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## INNOVATIVE VIEWPOINTS

# Reframing tropical savannization: linking changes in canopy structure to energy balance alterations that impact climate

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**Abstract.** Tropical ecosystems are undergoing unprecedented rates of degradation from deforestation, fire, and drought disturbances. The collective effects of these disturbances threaten to shift large portions of tropical ecosystems such as Amazon forests into savanna-like structure via tree loss, functional changes, and the emergence of fire (savannization). Changes from forest states to a more open savanna-like structure can affect local microclimates, surface energy fluxes, and biosphere–atmosphere interactions. A predominant type of ecosystem state change is the loss of tree cover and structural complexity in disturbed forest. Although important advances have been made contrasting energy fluxes between historically distinct old-growth forest and savanna systems, the emergence of secondary forests and savanna-like ecosystems necessitates a reframing to consider gradients of tree structure that span forest to savanna-like states at multiple scales. In this Innovative Viewpoint, we draw from the literature on forest–grassland continua to develop a framework to assess the consequences of tropical forest degradation on surface energy fluxes and canopy structure. We illustrate this framework for forest sites with contrasting canopy structure that ranges from simple, open, and savanna-like to complex and closed, representative of tropical wet forest, within two climatically distinct regions in the

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Amazon. Using a recently developed rapid field assessment approach, we quantify differences in cover, leaf area vertical profiles, surface roughness, albedo, and energy balance partitioning between adjacent sites and compare canopy structure with adjacent old-growth forest; more structurally simple forests displayed lower net radiation. To address forest–atmosphere feedback, we also consider the effects of canopy structure change on susceptibility to additional future disturbance. We illustrate a converse transition—recovery in structure following disturbance—measuring forest canopy structure 10 yr after the imposition of a 5-yr drought in the ground-breaking Seca Floresta experiment. Our approach strategically enables rapid characterization of surface properties relevant to vegetation models following degradation, and advances links between surface properties and canopy structure variables, increasingly available from remote sensing. Concluding, we hypothesize that understanding surface energy balance and microclimate change across degraded tropical forest states not only reveals critical atmospheric forcing, but also critical local-scale feedbacks from forest sensitivity to additional climate-linked disturbance.

Key words: Amazon; climate change; Earth System Models; energy balance; forest transitions; lidar; rapid field assessment; savannization; vegetation structure.

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#### INTRODUCTION

Tropical ecosystems are undergoing unprecedented rates of anthropogenically caused disturbance and conversion. For example, in Brazil in 2019, there was a roughly 50% increase from the previous year in deforestation followed by extensive fires (Escobar 2019), with similar forest loss rates recently recorded for Amazônia in other countries such as Colombia and Bolivia (Kalamandeen et al. 2018, Salazar et al. 2018). These changes impact ecosystem processes at local, regional, and global scales, including increasing atmospheric greenhouse gases such as CO<sub>2</sub>, CO,  $CH_4$ , and  $N_2O$  (Gash et al. 2004, Davidson et al. 2012, de Oliveira et al. 2019). Efforts to model the effects of climate change suggest that portions of Amazon forests are threatened with conversion into a savanna due to tree loss from deforestation, fire, and die-offs associated with extreme climate conditions and drought (Brando et al. 2008, 2019, Nepstad et al. 2008, Phillips et al. 2009, Aragão and Shimabukuro 2010, Allen et al. 2015). Savannization (sometimes called savannification) is the transformation of forest to lower biomass savanna structure, associated with the emergence of fire in the system (Silvério et al. 2013). Forest and savannas represent alternate forests states in

many areas, where savanna is maintained by fire feedbacks that promote grass, light-demanding fire-resilient trees, and open canopy structure, and thus fire recurrence (i.e., a fire trap; Desjardins et al. 1996, House et al. 2003, Hirota et al. 2011, Ratnam et al. 2011, Staver et al. 2011, Hoffmann et al. 2012, Oliveras and Malhi 2016). Now, a wider range of forest types are present in these regions because of changing disturbance regimes that create degraded and potentially pre-savannized or secondarized forest states (Barlow and Peres 2008, Nepstad et al. 2008; degraded forests we define as having lost one or more ecosystem functions over a period of time). To address the needs of forecasting future climates with Earth system approaches (IPCC 2013, 2014) and developing management strategies to reduce savannization (Malhi et al. 2009), it is now essential to develop a detailed understanding of forest-atmosphere interactions over this range of degraded forest types. This understanding requires expanding quantitative characterization of canopy function and microclimate changes within the spectrum of degraded states, and knowledge of how functional and microclimate changes will feedback to influence the sensitivity of forests to droughts, heatwaves, and fires that could cause additional degradation.

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Changes from a mature forest state to more open savanna-like structure, including secondary or transitional forest, can affect the local energy fluxes, tipping the balance and associated processes (including feedbacks) toward savannization (Cochrane and Laurance 2008, Aragão and Shimabukuro 2010, Hirota et al. 2010, Ordway and Asner 2020). Although advances have been made in quantifying energy fluxes in Amazon forests and in distant savannas in adjacent regions (da Rocha et al. 2009, Restrepo-Coupe et al. 2013), less is known about changes in surface energy fluxes and microclimates associated with forest disturbances. Furthermore, a predominant type of ecosystem state change is tree cover loss of different amounts in tropical forest due to human-related disturbances (Curtis et al. 2018, Bullock et al. 2020), while degraded forests are becoming more widespread and may become the dominant mode of Amazon forests in the future (Bullock et al. 2020). These changes necessitate a reframing of tropical forest energy fluxes and microclimates from the current perspective that primarily contrasts old-growth forest with savanna in a different region, to considering a multidimensional gradient of tree cover and structure that spans forest to grassland at multiple scales, including within a given location and climate. This reframing can complement ecological and biogeographic understanding that considers a wide spectrum of disturbance, recovery, and historical community assembly-related structural states that span tropical wet forests to savannas (Pennington et al. 2000, Barlow and Peres 2008, Berenguer et al. 2014, Chazdon 2014), as well as advances in remote detection of forest structure change (Rappaport et al. 2018, Smith et al. 2019, Bullock et al. 2020). Here, we propose a program for the conceptual and empirical steps needed to achieve this reframing-including providing new data on forest structure-energy balance and microclimate contrasts-to meet these needs. We draw from previously developed dryland literature on forest-grassland continua (Breshears 2006 and references therein) and expand that framework from a focus on cover to include canopy structural complexity (canopy cover, and vertical and horizontal variation), which can be retrieved from advanced remote sensing technologies (Chambers et al. 2007, Stark et al. 2012, 2015,

Rappaport et al. 2018, Shao et al. 2019, Tang et al. 2019, Almeida et al. 2019*a*).

Our specific objectives in this Innovative Viewpoint article are to, in Section 1: Reframing, propose a reframing of different types of forest transitions in tropical wet forest to highlight the need to understand the impacts of forest change on energy balance and the consequences for forest-atmosphere interactions; in Section 2: Contrasts, illustrate potential to aide in addressing this knowledge gap by presenting example data sets of vegetation differences and associated energy characterizations based on short field campaigns; and, in Section 3: Challenges and Prospects, discuss hypotheses about energy implications of vegetation change to more open and less complex structures, including the sensitivity of degraded forest to fire-driven savannization and other vegetation change feedbacks. We conclude suggesting steps to improve the savannization vegetation change pathways in Earth System models (ESMs) and to develop new remote sensing programs to closely monitor the changing structure and function of tropical canopies in Amazon forests and elsewhere.

## Section I: Reframing Tropical Forest Savannization as Transitions Along Canopy Structure and Energy Balance Gradients

We propose a simple conceptual framework that links disturbance and forest state transitions with gradients of canopy structural complexity and cover (Fig. 1A), and with surface energy balance components, to improve modeling of forest-atmosphere interactions (Fig. 1). The key global change drivers considered that can trigger transitions among these states include degradation from deforestation, fires, and drought and heatwaves, and forest regrowth (Fig. 1B). Structural predictor variables that may be detected remotely include forest canopy cover and canopy structure, tree size distribution, and leaf area index (LAI; Fig. 1C). The relationships between these predictor and response variables for microclimate and energy balance components-including albedo, net radiation, sensible to latent heat (Bowen ratio), surface roughness and boundary layer conductance, and near-ground incoming solar radiation-are incompletely

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Fig. 1. Conceptual figure of proposed framework for assessing the consequences of tropical forest disturbance and forest degradation on surface energy balance, and subsequent ecological and ecosystem properties, extending a temperate drylands framework focused on woody plant cover (Breshears 2006) to consider canopy structural changes more generally. This framework is useful for a variety of gradients of forest structure, including those related to deforestation and degradation in one direction and forest regrowth/regeneration in the other (A), and, most relevant to tropical forest savannization, decreases in structure and cover associated with tree die-off from droughts, heatwaves, and the emergence of fire (B). The characteristics to consider along these gradients are those integrally linked to microclimate and canopy function—forest cover and structure, tree size distribution, and LAI (C). As noted in Table 1, these characteristics influence energy balance components and associated microclimates in predictable ways, even if relationships are not completely characterized (D). These functions could increase or decrease in nonlinear as well as linear ways or could follow a peaked curve relationship where the maxima usually falls below 50% tree cover (Breshears 2006, Villegas et al. 2014; E). For nonpeaked relation-ships, the degree to which tree canopy units of a given structure interactively influence the area around them determines how linear or nonlinear and threshold like the functional responses are (Breshears 2006).

Table 1. Hypothesi	zed functional resp	onses for key pro	operties moving t	from closed,	mature lowland	tropical for-
est canopy to ve	ry open canopy str	ructure, driven b	y a combination	of fire, tree	mortality, defor	restation and
degradation.						

