

Commentary

Not the same old(-growth) forests

How will biodiverse tropical forest ecosystems respond to ongoing and future changes in climate and land use? While tropical forests play essential roles in the Earth's carbon (C), energy and water cycles, our understanding of how these cycles operate in tropical forests is limited. Tropical forest structure and function depend on the distribution of organisms and their environment governed by multiple factors such as climate, edaphic characteristics, nutrient availability, and natural and anthropogenic disturbance histories (Baraloto *et al.*, 2012; Quesada *et al.*, 2012; Longo *et al.*, 2016). Our understanding of the economic spectrum and the covariance of leaf and wood traits across tropical species and across environmental gradients is growing (Baraloto *et al.*, 2010). However, trait studies in tropical forests are biased toward old-growth forests, and this limits our understanding of how plant communities respond to the increasing influence of humans on tropical ecosystems (Lewis *et al.*, 2015). Seeking to represent tropical forests in a changing world, it is fundamental that we also understand and quantify the effects of anthropogenic disturbance on trait expression in all tropical forests. The comprehensive work and analysis by Both *et al.* published in this issue of *New Phytologist* (pp. 1853–1865) provides essential information on how soil characteristics and anthropogenic disturbance history modulate trait variability across selectively logged and intact forests in southeast Asia.

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In this comprehensive field survey, Both *et al.* measured 32 different traits for 651 individual trees (284 species). They complemented the trait information with data on 14 soil characteristics including nutrient concentration and nutrient availability. Their sampling approach included both common and rare species and a wide variety of traits ensuring a detailed characterization of functional diversity of the plant community regarding allocation to photosynthesis, defense, growth and nutrient acquisition. This sampling strategy allowed them to

quantify differences in the trait expression of the entire plant community in areas affected by selective logging.

The results from Both *et al.* revealed important differences in forest function between logged and intact forests despite their similar functional diversity. The authors applied principal component analysis on community-weighted mean traits for each of their 1-ha plots (four selectively logged, four intact), and found substantial shifts in forest functioning in logged forests as a result of changes in forest structure and composition (Fig. 1). The plant community in logged forests prioritized photosynthetic activity and growth (e.g. higher values of photosynthetic capacity, and area-based leaf nitrogen (N) content, carotenoids and chlorophyll) and invested less in structure and physical defense (e.g. lower values of branch density, physical strength of leaves, and cellulose concentration). While such shifts are expected and consistent with other studies in South America (Baraloto *et al.*, 2012), Both *et al.* identified another axis of trait variability associated with nutrient acquisition strategy (e.g. mass-based leaf N, phosphorus (P), calcium, magnesium, and C) that was mostly explained by soil characteristics rather than logging history. Together, the results from Both *et al.* suggest a more complex interaction between anthropogenic disturbances and the variability in abiotic controls in determining the shifts in the tropical forest functioning following disturbance.

Soil characteristics have long been recognized as a major controller of the forest structure and composition across intact tropical forests. For example, nutrient availability and physical properties of soils are associated with the regional variation of wood density and life strategies across the Amazon, where the relatively young, nutrient-rich soils in the west show higher abundance of fast-growing, high-turnover, low-wood-density species (Quesada *et al.*, 2012). Models that account for plant trait and soil heterogeneity substantially improved the representation of the spatial distribution of net primary productivity across the region (Castanho *et al.*, 2013). However, the mechanisms that dictate how nutrients affect the forest structure and composition of tropical forests are not yet resolved. For example, Turner *et al.* (2018) have challenged the venerable hypothesis that tropical forest communities on highly weathered soils are P-limited, despite the fact that individual species may show significant P limitation. Moreover, land-use change can effectively alter the nutrient dynamics in tropical ecosystems. For instance, N limits productivity in young secondary tropical forests even on old weathered soils, as a result of substantial N losses caused by deforestation (Davidson *et al.*, 2007).

