).

It is promising that many of the forests in our analysis exhibited signs of recovery 10-30 years after disturbance, suggesting a degree of resilience in Amazonian forests. Among recovering forests, we found that a change in one aspect of forest structure can be predictive of other, multidimensional structural changes, regardless of forest type or original impact. These coordinated structural changes may predict ecosystem function responses such as changing carbon stocks (Almeida *et al.* 2019a). The area of degraded forest in the Amazon is now larger than deforested (Matricardi *et al.* 2020) and yet carbon emissions from degradation are less well quantified (but see Berenguer *et al.* 2014; Longo *et al.* 2016, Aragão *et al.* 2018, Rappaport et al. 2018). Understanding fine-scale patterns and mechanisms of structural change in degraded forests builds capacity to estimate carbon stocks and emissions of these regions at larger scales via remote sensing (e.g., satellite-based lidar–GEDI), assisting in the growing effort to reduce the uncertainty associated with degraded forest emissions and incorporate them into national forest monitoring and policies (Junior *et al.* 2021). An integrated understanding of the structural signatures of disturbance will help to predict the risks of Amazon forest transitions, enhance identifiability of degradation types (Almeida *et al.* 2019a; Atkins *et al.* 2020), and projection of global ecosystem and climate functions.

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Figure legends

Figure 1. Leaf area density (LAD) profiles for disturbed (red) and undisturbed control (blue) forests for each treatment pair (a-k) and mean LAD profiles of all treatment pairs (m). The LAD profile of a natural savanna site (black), used as an outgroup, is shown in (e). Disturbance types are shown in gray boxes and plots are ordered by degree of disturbance-induced structural impact, from low (drought) to high (fire in *igapó*). Central lines are means within 95% CI envelopes.

Figure 2. (a) Violin plots displaying the distribution of 11 focal structural metrics within disturbed (red) and control (blue) forests of 11 treatment pairs, and across mature forest plots in the PCL-Am database, used to represent the 'natural background' of structural variation (gray, n=288, excludes plots grouped into Cluster 1 in panel b); points and error bars show means and 95% CIs. **(b)** Output from a hierarchical clustering on principal components analysis (HCPC) applied to the same 11 metrics shown in (a) across all disturbed (red, 79) and control (blue, 62) plots that make up our 11 treatment pairs, in addition to mature forest plots representing the natural background of Amazon forest structure (gray, n=229, from PCL-Am database). Treatment pairs are shown by blue squares (control forests) and red triangles (disturbed forests), positioned at the central point between survey plots; arrows indicate disturbance-induced structural shifts. Numbers indicate the disturbance treatment pair, namely, 1: fragmentation (Alter), 2: clearing and regrowth (BDFFP, *Cecropia*), 3: fragmentation (BDFFP), 4: clearing and regrowth (BDFFP, *Vismia*), 5: drought (Caxiuana), 6: fire (*igapó*), 7: logging (TNF K83), 8: drought (TNF Seca Floresta), 9: fire (*terra firme*), 10: clearing and regrowth (TNF K81), 11: fragmentation (UFAM). The dashed line connects the savanna plots with nearby forest plots. Structural metrics (and units) are as follows: elevation-relief ratio (ERR, unitless), gap fraction (unitless), heterogeneity fraction (unitless), height of 50% incident light (m), leaf area height volume (LAHV, m), leaf area index (LAI, m^2m^{-2}), height of 50% LAI (m), leaf area weighted height (LAWH, m), mean canopy height (m), maximum canopy height (m), and surface rugosity (m).

Figure 3. Structural impact of different disturbance types on **(a)** key structural metrics **(b)** summarized as the mean rank order impact, from least (drought and fragmentation) to most (burnt *igapó*) across all 11 focal metrics included in the HCPC. Structural impacts of burnt *igapó* closely align with the structural differences between the savanna vs. mature forest contrast (outgroup, black). In (a), impact is quantified as the difference in each structural metric relative to the control forest (disturbed - control), standardized by the standard deviation (SD); bars show means of transect sections and error bars indicate 95% confidence intervals; gray vertical lines at zero

indicate no change relative to the control. Disturbance types are broken into forest type where the latter has an important effect (fire in *terra firme* vs. *igapó* forests). Structural metrics are as follows: mean canopy height, maximum canopy height, surface rugosity, elevation relief ratio (ERR), gap fraction, leaf area index (LAI), leaf area height volume (LAHV), leaf area weighted height (LAWH), and height of 50% incident light.

Figure 4. Bivariate relationships between changes in structural metrics (relative to undisturbed control forest mean) across disturbance treatments and savanna outgroup for selected metric changes with (a) high correlations and (b) lower correlations. Gray horizontal and vertical lines indicate no change relative to undisturbed control forests. Regressions exclude points determined as outliers via the Inter-Quartile Range method of outlier detection. Outliers were as follows: Δ maximum canopy height: BDFFP *Vismia*; Δ ERR: savanna and TNF K81; Δ LAI: savanna and *igapó*. Significance levels: * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$).