Property	Functional response	Threshold strength	Feedback on future disturbance/ savannization	Representative temperate primarily dryland references	Representative tropical references
Albedo	Increasing with loss of cover and complexity allowing surface to reflect more solar radiation, but albedo may decrease following fire because of charring (Faria et al. 2018)	Expected nonlinearities, possible weak thresholds	Impact via alteration to energy budget. Increase with savannization of increasing sensible heat, enhancing resilience	Swann et al. 2012 (M), Bonan 2019 (O), Jin et al. 2012 (O, g)	Faria et al. 2018 (O, c); von Randow et al. 2004 (O, c); Loarie et al. 2011 (O, g); Houghton 2018 (M, g); de Oliveira et al. 2016 (O, M, g); de Oliveira et al. 2019 (O, M, g); de Oliveira and Moraes 2013 (O, M, g); this study
Net radiation (Rn)	Decreasing with loss of cover and complexity (higher albedo)	Expected nonlinearities, possible weak thresholds	With the increase of albedo after loss of cover, total energy available in the canopy to be partitioned into sensible and latent heat will decrease, while surface radiation and heat fluxes could increase. Altered microclimates impact plants	Morecroft et al. 1998 (O, c); Anthoni et al. 2000 (M, O); Jin et al. 2012 (O, g)	Gash and Nobre 1997 (O, M); von Randow et al. 2004 (O); de Oliveira et al. 2016 (O, M, g); de Oliveira et al. 2019 (O, M, g); de Oliveira and Moraes 2013 (O, M, g), Giambelluca et al. 2009 (O, c); this study
Bowen ratio, i.e., sensible/latent, heat flux partitioning	Potentially increasing as sensible heat flux increases, and latent heat flux decreases with loss of cover and complexity, but more complex relationship possible	Nonlinear with likely thresholds, may be weak or strong	Sensible heat increases can increase VPD, promoting fire spread (Ray et al. 2005, Cochrane and Laurance 2008) and increasing forest sensitivity. But reduction in fuel after fire can reduce potential for future fire (Balch et al. 2008)	Campbell and Norman 1998 (O); Villegas et al. 2017 (O); Villegas et al. 2014 (H)	Restrepo-Coupe et al. 2013 (O, g); da Rocha et al. 2009 (O, g); von Randow et al. 2004 (O, c); de Oliveira et al. 2019 (O, M, g); this study
Near-ground solar radiation	Increasing with cover and complexity loss	Nonlinear region of rapid change; moderate threshold-type response. Weak or more complex relationships with tree size and density in regeneration (Montgomery and Chazdon 2001)	Higher soil evaporation effect and hotter higher VPD near-ground environments may create a more stressful environment for early/small growth stages, promoting savannization	Breshears 2006 (H, g); Martens et al. 2001 (M, g); Royer et al. 2010 (O, g); Breshears and Ludwig 2010 (O, g) Royer et al. 2012 (O, g); Villegas et al. 2010 <i>a</i> (O, g), Villegas et al. 2010 <i>b</i> (O, g)	Galo et al. 1992 (O); Bellingham et al. 1996 (O); de Oliveira et al. 2016 (O, M, g); Montgomery and Chazdon 2001 (O, g); this study

(Table	1.	Continued.)
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Property	Functional response	Threshold strength	Feedback on future disturbance/ savannization	Representative temperate primarily dryland references	Representative tropical references
Surface roughness and boundary layer conductance	Increasing from closed mature canopy to gappy open forest, but may decrease moving to shorter statured savanna; possibly peaked or multimodal relationship	Nonlinear and high possibilities for thresholds, including in multiple response regions, and multimodality	An increase in boundary layer conductance over structure change has the potential to increase VPD, intensify water stress, and increase sensitivity to disturbance/ savannafication. If a complex relationship, the feedback will be weaker/limited	Villegas et al. 2014 (H, g); Campbell and Norman 1998 (O); Lee and Soliman 1977 (O); Lee 1991 <i>a</i> (O); Lee 1991 <i>b</i> (O), Wolfe and Nickling 1993 (O), as framed in Breshears et al. 2009 (H, g); Sankey et al. 2013 (O, g)	Tan et al. 2019 (O, M, g); Dickinson and Kennedy 1992 (M, c); Spracklen and Garcia-Carreras 2015 (M, c); this study (via roughness quantification)

*Notes:* Source abbreviations are H, hypothesized; O, observations; M, modeled. Study type abbreviations are c, contrast of two points; g, gradient of vegetation structure–function was considered.

characterized (Fig. 1D). These relationships could either decrease, increase, or intermediately peak with decreasing forest canopy complexity and cover; linear and nonlinear responses are possible within response types (Fig. 1E).

In this conceptual framework, we draw on the rich literature from forest-grassland continua in temperate systems-often dryland gradients from semi-arid grassland through semiarid forest (Breshears 2006, and references therein, including Archer et al. 1988, Belsky and Danham 1994, Scholes and Archer 1997, Breshears and Barnes 1999, Martens et al. 2001, House et al. 2003, Sankaran et al. 2004, 2005; see also Wang et al. 2010, Villegas et al. 2014, Villegas et al. 2015, Ratajczak et al. 2017)-that describe connections between microclimate, components of energy balance, canopy cover, and structural complexity. A central premise of this framework is that woody plants (shrubs and trees) have a disproportionately large influence on the microclimate and associated energy balance beneath and around them and that this influence changes, often in nonlinear ways, with the increasing prevalence of woody plants and an elevated vegetation canopy. In woodland and savanna systems, gradients in the vegetation canopy can often be conceptualized as changes in canopy cover, though other structural factors may also be important (which we will elaborate in the context of tropical forest below).

We highlight relevant findings from dryland and tropical research to illustrate this canopy structure-function framework including patterns that have been hypothesized, documented, and predicted for a diverse range of properties such as albedo, net radiation (Rn), surface roughness, and near-ground (below woody canopy) solar radiation patterns, among others (Table 1). For example, as woody plant cover decreases, albedo and near-ground solar radiation increase, which increases the Bowen ratio (von Randow et al. 2004, Villegas et al. 2014; citations in Table 1). Additionally, these patterns are often nonlinear, potentially displaying a range of threshold-type rapid change responses (Fig. 1E), depending on the degree of interactivity between vegetation units (determining beneath canopy vs. intercanopy space in Breshears 2006). Near-ground solar radiation, for example, decreases nonlinearly in plots with increasing canopy cover; in one instance, near-ground areas receiving the maximum amount of daily solar radiation in a semi-arid woodland made up more than a third of the ground surface at 21% tree cover, but dropped to just a tenth of the area at 34% tree cover, and were completely absent by 41% tree cover (Martens et al. 2001). Maximum canopy height and vertical foliage distribution also impact near-ground radiation (Sankey et al. 2013, Villegas et al. 2014). Similarly, surface roughness and associated wind flow category-impacting mixing and canopy conductance (Bonan 2015)-

change nonlinearly with increasing cover. While natural vegetation canopy data is needed, one wind tunnel study using solid cylinders found isolated wake flow at less than 14% cover, wake interference flow at 14–40% cover, and skimming flow at >40% cover (Wolfe and Nickling 1993; and see Breshears et al. 2009). Ultimately, structural properties impact the full range of components of surface energy and its partitioning into sensible and latent heat fluxes.

Gradient analyses considering elements of canopy structure (e.g., cover or LAI) in relation to microclimate and energy balance consequences of these gradients, and forest change more broadly, remain relatively rare in Amazon forests. However, a number of tropical site contrast studies, experimental disturbance manipulations, analyses tracking the after effects of uncontrolled disturbances, and modeling results offer insight on structure-function relationships (Table 1). Investigations of the impact of forest structure gradients and change on albedo typically contrast forest with highly altered vegetation types canopies. For example, higher albedo is typically found in pasture, crops, and cleared lands, relative to forest, at least after initial postfire increases in absorptive charred materials subside (de Oliveira and Moraes 2013, de Oliveira et al. 2016, 2019, Faria et al. 2018). The albedo of regenerating secondary forest appears to converge toward mature forest values (low values, i.e.,  $\sim 0.1$ ); however, seasonal differences in albedo and net radiation appear linked to structure in these forests (de Oliveira and Moraes 2013, de Oliveira et al. 2016, 2019). Foundational energy and materials flux network studies highlight large scale gradients in Amazon forest function, including variation in seasonal patterns and the roles of water vs. radiation limitation of photosynthesis and latent and sensible heat fluxes (da Rocha et al. 2009, Restrepo-Coupe et al. 2013). The broad gradients studied to date include major tropical forest biome transitions, including forest to savanna and forest to the drier cerrado vegetation, which may also be associated with differences in canopy structure (Marselis et al. 2018, Shao et al. 2019, Tang et al. 2019). Ultimately, discerning the detailed links between canopy structure and ecosystem functions including surface energy dynamics remains an area of emerging research requiring greater empirical and theoretical development (Wehr et al. 2017, Wu et al. 2018). However, the results presented above, and theoretical foundations (Bonan 2008), suggest strong predictive quantitative links between forest canopy structure and function; with additional development, these links should open transformative remote observation data streams on degraded forest function.

Soil factors may also impact surface energy fluxes (Bonan 2008) and influence the distribution of savannas (Lloyd et al. 2008, Lehmann et al. 2011) and canopy structure and function gradients (Schietti et al. 2016). Lehmann et al. 2011, for example, identify soil fertility as a key factor influencing arid savanna forest transitions, though no single fertility threshold was identified for savanna. Furthermore, soil structural factors such as sand content influence patterns of soil water availability and plant water relations (Sperry and Hacke 2002, Oliveras and Malhi 2016). Seasonally flooded forests are also at risk of transitions to degraded savanna-like states as a result of high fire sensitivity and susceptibility due to superficial root mats and other factors (Almeida et al. 2016, Flores et al. 2017). Together, soil structure and nutrients likely impact the chances of long-term savannization following disturbance and may alter relations between vegetation structure and energy balance components, but more studies are needed.

Energy balance and forest structural attributes have been shown to change with forest disturbance; however, not enough information is available for robust characterizations of the functional relationships highlighted by our framework in tropical forests. The seasonal dynamics of the sensible to latent heat flux partitioning, the Bowen ratio, varies between wetter and drier forests; dry forest and savanna exhibit strong increases in the Bowen ratio in the dry season, while wet forest remains relatively insensitive to rainfall seasonality (da Rocha et al. 2009, Restrepo-Coupe et al. 2013). Brando et al. 2019 detail the impacts of 13 yr of fire impact and recovery in a controlled experiment in south central Amazônia; contrasting flux measurements in burned and unburned (control) plots, evapotranspiration (ET) was similar even though LAI in the control was 70% higher, potentially consistent with a nonlinear functional response. A foundational study that imposed a drought

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experimentally for 5 yr in the central Amazon found a 30% reduction in leaf area by the end of measurements (Brando et al. 2008; see discussion below of our canopy resurvey of this study site). Patterns of light transmission through the forest are also impacted by disturbance and local canopy structure gradients. Montgomery and Chazdon (2001), working in Costa Rican mature and secondary forests, found relationships between stem densities and near-surface radiation transmittance in mature forest but not for regenerating forest; also observing vertical heterogeneity in radiation environments, these authors concluded that the multilayered heterogeneity of the canopy played a complex role in radiation transmission dynamics. Little direct work is available on the role of canopy structure gradients in surface roughness and boundary layer conductances; models generally assume that deforestation will reduce roughness and thus mixing (Lean and Warrilow 1989, Shukla et al. 1990, Spracklen and Garcia-Carreras 2015). While we do not consider larger scale climate processes in depth here, it is important to note that these processes contribute to several additional near-surface atmosphere impacts including the local formation of clouds, aerosols, and rainfall, which alter albedo and heating processes in the atmosphere (Bonan 2015, Laguë et al. 2019). Deforestation generally decreases rainfall over the Amazon in model-based studies (Knox et al. 2011, Davidson et al. 2012, Lawrence and Vandecar 2015, Spracklen and Garcia-Carreras 2015), including threshold-type nonlinear reductions and bioclimatic savannization in the southern and eastern Amazon (Pires and Costa 2013).