Intact forests are more the exception than the rule across the tropics. Only 30% of the remaining tropical forests are sufficiently far from direct human influence to be considered intact (Lewis *et al.*, 2015; Tyukavina *et al.*, 2016); with the remaining forests being subject to degradation from

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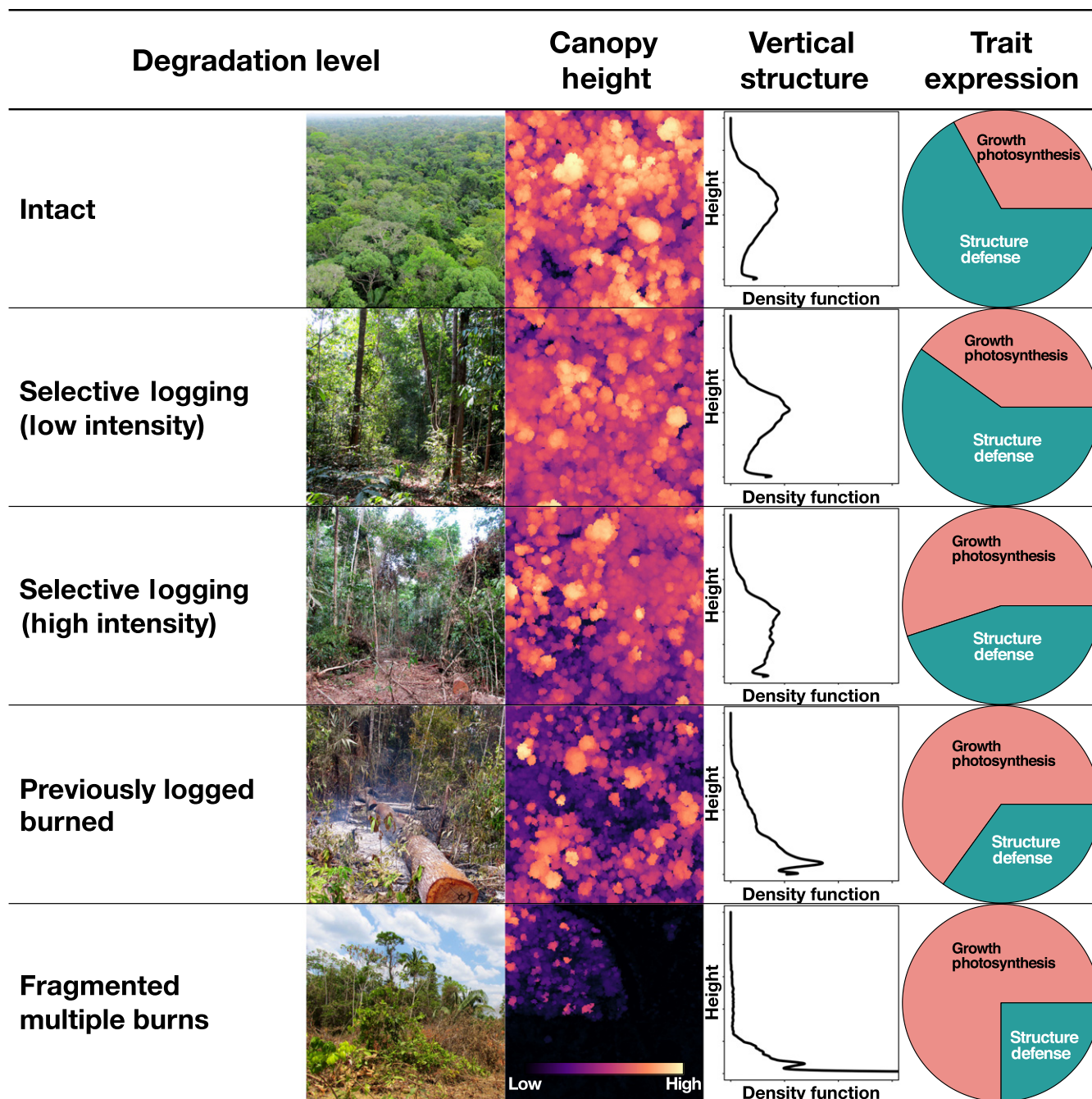