Forest disturbance can have significant influence on the future ecological state of the impacted forest, including by enhancing the risk of savannization (Cochrane and Laurance 2008, Aragão and Shimabukuro 2010, Silva et al. 2018). Disturbance broadly impacts the landscape structure of forest and savanna mosaics, as well as continua of structural gradients within vegetation types. For example, Soares-Filho et al. (2012) found that a deforestation-related feedback is the primary driver of increased fire frequency in a data-driven model of a highly disturbed central Amazonian landscape. Feedbacks are also linked to microclimate and energy balance impacts associated with forest structural change and arise when disturbed forest is more susceptible to additional disturbance, and when ecological recovery trajectories are altered. One of the most consequential feedbacks occurs when structural change promotes fire because of the capacity of fire to profoundly reorganize ecosystem and community structure, including by converting wet forest to savanna (Malhi et al. 2009, Silvério et al. 2013), or secondarized low biomass forest comprised of pioneer trees (Barlow and Peres 2008), or creating alternate regeneration pathways (Mesquita et al. 2001, Norden et al. 2011). Disturbances that open the forest canopy create conditions favorable to fire spread following human-driven ignition, increasing boundary layer conductance, reducing humidity, and increasing air speed and temperatures (Ray et al. 2005, Cochrane and Laurance 2008). Fire itself may cause these alterations, but an important caveat is that fires also reduce fuel loads, which has a negative feedback on fire spread in the near term (Balch et al. 2008). Canopy opening disturbances such as fires promote grass establishment which can facilitate future fire ignition and spread, particularly if the newly established grass species are fire adapted (Silvério et al. 2013). The recurrence of burning promotes the establishment of fire-resilient savanna species with thick bark that coexist with grasses, creating a positive feedback to fire susceptibility enhancing savannization (Ratnam et al. 2011, Hoffmann et al. 2012).

The reduction of forest cover and structural complexity from disturbance can promote additional canopy simplification through positive forest change feedback mechanisms. The loss of cover and increased canopy openness can increase the vulnerability of trees not only to fire but also to wind throw during storms (Silvério et al. 2019). Increasing openness, light penetration, and understory vapor pressure deficit (VPD) were associated with edge effects in the **Biological Dynamics of Forests Fragments Project** (BDFFP), which led to the establishment of light wooded faster growing and faster dying trees in the years that followed fragmentation (Nascimento and Laurance 2004, Almeida et al. 2019b). Lianas may also increase after disturbance (Laurance et al. 2001) and can lead to additional tree fall (Hunter et al. 2015). Negative feedbacks between disturbance and canopy change may

also be at play; particularly, disturbance enhances light environments in the lower strata of forests, promoting tree growth and the infilling of gaps (via gap regeneration dynamics; Brokaw 1985), which can also suppress fire (Oliveras and Malhi 2016). Linking specific microclimate impacts and the enhancement of regeneration potential in vertically structured canopies remains an emerging area of research (Stark et al. 2015). However, the interplay of microclimates, light-limited tree regeneration, and drought and fire disturbances is not yet fully understood (see also Oliveras and Malhi 2016), which precludes more informed predictions about forest change trajectories, including recovery and savannization, and associated longer term ecosystem impacts (Fig. 1A). Recent work has suggested that tree functional composition change over succession, in terms of differentiation on growthsurvival and stature-recruitment tradeoffs, can explain forest structural change, highlighting the likely importance of community and demographic dynamics in forest transitions (Rüger et al. 2020). Furthermore, understanding the specific long-term impacts of forest disturbances on demographic components, recruitment, growth, and mortality is increasingly recognized as central to predicting climate forcing (McDowell et al. 2020).

## Section 2: Tropical Site Contrasts Within Canopy Structure–Energy Gradients

A key challenge for understanding changes along forest structure gradients and their consequences for energy balance is the ability to quickly detect and assess these changes across heterogeneous landscapes. This is particularly relevant where changes from disturbance are occurring rapidly or have novel impacts relative to long-term patterns of vegetation heterogeneity, such as in the central Amazon. The conventional approach to understanding these gradients is through the establishment of long-term towerbased eddy covariance flux monitoring networks (Baldocchi et al. 2001), which limits the scope of assessment in large and quickly changing systems. A recently developed rapid campaign approach can supplement these long-term monitoring networks for the characterization of surface properties associated with vegetation structure, particularly those related to energy balance and radiation fluxes (Villegas et al. 2017). Although sacrificing accuracy and temporal scope relative to long-term tower installation and flux monitoring approaches, this approach offers the potential to more rapidly assess energy balance partitioning in multiple sites and potentially multiple stages of degradation and forest-savanna gradients. This capacity can help close gaps in the scope of assessment of the consequences of forest structural change, offering field measurements in recently disturbed forest, and degraded forests undergoing recovery or savannization. Ecosystem and atmospheric functions assessed with this rapid approach were comparable to long-term quantification of similar vegetation change impacts within the ecosystems studied (boreal and semi-arid North American forest in Villegas et al. 2017), though additional validation and development may offer improvement. Here, we applied this approach in Amazon forests for the first time to obtain example comparisons among sites, providing patterns consistent with our framework for the investigation of forest functional and structural gradients.

To quantify structural and functional contrasts across forest disturbance and savanna transitions, we estimated changes in structural complexity (tree cover, LAI, tree size structure, and vertical leaf area heterogeneity) and energy balance variables (surface roughness, Bowen partitioning ratio, and albedo) in paired simultaneous measurement plots. The rapid assessment method detailed in Villegas et al. 2017, and in the context of this Amazon forest study, in Supporting Information Appendix S1, is based on the following components: (1) the establishment of focal forest plots where tree surveys provided diameter distributions and basal area; (2) the measurement of canopy structure with a combination of hemispherical photos (used to calculate direct site factor, DSF, a metric of incident radiation) and a profiling lidar (PCL) to quantify the vertical and horizontal variation of canopy surface areas, of which leaves are the primary component (Parker et al. 2004); and, (3) the quantification of surface energy dynamics with incoming and outgoing above-canopy solar radiation from a net radiometer-and, in profile, wind speed, humidity, and temperature-that

utilized lightweight sensors and a portable mast system secured above the canopy. From these measurements, we estimate Bowen ratio by assuming that vertical fluxes of sensible and latent heat are proportional to vertical gradients of temperature and humidity (Shuttleworth 2012). Soil heat flux is also measured in the tower footprint (Appendix S1).

We considered two study regions in the central Amazon with gradients of structural complexity and tree cover, including large-statured mature rainforest, smaller-statured closed canopy forest with disturbance histories, and open savanna (or savannized forest) sites. Climate variables and, to the extent possible, soil conditions at a given study region were held constant. In the first region, near the confluence of the Tapajós and Amazon rivers near the city of Santarém (Pará, Brazil), in the village of Alter do Chão, we conducted a rapid assessment of differences between natural savanna, nearby forest fragments-here natural island-like patches-disturbed periodically by fire (Magnusson et al. 2008), and mature rainforest 45 km away at the K67 site of the Tapajós National Forest (TNF; where there is long-term tower-based eddy covariance flux monitoring; Saleska et al. 2003). We note that Alter do Chão has sandy soil, while soil is clay-rich in the TNF. In a second region ~50 km north of the city of Manaus (Amazônas, Brazil), we investigated the impacts of recent forest clearing in a regrowing pasture with remnant trees and in an ~20-yr-old secondary forestareas cleared and under study as part of the long-term BDFFP project (Laurance et al. 2002). We compared these disturbed areas to nearby (within 20 km) mature rainforest contiguous with extensive undisturbed rainforest; here, all sites were characterized by clay-rich soil. Gradients in forest structural complexity were multidimensional, but broadly similar in the two regions, as revealed by the data (and described below). Within each area, mature vs. disturbed forest contrasts were collected through simultaneous deployment of rapid assessment towers and instrumentation.

Measurements revealed differences in the numbers and distributions of stem sizes, the vertical and horizontal structure of leaf area, and the canopy surface layer, over vegetation contrasts (Figs. 2, 3). Rugosity, a metric of surface roughness, derived from lidar data appeared higher in savanna/savannized forest (BDFFP savannized forest, 2.92 m; Alter do Chão savanna, 3.47 m), relative to fragments and regenerating forest (BDFFP regenerating forest, 2.74 m; Alter forest fragment, 1.84 m), though reconstructed areas were too small for spatially controlled statistical comparison. Interestingly, tall vertically heterogeneous canopies of old-growth forest were more rugose (Manaus-Reserva Ducke, 4.79 m, 95% confidence intervals, CI 4.44-5.14; Manaus-ZF2, 4.65 m, CI 4.16-5.13; Tapajós-K67, 7.55 m, CI 7.11-7.99; sites and PCL lidar collection described in Stark et al. 2012), which highlights the possibility of multimodality of rugosity over structural gradients. Similarities were apparent when comparing estimated vertical leaf area density profiles; in particular, both gradients displayed tall vertically complex mature rainforest structure with maximum foliage heights near 50 m, shorter intermediate complexity forests around 20 m tall with developed upper canopy layers, and open savanna (or savanna-like) structure with a few trees or treelets reaching between 10 and 15 m (Fig. 3). Both gradients displayed correspondence between stem diameter size structure and vertical leaf area structure (consistent with prior findings Stark et al. 2012, 2015). Similar contrasts were apparent comparing leaf area estimated from lidar leaf area density profiles across the structural gradients, wherein mature forests displayed LAI values around six, intermediate complexity recovering forest and forest fragments, were slightly lower, with LAI closer to five, and savannized/savanna sites were open-canopied with LAI between 0.5 and 2 (Table 2, Fig. 4). LAI and vertical patterns of leaf area were, thus, similar in our two study regions, but structural differences were also apparent. Most notably, the BDFFP region displays a more developed mature forest upper canopy, as has been noted previously (Stark et al. 2012). The historical savanna site of Alter do Chão also appeared to differ relative to the savannized forest/pasture of the BDFFP. Specifically, in the BDFFP, a thicket of a vine locally known as cipó-de-fogo (genera Davilla and Doliocarpus) formed around persistent woody vegetation, while tall herbaceous dicots dominated the vegetation at ground level. In contrast, Alter do Chão was grass-dominated



Fig. 2. Three-dimensional canopy surfaces derived from ground-based lidar at (disturbed) Alter do Chão forest fragment, and savanna sites (top) and Biological Dynamics of Forest Fragments Project (BDFFP) recovering forest and savannized forest/pasture sites illustrate the impacts of forest disturbance on canopy height and rugosity. Canopy height is higher in less disturbed sites, while rugosity may be higher in more disturbed sites (though the sample size precludes statistical comparison of the rugosity metric calculated as the standard deviation of canopy surface height).

and trees and shrubs were sparse, had open canopies, and represented fire-tolerant species typical of savanna (Miranda 1993, Magnusson et al. 2008); this translated to a lower LAI and lower near-ground leaf area in Alter do Chão.

Canopy structural differences among sites had apparent consequences for radiation transmission, and other microclimate and surface energy canopy functions. The progression of decreasing LAI from mature to degraded to savannized forest corresponded with patterns in other variables, in the same or opposing directions (Table 2, Fig. 4). All contrasts were significant and consistent in direction over the comparable forest structural gradients in the two regions, with the exception of the Bowen ratio (Table 2, Fig. 4). The proportion of potential near-ground solar radiation reaching the soil surface—the

DSF (Royer et al. 2010, Villegas et al. 2010*a*, *b*) increased in the low LAI open sites. Lower DSF, albedo, and ground heat fluxes correspond with higher available radiation/energy (for latent and sensible heat flux; Rn - G) in the closed canopy disturbed forest relative to the savanna/savannized sites. Over the short observation window of this study, we did not identify differences in the sensible to latent heat fluxes (Bowen ratio). However, available energy is partitioned to latent heat with primacy over sensible heat when water is available, as it was during our study. Since there was higher available net radiation in the forest sites (particularly morning through midday, Fig. 5), corresponding with lower albedo and soil heat flux, the similar Bowen ratio values mean that there were higher latent than sensible heat fluxes overall. Higher latent heat fluxes, and



Fig. 3. Vegetation structure—integration of stem diameter and lidar vertical vegetation information. Panels from left to right move from mature tropical rainforest (control/comparison sites), to disturbed, and then

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#### (Fig. 3. Continued)

savanna/savannized forest. Top two rows present the Alter do Chão region gradient (mature forest comparison in the Tapajós National Forest, K67 site), and the bottom two rows, the BDFFP gradient. Basal area profiles are derived from the stem frequency distributions shown in each panel pair (pink). Frequency panels also include forest type information. Lidar-derived leaf area density profiles are shown in green; ribbons display 95% confidence intervals around mean values. Gray shaded regions are size class basal area plotted vs expected height of the size group (Feldpausch et al. 2011, Stark et al. 2012), highlighting (partial) correspondence with vertical leaf area profiles. Bottom panels for each region show the tree size frequency distributions (purple bars). Abbreviation regen. indicates regenerating.

net radiation differences, suggested greater (and generally high) transfer of water to the atmosphere in the forest fragments and regenerating forest relative to savanna and savannized forest. Temporally and climatically coincident data were not available from mature forest eddy covariance sites. Albedo values of the disturbed forest sites, however, were close to those reported for the old-growth forest sites (Araújo et al. 2002, von Randow et al. 2004, Miller et al. 2011), suggesting that even with apparently slightly reduced LAI, the low albedo of these closed canopy disturbed sites was comparable to mature closed canopy tropical forest.

We also leveraged research infrastructure previously developed in the Seca floresta experiment at the TNF. We tested whether there were persistent or even elevated canopy impacts 10 yr after the cessation of 5 yr of experimental drought from rain throughfall exclusion (Nepstad et al. 2007, Brando et al. 2008). This contrast (pre- and post-drought) enabled us to consider temporal changes in addition to the structural spatial contrasts illustrated above, to highlight potential forest change feedback. From the end of the manipulated drought in 2005 to our resurvey in 2015, the LAI in the control plot did not change significantly, whereas the drought plot had a reduced LAI in 2005 that recovered to control levels by 2015 (Fig. 6, top row; 2015 control mean 5.64 with 95% CI 5.34-5.94, and experimental 5.71 with CI 5.45–5.97). We were also able to confirm that this recovery was complete in terms of the height profile of vegetation, with very similar leaf area profiles occurring in the control and the drought plots in 2015 (Fig. 6, bottom row). We note that though vegetation profile data are not available from the experimental period, higher mortality of large trees in the drought plot was reported (Nepstad et al. 2007),

suggesting a likely reduction of leaf area in upper strata at that time.

Collectively, these examples highlight expected but to date rarely quantified patterns of canopy structural, functional change in tropical forests that relate directly to savannization and help reveal structure–energy relationships, though expanding sampling over broader gradients is needed to quantify functional responses essential for predictive ecosystem science (see Fig. 1). Although these examples are insufficient to span full gradients of canopy structure, they provide initial insights into how such differences might be placed within the proposed framework.

### Section 3: Reframing Tropical Forest Savannization, Challenges and Prospects

Studies in tropical forest structure and function can be particularly challenging due to vegetation height, accessibility, and infrastructural limitations. Limited funding has further constrained studies of vegetation structure in Amazon Basin tropical forests. Despite the enormous importance of the Amazon forests and concerns about the potential for savannization-highlighted prominently in the recent IPCC assessment (IPCC 2013, 2014)-there are to date fewer than 10 flux towers currently operating in this region. Flux towers are extremely valuable for studying differences between forest types over major vegetation gradients, including forest vs. savanna contrasts (da Rocha et al. 2009, Restrepo-Coupe et al. 2013), and in rare cases over local vegetation contrasts (Brando et al. 2019). However, distant comparisons over major gradients are confounded by climate and variation in vegetation types (functional composition) when used as proxies to investigate changes that might occur in the process of savannization.

Region Forest Mature/ type old-growt		BDFFP/Manaus		Alter do Chão/Santarém		
	Mature/ old-growth	Degraded/ secondary	Savannized	Mature/ old-growth	Degraded	Savanna
LAI	6.20 (6.05–6.35)	4.60 (4.26–4.93)	1.25 (0.93–1.57)	5.73 (5.57–5.89)	4.97 (4.69–5.25)	0.23 (0.16–0.31)
DSF		0.26 (0.24-0.28)	0.64 (0.57-0.72)		0.32 (0.00-0.65)	0.93 (0.90-0.95)
Rn-G (W/m <sup>2</sup> ·s)		104.42 (80.17–128.68)	37.21 (1.30–73.12)		144.15 (102.62–185.68)	31.94 (0.39–63.50)
Bowen Ratio		0.13 (0.05–0.21)	0.72 (0.22–1.21)		1.86 (0.93–2.80)	2.77 (1.31–4.24)
Albedo		0.100 (0.097–0.102)	0.165 (0.160–0.171)		0.092 (0.090–0.095)	0.143 (0.135–0.150)

Table 2. Means and 95% confidence intervals (parentheses) for structural, energy balance, and associated microclimate variables in forest contrasts.

Note: See Fig. 4.

Furthermore, flux network comparisons lack perspectives on local vegetation structure gradients associated with disturbance (the local flux contrasts offered by the Fazenda Tanguro fire experiment are an exception to these generalizations; Brando et al. 2019). Disturbed and degraded forests account for a large fraction of Amazon Basin -recently reported by Bullock et al. 2020 as 17% of the ecoregion in 2017 (in contrast to 11% of Amazon forest cleared for agriculture, and 52% higher than previously estimated)-while secondary growth may account for 28% of Neotropical forest (Chazdon et al. 2016). Degraded forest types represent a significant risk for savannization (Cochrane and Laurance 2008, Aragão and Shimabukuro 2010), which could have critical impacts, including lowering the Amazon forest carbon sink, altering global temperature (Cox et al. 2004, Malhi et al. 2008), and altering other climate patterns (Garcia et al. 2016).

Gradient studies are a critical source of ecological information in tropical forests, as highlighted by the BDFFP project, which investigates fragment size and distance-to-edge effects (Nascimento and Laurance 2004, Almeida et al. 2019b). However, to date, there have not been specifically designed and implemented studies that focus on canopy structure gradients of degraded tropical forest and secondary growth at risk of savannization and the associated relationships between canopy structure, microclimate, and surface energy dynamics. Our proposed framework (Fig. 1) could help guide the development and installation of one or more gradients to specifically evaluate canopy structure-energy relationships. This could be accomplished with

field campaigns such as the one presented, but expanded beyond the pilot demonstration to cover more complete canopy structure gradients (e.g., related to age of regeneration, impact level, or disturbance type), while also controlling for environmental and climate variation. The objective of field campaigns would be to quantify the functional relationships between elements of canopy structure and surface energy balance and, ideally, to evaluate additional environmental and biogeographic dependencies, needed to transform Earth system approaches. With a larger investment, this could also be studied with a network of flux towers, which would provide additional longer term information on energy, water, and carbon fluxes. The Fazenda Tanguro fire experiment contrasting paired fire impacted and control forests partially addresses this gap (Brando et al. 2019). There is a critical need, however, to move beyond contrasts toward understanding of gradients and functional responses, for which a range of structural states must be considered (Berenguer et al. 2014, 2018). As with temperate grassland-forest gradients, many microclimate and associated energy balance impacts of forest structural change will display nonlinear functional responses, including decreasing, increasing or peaked relationships (Fig. 1; Breshears 2006). Nonlinearities and thresholds in functional responses of energy balance, and related microclimates, may determine whether a site or region will transition to a savanna or recovered forest state over the long term (Fig. 1; Staver et al. 2011, Hoffmann et al. 2012, da Silva Junior et al. 2019). In the future, combinations of targeted gradient studies and



Fig. 4. Structural, energy balance, and associated microclimate variables over gradients of decreasing structural complexity and cover. Horizontal lines are means, while shaded bars are estimated 95% confidence regions. All contrasts are significant at the P < 0.05 level by *t*-tests (or comparison of confidence region in the case of LAI), excepting Bowen ratios, which did not appear to differ. Leaf area index was estimated from lidar and, in this case, included the mature forest site data for comparison. LAI and vegetation structure impacts on incoming solar radiation are illustrated by direct site factor (DSF; proportion of annual direct solar radiation that reaches the surface relative to the open-sky expectation)-and here, higher DSF may have contributed to higher albedo, with the ground more reflective than leaf area. Rn-G, available net radiation, and other energy balance components are taken from half-hour mean values between 10 a.m. and 2 p.m. in two observed daily cycles. See Table 2.

networks of comparable field contrasts, with detailed structural predictor and energy and microclimate response variable measurements, can directly reveal thresholds and functional responses, and their associated dependencies.

Canopy structure-energy relationships in tropical forests are essential to global climate function; tropical forests are not simply important for their carbon sequestration value (IPCC 2014). Rather, as we have illustrated (Figs. 2–6), changes in canopy structure have pronounced impacts on energy balance and associated local microclimate. This has implications for locally mediated, and large scale, vegetation change feedbacks. First, at the local scale, sites with less cover and simplified structure create a hotter microclimate that can impact understory vegetation (Nascimento and Laurance 2004, Allen et al. 2015). In harsher microclimates, stress may be amplified for remaining trees, potentially triggering additional tree mortality and creating environments favorable to fire ignition and spread (Nascimento and Laurance 2004, Ray et al. 2005, Allen et al. 2015). Next, widespread vegetation change impacts on local climates alter large scale temperature, precipitation, and pressure gradients (Spracklen and Garcia-Carreras 2015, Villegas et al. 2015), which may cause large scale vegetation feedbacks (Friedlingstein et al. 2014). Changes in climate within one subregion can also alter climate teleconnections and thereby impact vegetation elsewhere-termed an ecoclimate teleconnection (Swann et al. 2012, Stark et al. 2016). Thus, if savannization is sufficiently extensive, it can potentially affect energy balance and local climate in both the region of tree loss as well as in other regions via climate connections (Swann et al. 2012, Medvigy et al. 2013, Garcia et al. 2016, Stark et al. 2016, Molina et al. 2019).

Structure–energy relationships appear integral to the sensitivity and resilience of tropical forest to structural change from droughts, heatwaves, fires, deforestation, and other increasing environmental disturbances at local scales, because of microclimate alteration and the influence of microclimates on disturbance impacts. However, we generally lack rigorous quantitative sensitivity and resilience relationships that can translate how a particular forest state will respond to a particular disturbance, under a given climate. In this context, the unresolved sensitivity and



Fig. 5. Diurnal time-series of available energy at the surface (Rn-G) contrasted over forest structural gradients in the central Amazon. Red stars represent savanna or savannized sites, while blue triangles are disturbed but closed canopy forest sites. Note that the averages of these diurnal patterns are the values presented in Table 2, Fig. 4.



Fig. 6. Temporal contrast addressing forest resilience/sensitivity. Forest recovery 10 yr after the Seca Floresta drought throughfall experiment (Nepstad et al. 2007). Drought is red and control, blue. LAI of drought plot in 2005 reported in Brando et al. 2008 falls below resampling-determined LAI confidence intervals (2015) suggesting significant recovery (denoted as \*).

resilience of tropical forest to droughts, heatwaves, and fires significantly limits Earth System model forecasting of climate change (IPCC 2013, 2014, Friedlingstein et al. 2014, Kloster and Lasslop 2017, Fisher et al. 2018). To address this uncertainty, we advance here the specific hypothesis that canopy structure, surface energy balance, and the sensitivity of tropical forest to droughts, heatwaves, and fires are mechanistically interrelated by the impacts of canopy structure on vegetation microclimates, and the roles of microclimates in vegetation disturbance (e.g., impacting drought mortality and fire spread; Nascimento and Laurance 2004, Ray et al. 2005, Allen et al. 2015). It follows that the relationships explored in our framework (Fig. 1, Table 1) could then be extended to predict sensitivities, and that data on both forest canopy structure and energy balance would improve this prediction (Fig. 7). To expand our conceptual framework to include sensitivity, we consider two forest change time steps, an initial degradation event driven by deforestation or another disturbance (Fig. 7 left), and a second step that could include forest recovery, or continued degradation (Fig. 7 right). The outcome of this second time step-recovery or collapse-hinges on forest sensitivity to the disturbances likely to be present, including drought and fire. Thus, as we have hypothesized, a first feedback to change is possible from the local-scale impacts of degradation



Fig. 7. Hypothesis and proposed research program to address the sensitivity and resilience of tropical forest to future change from structure, energy balance, and microclimate relationships. ΔT1 is a time step of initial disturbance, such as deforestation, that causes an old-growth tropical forest to become secondarized or otherwise degraded, with changing energy partitioning (blue to red gradient, with more red indicating more savanna-like energy characteristics). In this time step, rapid field assessment and remote observation of forest structure (lidar) and energy balance (multispectral and thermal approaches) offer the development of quantitative models linking structure and energy balance. In the  $\Delta T2$  second time step, forests may recover, or collapse and be further degraded from additional disturbances. Initiated by the disturbance in time step 1, two feedback pathways mediated by forest sensitivity and resilience may affect forest transitions in the second time step. The first, we hypothesize, is a local-scale disturbance feedback wherein forest structure and energy balance influence forest sensitivity to drought, heatwave, and fire disturbance because of cross-linking microclimate relationships (e.g., open canopies are drier and hotter, facilitating fire). The second feedback is the well-known large scale vegetation-climate feedback arising when widespread energy balance changes affect climate gradients and processes that in turn impact the forest. Remote and field monitoring over this second time step would test the disturbance feedback hypothesis and allow quantitative model development of forest disturbance sensitivity relationships, that should also account for climate and functional traits.

on disturbance sensitivity. The larger scale vegetation–atmosphere interactions typically addressed in Earth System models (Friedlingstein et al. 2014) represent a second feedback. In this case, the feedback results from regional alterations of temperature and precipitation, which impacts the forest via its sensitivity to variations in these factors. Other factors influencing forest sensitivity and resilience to disturbance such as forest functional composition (Brum et al. 2019, Rüger et al. 2020) would also play a critical role.

Advanced fine-grained remote sensing may allow for the rapid application of this framework to reduce uncertainty in tropical forest transitions (highlighted in Fig. 7). The quantity and arrangement of canopy surface areas, shortwave albedo, and thermal near infrared emission components of energy balance are already directly observable at fine (few meter) scales from remote sensing technologies (lidar and multispectral radiometric imaging respectively). From these raw remote observations, approaches to estimate surface and canopy microclimates (Zellweger et al. 2019), tree sizestructured dynamics (Stark et al. 2012, 2015, Smith et al. 2019), and full surface energy partitioning (de Oliveira et al. 2016) have been elaborated. Thus, an implication of our framework is that, if correct, advances in remote sensing will open a wide new avenue to monitor both atmospheric forcing relevant to predicting large scale climate feedbacks and changing forest sensitivities, relevant to predicting local-scale disturbance sensitivity feedbacks (Fig. 7). Field

measurements such as those presented in this article will also be essential to develop faster high-throughput remote observation-based approaches to quantify structure, surface energy balance, and microclimates across forest degradation and savannization gradients.

In the context of changes related to forest resilience (Fig. 7 right), the temporal change we documented at the Seca Floresta experimental drought study (Fig. 6) provides one example of forest recovery. In that study, rain throughfall was excluded from 1 ha of forest for 5 yr; our resurvey 10 yr after cessation showed that there was no apparent impact on leaf area-that leaf area had recovered from an initially reported 30% loss—and that there were no discernable differences in the vertical canopy structure. This forest experiences significant seasonal drought, with a likely stronger than average drought event in 2010 (Lewis et al. 2011; though, we note this region did not experience the severe drought of others), but, nevertheless, was able to recover. This may be consistent with findings of Brando et al. (2008) in the initial study: The forest appeared to shift allocation to maintain leaf area (estimated with litter production) during the drought, at the expense of wood growth. Furthermore, wood growth appeared to recover quickly in the first year after drought cessation. More recently, detailing responses to experimental fire in the southern central Amazon, Brando et al. (2019) describe a surprising resilience of function in forest undergoing apparent savannization—even with a 70% decrease in leaf area, fire impacted forests were able to maintain similar transpiration as control vegetation. This highlights the need to include not just physical structural information but also vegetation functional characterization. A more complete understanding of structure-energy balance change and forest resilience would link variation in leaf function and water strategies over canopy strata and canopy microenvironments with the risks of fire, mortality, and other factors under droughts and heatwaves (McDowell et al. 2018, Smith et al. 2019, Brum et al. 2019).

In conclusion, global change-related droughts, deforestation, and fire are rapidly converting previously structurally complex mature forests into a matrix of degraded states that range in vertical and horizontal variation of leaf area and canopy cover (Asner et al. 2010, Tyukavina et al. 2017, Almeida et al. 2019b). Because savannization of tropical wet forests is of such concern both locally and globally (IPCC 2014), we need to move past historical savanna and forest contrasts to the huge areas at risk of savannization, to understand threshold type and nonlinear response to forest gradients associated with savannization and other types of forest change. Given that changes in tree cover and structure have large impacts on energy balance and ecosystem properties, there is an urgent need to quantify these properties not only for primary forests, but also for forests with lower, less complex cover and structure. The proposed framework (Table 1, Fig. 1), along with the recently developed field campaign protocol, provides a means for achieving this broader characterization. In addition, recent advances in remote sensing offer new opportunities to quantify and link canopy structure to components of energy balance, and forest sensitivity and recovery from disturbance (Fig. 7)-these include multispectral based approaches to mapping components of energy balance, microclimates, canopy functional parameters, and airborne and spaceborne lidar for forest three-dimensional canopy structure characterization, including the new GEDI mission (Chambers et al. 2007, Stark et al. 2012, 2015, de Oliveira et al. 2016, Shao et al. 2019, Tang et al. 2019, Zellweger et al. 2019). Further, many forest disturbance factors including intensification of ENSO, and drought generally, as well as direct human alterations, and related fires are currently increasing in the Amazon (Davidson et al. 2012). Smoke pollution from land use change related fires also causes widespread adverse respiratory health impacts, which in 2020 may worsen the COVID-19 pandemic (de Oliveira et al. 2020). The much publicized 2019 crisis of Amazon fire and land conversion (Escobar 2019), and emerging 2020 crisis (de Oliveira et al. 2020), in this light represent a clear call for action to safeguard human health and Amazon forest climate function, including by better understanding the factors that could contribute to restoration and recovery of high biomass tropical forest, instead of long-term savannization (and see Barlow et al. 2020). There is need to both quantify the consequences of degradation and understand feedbacks to longer term forest

change, particularly to track and monitor ecological trajectories that can provide early warning for forest state transitions from high biomass forest to low biomass and high sensible heat flux savanna. Ultimately, energy and carbon budgets of disturbed and degraded forest types, and their sensitivities to forest state transitions, must be included in ecosystem model forecasts of coupled vegetation–climate change.

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## LITERATURE CITED

- Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6:1–55.
- Almeida, D. R. A., et al. 2019a. The effectiveness of lidar remote sensing for monitoring forest cover attributes and landscape restoration. Forest Ecology and Management 438:34–43.
- Almeida, D. A., et al. 2019b. Persistent effects of fragmentation on tropical rainforest canopy structure after 20 years of isolation. Ecological Applications 29:e01952.
- Almeida, D. A., B. W. Nelson, J. Schietti, E. B. Gorgens, A. F. Resende, S. C. Stark, and R. Valbuena. 2016. Contrasting fire damage and fire susceptibility between seasonally flooded forest and upland forest in the Central Amazon using portable profiling LiDAR. Remote Sensing of Environment 184:153– 160.
- Anthoni, P. M., B. E. Law, M. H. Unsworth, and R. J. Vong. 2000. Variation of net radiation over heterogeneous surfaces: measurements and simulation in a juniper–sagebrush ecosystem. Agricultural and Forest Meteorology 102:275–286.
- Aragão, L. E., and Y. E. Shimabukuro. 2010. The incidence of fire in Amazonian forests with implications for REDD. Science 328:1275–1278.
- Araújo, A. C., et al. 2002. Comparative measurements of carbon dioxide fluxes from two nearby towers in a central Amazonian rainforest: the Manaus LBA site. Journal of Geophysical Research: Atmospheres. 107:LBA-58.
- Archer, S., C. Scifres, C. R. Bassham, and R. Maggio. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecological Monographs 58:111–127.
- Asner, G. P., et al. 2010. High-resolution forest carbon stocks and emissions in the Amazon. Proceedings of the National Academy of Sciences USA 107:16738–16742.
- Balch, J. K., D. C. Nepstad, P. M. Brando, L. M. Curran, O. Portela, O. de Carvalho Jr, and P. Lefebvre. 2008. Negative fire feedback in a transitional forest of southeastern Amazonia. Global Change Biology 14:2276–2287.
- Baldocchi, D., et al. 2001. FLUXNET: a new tool to study the temporal and spatial variability of

ECOSPHERE \* www.esajournals.org

19

ecosystem-scale carbon dioxide, water vapor, and energy flux densities. Bulletin of the American Meteorological Society 82:2415–2434.

- Barlow, J., E. Berenguer, R. Carmenta, and F. França. 2020. Clarifying Amazonia's burning crisis. Global Change Biology 26:319–321.
- Barlow, J., and C. A. Peres. 2008. Fire-mediated dieback and compositional cascade in an Amazonian forest. Philosophical Transactions of the Royal Society B: Biological Sciences 363:1787–1794.
- Bellingham, P. J., E. V. J. Tanner, P. M. Rich, and T. C. R. Goodland. 1996. Changes in light below the canopy of a Jamaican montane rainforest after a hurricane. Journal of Tropical Ecology 12:699–722.
- Belsky, A. J., and C. D. Danham. 1994. Forest gaps and isolated savanna trees. BioScience 44:77–84.
- Berenguer, E., J. Ferreira, T. A. Gardner, L. E. O. C. Aragão, P. B. De Camargo, C. E. Cerri, M. Durigan, R. C. D. Oliveira, I. C. G. Vieira, and J. Barlow. 2014. A large-scale field assessment of carbon stocks in human-modified tropical forests. Global Change Biology 20:3713–3726.
- Berenguer, E., Y. Malhi, P. Brando, A. Cardoso Nunes Cordeiro, J. Ferreira, F. França, L. Chesini Rossi, M. Maria Moraes de Seixas, and J. Barlow. 2018. Tree growth and stem carbon accumulation in humanmodified Amazonian forests following drought and fire. Philosophical Transactions of the Royal Society B: Biological Sciences 373:20170308.
- Bonan, G. B. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320:1444–1449.
- Bonan, G. 2015. Ecological climatology: concepts and Applications. Cambridge University Press, Cambridge, UK.
- Bonan, G. 2019. Climate change and terrestrial ecosystem modeling. Cambridge University Press, Cambridge, UK.
- Brando, P. M., D. C. Nepstad, E. A. Davidson, S. E. Trumbore, D. Ray, and P. Camargo. 2008. Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: results of a throughfall reduction experiment. Philosophical Transactions of the Royal Society B: Biological Sciences 363:1839–1848.
- Brando, P. M., et al. 2019. Prolonged tropical forest degradation due to compounding disturbances: implications for CO2 and H2O fluxes. Global Change Biology 25:2855–2868.
- Breshears, D. D. 2006. The grassland–forest continuum: trends in ecosystem properties for woody plant mosaics? Frontiers in Ecology and the Environment 4:96–104.
- Breshears, D. D., and F. J. Barnes. 1999. Interrelationships between plant functional types and soil

moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. Landscape Ecology 14:465–478.

- Breshears, D. D., and J. A. Ludwig. 2010. Near-ground solar radiation along the grassland–forest continuum: Tall-tree canopy architecture imposes only muted trends and heterogeneity. Austral Ecology 35:31–40.
- Breshears, D. D., J. J. Whicker, C. B. Zou, J. P. Field, and C. D. Allen. 2009. A conceptual framework for dryland aeolian sediment transport along the grassland–forest continuum: effects of woody plant canopy cover and disturbance. Geomorphology 105:28–38.
- Brokaw, N. V. 1985. Gap-phase regeneration in a tropical forest. Ecology 66:682–687.
- Brum, M., M. A. Vadeboncoeur, V. Ivanov, H. Asbjornsen, S. Saleska, L. F. Alves, D. Penha, J. D. Dias, L. E. Aragão, F. Barros, and P. Bittencourt. 2019. Hydrological niche segregation defines forest structure and drought tolerance strategies in a seasonal Amazon forest. Journal of Ecology 107:318– 333.
- Bullock, E. L., C. E. Woodcock, C. Souza Jr., and P. Olofsson. 2020. Satellite-based estimates reveal widespread forest degradation in the Amazon. Global Change Biology 26:2956–2969.
- Campbell, G. S., and J. M. Norman. 1998. An introduction to environmental biophysics. Second edition. Springer, New York, New York, USA.
- Chambers, J. Q., G. P. Asner, D. C. Morton, L. O. Anderson, S. S. Saatchi, F. D. Espírito-Santo, M. Palace, and C. Souza Jr. 2007. Regional ecosystem structure and function: ecological insights from remote sensing of tropical forests. Trends in Ecology & Evolution 22:414–423.
- Chazdon, R. L. 2014. Second growth: the promise of tropical forest regeneration in an age of deforestation. University of Chicago Press, Chicago, Illinois, USA.
- Chazdon, R. L., et al. 2016. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. Science Advances 2: e1501639.
- Cochrane, M. A., and W. F. Laurance. 2008. Synergisms among fire, land use, and climate change in the Amazon. Ambio 37:522–527.
- Cox, P. M., R. A. Betts, M. Collins, P. P. Harris, C. Huntingford, and C. D. Jones. 2004. Amazonian forest dieback under climate-carbon cycle projections for the 21st century. Theoretical and Applied Climatology 78:137–156.
- Curtis, P. G., C. M. Slay, N. L. Harris, A. Tyukavina, and M. C. Hansen. 2018. Classifying drivers of global forest loss. Science 361:1108–1111.

20

- da Rocha, H. R., et al. 2009. Patterns of water and heat flux across a biome gradient from tropical forest to savanna in Brazil. Journal of Geophysical Research. Biogeosciences 114:G00B12.
- da Silva Junior, C. A., G. de Medeiros Costa, F. S. Rossi, J. C. E. Vale, R. B. de Lima, M. Lima, J. F. de Oliveira-Junior, P. E. Teodoro, and R. C. Santos. 2019. Remote sensing for updating the boundaries between the Brazilian Cerrado-Amazonia biomes. Environmental Science & Policy. 101:383–392.
- Davidson, E. A., et al. 2012. The Amazon basin in transition. Nature 481:321.
- de Oliveira, G., N. Brunsell, E. Moraes, G. Bertani, T. dos Santos, Y. Shimabukuro, and L. Aragão. 2016. Use of MODIS sensor images combined with reanalysis products to retrieve net radiation in Amazonia. Sensors 16:956.
- de Oliveira, G., N. A. Brunsell, E. C. Moraes, Y. E. Shimabukuro, T. V. dos Santos, C. von Randow, R. G. de Aguiar, and L. E. Aragao. 2019. Effects of landcover changes on the partitioning of surface energy and water fluxes in Amazonia using high-resolution satellite imagery. Ecohydrology 12:e2126.
- de Oliveira, G., J. M. Chen, S. C. Stark, E. Berenguer, P. Moutinho, P. Artaxo, L. O. Anderson, and L. E. O. C. Aragão. 2020. Smoke pollution's impacts in Amazonia. Science 369:634–635.
- de Oliveira, G., and E. C. Moraes. 2013. Validation of net radiation obtained from MODIS/TERRA data in Amazonia with LBA surface measurements. Acta Amazonica 43:353–363.
- Desjardins, T., A. Mariotti, C. Girardin, and A. Chauvel. 1996. Changes of the forest-savanna boundary in Brazilian Amazonia during the Holocene revealed by stable isotope ratios of soil organic carbon. Oecologia 108:749–756.
- Dickinson, R. E., and P. Kennedy. 1992. Impacts on regional climate of Amazon deforestation. Geophysical Research Letters 19:1947–1950.
- Escobar, H. 2019. Amazon fires clearly linked to deforestation, scientists say. Science 365:853.
- Faria, T. D. O., T. R. Rodrigues, L. F. A. Curado, D. C. Gaio, and J. D. S. Nogueira. 2018. Surface albedo in different land-use and cover types in Amazon forest region. Revista Ambiente & Água 13:1.
- Feldpausch, T. R., et al. 2011. Height-diameter allometry of tropical forest trees. Biogeosciences 8:1081– 1106.
- Fisher, R. A., et al. 2018. Vegetation demographics in Earth System Models: a review of progress and priorities. Global Change Biology 24:35–54.
- Flores, B. M., M. Holmgren, C. Xu, E. H. van Nes, C. C. Jakovac, R. C. Mesquita, and M. Scheffer. 2017. Floodplains as an Achilles' heel of Amazonian

forest resilience. Proceedings of the National Academy of Sciences USA 114:4442–4446.

- Friedlingstein, P., M. Meinshausen, V. K. Arora, C. D. Jones, A. Anav, S. K. Liddicoat, and R. Knutti. 2014. Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks. Journal of Climate 27:511–526.
- Galo, A. T., P. M. Rich, and J. J. Ewel. 1992. Effects of forest edges on the solar radiation regime in a series of reconstructed tropical ecosystems. Pages 98– 108 *in* American Society for Photogrammetry and Remote Sensing Annual Meeting. Albuquerque, New Mexico, USA.
- Garcia, E. S., A. L. Swann, J. C. Villegas, D. D. Breshears, D. J. Law, S. R. Saleska, and S. C. Stark. 2016. Synergistic ecoclimate teleconnections from forest loss in different regions structure global ecological responses. PLOS ONE 11:e0165042.
- Gash, J. H. C., et al. 2004. Amazonian climate: results and future research. Theoretical and Applied Climatology 78:187–193.
- Gash, J. H. C., and C. A. Nobre. 1997. Climatic effects of Amazonian deforestation: some results from ABRACOS. Bulletin of the American Meteorological Society 78:823–830.
- Giambelluca, T. W., F. G. Scholz, S. J. Bucci, F. C. Meinzer, G. Goldstein, W. A. Hoffmann, A. C. Franco, and M. P. Buchert. 2009. Evapotranspiration and energy balance of Brazilian savannas with contrasting tree density. Agricultural and Forest Meteorology 149:1365–1376.
- Hirota, M., M. Holmgren, E. H. Van Nes, and M. Scheffer. 2011. Global resilience of tropical forest and savanna to critical transitions. Science 334:232– 235.
- Hirota, M., C. Nobre, M. D. Oyama, and M. M. Bustamante. 2010. The climatic sensitivity of the forest, savanna and forest–savanna transition in tropical South America. New Phytologist 187:707–719.
- Hoffmann, W. A., E. L. Geiger, S. G. Gotsch, D. R. Rossatto, L. C. Silva, O. L. Lau, M. Haridasan, and A. C. Franco. 2012. Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. Ecology Letters 15:759–768.
- Houghton, R. A. 2018. Interactions between land-use change and climate-carbon cycle feedbacks. Current Climate Change Reports 4:115–127.
- House, J. I., S. Archer, D. D. Breshears, R. J. Scholes, and NCEAS Tree–Grass Interactions Participants. 2003. Conundrums in mixed woody–herbaceous plant systems. Journal of Biogeography 30:1763– 1777.
- Hunter, M. O., M. Keller, D. Morton, B. Cook, M. Lefsky, M. Ducey, S. Saleska, R. C. de Oliveira Jr, and

ECOSPHERE \* www.esajournals.org

21

J. Schietti. 2015. Structural dynamics of tropical moist forest gaps. PLOS ONE 10:e0132144.

- IPCC. 2013. Climate change 2013: the physical science basis. *In* Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- IPCC. 2014. Climate change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. *In* Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Jin, Y., J. T. Randerson, M. L. Goulden, and S. J. Goetz. 2012. Post-fire changes in net shortwave radiation along a latitudinal gradient in boreal North America. Geophysical Research Letters 39. https://doi. org/10.1029/2012GL051790
- Kalamandeen, M., E. Gloor, E. Mitchard, D. Quincey, G. Ziv, D. Spracklen, B. Spracklen, M. Adami, L. E. Aragão, and D. Galbraith. 2018. Pervasive rise of small-scale deforestation in Amazonia. Scientific Reports 8:1600.
- Kloster, S., and G. Lasslop. 2017. Historical and future fire occurrence (1850 to 2100) simulated in CMIP5 Earth System Models. Global and Planetary Change 150:58–69.
- Knox, R., G. Bisht, J. Wang, and R. Bras. 2011. Precipitation variability over the forest-to-nonforest transition in southwestern Amazonia. Journal of Climate 24:2368–2377.
- Laguë, M. M., G. B. Bonan, and A. L. Swann. 2019. Separating the impact of individual land surface properties on the terrestrial surface energy budget in both the coupled and uncoupled land–atmosphere system. Journal of Climate 32:5725–5744.
- Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. G. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conservation Biology 16:605–618.
- Laurance, W. F., D. Pérez-Salicrup, P. Delamônica, P. M. Fearnside, S. D'Angelo, A. Jerozolinski, L. Pohl, and T. E. Lovejoy. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology 82:105–116.
- Lawrence, D., and K. Vandecar. 2015. Effects of tropical deforestation on climate and agriculture. Nature Climate Change 5:27.
- Lean, J., and D. A. Warrilow. 1989. Simulation of the regional climatic impact of Amazon deforestation. Nature 342:411.
- Lee, B. E., and B. F. Soliman. 1977. An investigation of the forces on three dimensional bluff bodies in

rough wall turbulent boundary layers. Journal of Fluids Engineering 99:503–509.

- Lee, J. A. 1991*a*. Near-surface wind flow around desert shrubs. Physical Geography 12:140–146.
- Lee, J. A. 1991b. The role of desert shrub size and spacing on wind profile parameters. Physical Geography 12:72–89.
- Lehmann, C. E., S. A. Archibald, W. A. Hoffmann, and W. J. Bond. 2011. Deciphering the distribution of the savanna biome. New Phytologist 191:197–209.
- Lewis, S. L., P. M. Brando, O. L. Phillips, G. M. van der Heijden, and D. Nepstad. 2011. The 2010 amazon drought. Science 331:554.
- Lloyd, J., M. I. Bird, L. Vellen, A. C. Miranda, E. M. Veenendaal, G. Djagbletey, H. S. Miranda, G. Cook, and G. D. Farquhar. 2008. Contributions of woody and herbaceous vegetation to tropical savanna ecosystem productivity: a quasi-global estimate. Tree Physiology 28:451–468.
- Loarie, S. R., D. B. Lobell, G. P. Asner, and C. B. Field. 2011. Land-cover and surface water change drive large albedo increases in South America. Earth Interactions 15:1–16.
- Magnusson, W. E., A. P. Lima, A. L. K. M. Albernaz, T. M. Sanaiotti, and J. L. Guillaumet. 2008. Composição florística e cobertura vegetal das savanas na região de Alter do Chão, Santarém - PA. Revista Brasileira De Botânica 31:165–177.
- Malhi, Y., L. E. Aragão, D. Galbraith, C. Huntingford, R. Fisher, P. Zelazowski, S. Sitch, C. McSweeney, and P. Meir. 2009. Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. Proceedings of the National Academy of Sciences USA 106:20610–20615.
- Malhi, Y., J. T. Roberts, R. A. Betts, T. J. Killeen, W. Li, and C. A. Nobre. 2008. Climate change, deforestation, and the fate of the Amazon. Science 319:L169– L172.
- Marselis, S. M., H. Tang, J. D. Armston, K. Calders, N. Labrière, and R. Dubayah. 2018. Distinguishing vegetation types with airborne waveform lidar data in a tropical forest-savanna mosaic: a case study in Lopé National Park, Gabon. Remote Sensing of Environment 216:626–634.
- Martens, S. N., D. D. Breshears, and F. J. Barnes. 2001. Development of species dominance along an elevational gradient: population dynamics of *Pinus edulis* and *Juniperus monosperma*. International Journal of Plant Sciences 162:777–783.
- McDowell, N. G., et al. 2020. Pervasive shifts in forest dynamics in a changing world. Science. 368: eaaz9463.
- McDowell, N., et al. 2018. Drivers and mechanisms of tree mortality in moist tropical forests. New Phytologist 219:851–869.

22

- Medvigy, D., R. L. Walko, M. J. Otte, and R. Avissar. 2013. Simulated changes in northwest US climate in response to Amazon deforestation. Journal of Climate 26:9115–9136.
- Mesquita, R. C., K. Ickes, G. Ganade, and G. B. Williamson. 2001. Alternative successional pathways in the Amazon Basin. Journal of Ecology 89:528– 537.
- Miller, S. D., M. L. Goulden, L. R. Hutyra, M. Keller, S. R. Saleska, S. C. Wofsy, A. M. S. Figueira, H. R. Da Rocha, and P. B. De Camargo. 2011. Reduced impact logging minimally alters tropical rainforest carbon and energy exchange. Proceedings of the National Academy of Sciences USA 108:19431– 19435.
- Miranda, I. S. 1993. Estrutura do estrato arbóreo do cerrado amazônico em Alter do Chão, Pará, Brasil. Revista Brasileira De Botânica 16:143–150.
- Molina, R. D., J. F. Salazar, J. A. Martínez, J. C. Villegas, and P. A. Arias. 2019. Forest-induced exponential growth of precipitation along climatological wind streamlines over the Amazon. Journal of Geophysical Research: Atmospheres 124:2589– 2599.
- Montgomery, R. A., and R. L. Chazdon. 2001. Forest structure, canopy architecture, and light transmittance in tropical wet forests. Ecology 82:2707–2718.
- Morecroft, M. D., M. E. Taylor, and H. R. Oliver. 1998. Air and soil microclimates of deciduous woodland compared to an open site. Agricultural and Forest Meteorology 90:141–156.
- Nascimento, H. E., and W. F. Laurance. 2004. Biomass dynamics in Amazonian forest fragments. Ecological Applications 14:127–138.
- Nepstad, D. C., C. M. Stickler, B. S. Filho, and F. Merry. 2008. Interactions among Amazon land use, forests and climate: prospects for a near-term forest tipping point. Philosophical Transactions of the Royal Society B: Biological Sciences 363:1737–1746.
- Nepstad, D. C., I. M. Tohver, D. Ray, P. Moutinho, and G. Cardinot. 2007. Mortality of large trees and lianas following experimental drought in an Amazon forest. Ecology 88:2259–2269.
- Norden, N., R. C. Mesquita, T. V. Bentos, R. L. Chazdon, and G. B. Williamson. 2011. Contrasting community compensatory trends in alternative successional pathways in central Amazonia. Oikos 120:143–151.
- Oliveras, I., and Y. Malhi. 2016. Many shades of green: the dynamic tropical forest–savannah transition zones. Philosophical Transactions of the Royal Society B: Biological Sciences 371:20150308.
- Ordway, E. M., and G. P. Asner. 2020. Carbon declines along tropical forest edges correspond to heterogeneous effects on canopy structure and function.

Proceedings of the National Academy of Sciences USA 117:7863–7870.

- Parker, G. G., D. J. Harding, and M. L. Berger. 2004. A portable LIDAR system for rapid determination of forest canopy structure. Journal of Applied Ecology 41:755–767.
- Pennington, T. R., D. E. Prado, and C. A. Pendry. 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. Journal of Biogeography 27:261–273.
- Phillips, O. L., et al. 2009. Drought sensitivity of the Amazon rainforest. Science 323:1344–1347.
- Pires, G. F., and M. H. Costa. 2013. Deforestation causes different subregional effects on the Amazon bioclimatic equilibrium. Geophysical Research Letters 40:3618–3623.
- Rappaport, D. I., D. C. Morton, M. Longo, M. Keller, R. Dubayah, and M. N. dos-Santos. 2018. Quantifying long-term changes in carbon stocks and forest structure from Amazon forest degradation. Environmental Research Letters 13:065013.
- Ratajczak, Z., P. D'Odorico, J. B. Nippert, S. L. Collins, N. A. Brunsell, and S. Ravi. 2017. Changes in spatial variance during a grassland to shrubland state transition. Journal of Ecology 105:750–760.
- Ratnam, J., W. J. Bond, R. J. Fensham, W. A. Hoffmann, S. Archibald, C. E. Lehmann, M. T. Anderson, S. I. Higgins, and M. Sankaran. 2011. When is a 'forest' a savanna, and why does it matter? Global Ecology and Biogeography 20:653–660.
- Ray, D., D. Nepstad, and P. Moutinho. 2005. Micrometeorological and canopy controls of fire susceptibility in a forested Amazon landscape. Ecological Applications 15:1664–1678.
- Restrepo-Coupe, N., et al. 2013. What drives the seasonality of photosynthesis across the Amazon basin? A cross-site analysis of eddy flux tower measurements from the Brazil flux network. Agricultural and Forest Meteorology 182:128–144.
- Royer, P. D., D. D. Breshears, C. B. Zou, N. S. Cobb, and S. A. Kurc. 2010. Ecohydrological energy inputs in semiarid coniferous gradients: responses to management-and drought-induced tree reductions. Forest Ecology and Management 260:1646– 1655.
- Royer, P. D., D. D. Breshears, C. B. Zou, J. C. Villegas, N. S. Cobb, and S. A. Kurc. 2012. Density-dependent ecohydrological effects of piñon–juniper woody canopy cover on soil microclimate and potential soil evaporation. Rangeland Ecology & Management 65:11–20.
- Rüger, N., R. Condit, D. H. Dent, S. J. DeWalt, S. P. Hubbell, J. W. Lichstein, O. R. Lopez, C. Wirth, and C. E. Farrior. 2020. Demographic trade-offs predict tropical forest dynamics. Science 368:165–168.

ECOSPHERE \* www.esajournals.org

23

- Salazar, A., et al. 2018. The ecology of peace: preparing Colombia for new political and planetary climates. Frontiers in Ecology and the Environment 16:525– 531.
- Saleska, S. R., et al. 2003. Carbon in Amazon forests: unexpected seasonal fluxes and disturbance-induced losses. Science 302:1554–1557.
- Sankaran, M., et al. 2005. Determinants of woody cover in African savannas. Nature 438:846.
- Sankaran, M., J. Ratnam, and N. P. Hanan. 2004. Treegrass coexistence in savannas revisited–insights from an examination of assumptions and mechanisms invoked in existing models. Ecology Letters 7:480–490.
- Sankey, J. B., D. J. Law, D. D. Breshears, S. M. Munson, and R. H. Webb. 2013. Employing lidar to detail vegetation canopy architecture for prediction of aeolian transport. Geophysical Research Letters 40:1724–1728.
- Schietti, J., et al. 2016. Forest structure along a 600 km transect of natural disturbances and seasonality gradients in central-southern Amazonia. Journal of Ecology 104:1335–1346.
- Scholes, R. J., and S. R. Archer. 1997. Tree-grass interactions in savannas. Annual Review of Ecology and Systematics 28:517–544.
- Shao, G., S. C. Stark, D. R. de Almeida, and M. N. Smith. 2019. Towards high throughput assessment of canopy dynamics: the estimation of leaf area structure in Amazonian forests with multitemporal multi-sensor airborne lidar. Remote Sensing of Environment 221:1–13.
- Shukla, J., C. Nobre, and P. Sellers. 1990. Amazon deforestation and climate change. Science 247:1322–1325.
- Shuttleworth, W. J. 2012. Terrestrial hydrometeorology. Wiley, Chichester, UK.
- Silva, C. V., et al. 2018. Drought-induced Amazonian wildfires instigate a decadal-scale disruption of forest carbon dynamics. Philosophical Transactions of the Royal Society B: Biological Sciences 373:20180043.
- Silvério, D. V., P. M. Brando, J. K. Balch, F. E. Putz, D. C. Nepstad, C. Oliveira-Santos, and M. M. Bustamante. 2013. Testing the Amazon savannization hypothesis: fire effects on invasion of a neotropical forest by native cerrado and exotic pasture grasses. Philosophical Transactions of the Royal Society B: Biological Sciences 368:20120427.
- Silvério, D. V., P. M. Brando, M. M. Bustamante, F. E. Putz, D. M. Marra, S. R. Levick, and S. E. Trumbore. 2019. Fire, fragmentation, and windstorms: a recipe for tropical forest degradation. Journal of Ecology 107:656–667.
- Smith, M. N., et al. 2019. Seasonal and drought-related changes in leaf area profiles depend on height and

light environment in an Amazon forest. New Phytologist 222:1284–1297.

- Soares-Filho, B., et al. 2012. Forest fragmentation, climate change and understory fire regimes on the Amazonian landscapes of the Xingu headwaters. Landscape Ecology 27:585–598.
- Sperry, J. S., and U. G. Hacke. 2002. Desert shrub water relations with respect to soil characteristics and plant functional type. Functional Ecology 16:367– 378.
- Spracklen, D. V., and L. Garcia-Carreras. 2015. The impact of Amazonian deforestation on Amazon basin rainfall. Geophysical Research Letters 42:9546–9552.
- Stark, S. C., et al. 2012. Amazon forest carbon dynamics predicted by profiles of canopy leaf area and light environment. Ecology Letters 15:1406– 1414.
- Stark, S. C., et al. 2016. Toward accounting for ecoclimate teleconnections: intra-and inter-continental consequences of altered energy balance after vegetation change. Landscape Ecology 31:181–194.
- Stark, S. C., B. J. Enquist, S. R. Saleska, V. Leitold, J. Schietti, M. Longo, L. F. Alves, P. B. Camargo, and R. C. Oliveira. 2015. Linking canopy leaf area and light environments with tree size distributions to explain Amazon forest demography. Ecology Letters 18:636–645.
- Staver, A. C., S. Archibald, and S. A. Levin. 2011. The global extent and determinants of savanna and forest as alternative biome states. Science 334:230–232.
- Swann, A. L., I. Y. Fung, and J. C. Chiang. 2012. Midlatitude afforestation shifts general circulation and tropical precipitation. Proceedings of the National Academy of Sciences USA 109:712–716.
- Tan, Z. H., et al. 2019. Surface conductance for evapotranspiration of tropical forests: calculations, variations, and controls. Agricultural and Forest Meteorology 275:317–328.
- Tang, H., J. Armston, S. Hancock, S. Marselis, S. Goetz, and R. Dubayah. 2019. Characterizing global forest canopy cover distribution using spaceborne lidar. Remote Sensing of Environment 231:111262.
- Tyukavina, A., M. C. Hansen, P. V. Potapov, S. V. Stehman, K. Smith-Rodriguez, C. Okpa, and R. Aguilar. 2017. Types and rates of forest disturbance in Brazilian Legal Amazon, 2000–2013. Science Advances 3:e1601047.
- Villegas, J. C., et al. 2015. Sensitivity of regional evapotranspiration partitioning to variation in woody plant cover: insights from experimental dryland tree mosaics. Global Ecology and Biogeography 24:1040–1048.
- Villegas, J. C., et al. 2017. Prototype campaign assessment of disturbance-induced tree loss effects on

ECOSPHERE \* www.esajournals.org

24

surface properties for atmospheric modeling. Ecosphere 8:e01698.

- Villegas, J. C., D. D. Breshears, C. B. Zou, and D. J. Law. 2010a. Ecohydrological controls of soil evaporation in deciduous drylands: how the hierarchical effects of litter, patch and vegetation mosaic cover interact with phenology and season. Journal of Arid Environments 74:595–602.
- Villegas, J. C., D. D. Breshears, C. B. Zou, and P. D. Royer. 2010b. Seasonally pulsed heterogeneity in microclimate: phenology and cover effects along deciduous grassland–forest continuum. Vadose Zone Journal 9:537–547.
- Villegas, J. C., J. E. Espeleta, C. T. Morrison, D. D. Breshears, and T. E. Huxman. 2014. Factoring in canopy cover heterogeneity on evapotranspiration partitioning: beyond big-leaf surface homogeneity assumptions. Journal of Soil and Water Conservation 69:78A–83A.
- von Randow, C., et al. 2004. Comparative measurements and seasonal variations in energy and carbon exchange over forest and pasture in South West Amazonia. Theoretical and Applied Climatology 78:5–26.

- Wang, L., K. K. Caylor, J. C. Villegas, G. A. Barron-Gafford, D. D. Breshears, and T. E. Huxman. 2010. Partitioning evapotranspiration across gradients of woody plant cover: assessment of a stable isotope technique. Geophysical Research Letters 37. https://doi.org/10.1029/2010GL043228
- Wehr, R., R. Commane, J. W. Munger, J. B. McManus, D. D. Nelson, M. S. Zahniser, S. R. Saleska, and S. C. Wofsy. 2017. Dynamics of canopy stomatal conductance, transpiration, and evaporation in a temperate deciduous forest, validated by carbonyl sulfide uptake. Biogeosciences 14:389– 401.
- Wolfe, S. A., and W. G. Nickling. 1993. The protective role of sparse vegetation in wind erosion. Progress in Physical Geography 17:50–68.
- Wu, J., et al. 2018. Biological processes dominate seasonality of remotely sensed canopy greenness in an Amazon evergreen forest. New Phytologist 217:1507–1520.
- Zellweger, F., P. De Frenne, J. Lenoir, D. Rocchini, and D. Coomes. 2019. Advances in microclimate ecology arising from remote sensing. Trends in Ecology & Evolution 34:327–341.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2. 3231/full