Fig. 1 Schematic diagram representing the impacts of degradation in tropical forest structure and function. Rows are sorted by degradation intensity, with the top row representing nondegraded forests. Changes in forest structure are exemplified by expected changes in canopy height and the vertical distribution of returns from airborne LiDAR measurements. Changes in trait expression are expressed by community-level allocation to growth and photosynthesis vs allocation to structure and physical defense, building on the results from Both *et al.* (in this issue of *New Phytologist*, pp. 1853–1865) and expanding with the expectation to more degraded landscapes.

fragmentation, defaunation, understory fires, and selective logging. Degradation profoundly impacts forest structure and C stocks (Fig. 1), with overall reduction in multi-trophic level biodiversity even at relatively low (*c.* 20%) forest cover loss (Barlow *et al.*, 2016), and increased abundance of fast-growing, low-wood-density trees that invest more in light harvesting than in defense mechanisms (Baraloto *et al.*, 2012; Barlow *et al.*, 2016; Both *et al.*); the impacts of degradation in ecosystem

structure and function can persist for decades (Baraloto *et al.*, 2012; Longo *et al.*, 2016). Importantly, the results from Both *et al.* indicate that the impacts of forest degradation on ecosystem function were effectively independent of the tested abiotic controls on the community-level trait expression; this independence suggests that the impact of anthropogenic disturbances on tropical forest functioning is also unlikely to be compensated by other environmental controls.

Because of the growing anthropogenic influence in tropical ecosystems, the future of tropical forests will be modulated by the impacts of current and future tropical forest degradation. Yet, most Earth System Models represent biomes with the highly aggregated 'big leaf' approach, often with a single plant functional type describing the average tropical forest tree (Fisher *et al.*, 2018, and references cited therein). Big leaf models are computationally advantageous, but they can only represent a few impacts of tropical forest degradation. For example, in the case of logging it may be possible to represent reductions of C stocks based on timber demand, and loss of forest cover. However, to mechanistically represent the impacts of tropical forest degradation in models, one must account for the acute disturbance that selectively kills trees (e.g. diffuse felling of a few large-sized and marketable trees) and chronic change in forest structure and function as the disturbed forests respond to the changes in the micro-environment caused by the disturbance.

The development of cohort-based vegetation models, which are able to efficiently represent structural and functional diversity within forest ecosystems at regional and global scales (Fisher *et al.*, 2018), may provide a feasible way to account for the main mechanisms that drive the dynamics of human-disturbed ecosystems. In these models, the emerging forest structure and composition depends on the distribution of traits and trade-offs that are implemented for each functional group. These models are capable of representing a variety of micro-environments by decomposing the landscape into patches of similar age since last disturbance (Fisher *et al.*, 2018). However, the ability of cohort-based models to successfully represent functional diversity in tropical forests depends on the ability to link observable traits to their definition of functional groups. The results from Both *et al.* suggest that anthropogenic disturbances associated with forest degradation may dictate most of the observed variance in community-level traits in tropical forests. These results should serve as a caution to practitioners who seek trait information for models mainly from the increasingly uncommon range of intact forests. Propagating the excessive focus toward study of old-growth end-members assumes that we understand the future trajectories of tropical forest succession and could easily bias the next generation of dynamic vegetation models.

The extensive data set obtained by Both *et al.* in Sabah (northern Borneo) is an important scientific contribution in itself because few studies have investigated how degradation changes the functioning of tropical forest in southeast Asia, despite more extensive degradation of southeast Asian forests compared to Amazonian forests (Edwards *et al.*, 2014). However, the limited number of plots included in Both *et al.* likely resulted in few statistically significant associations between community-weighted mean traits and disturbance history or soil characteristics. There is a need to expand trait data collection in selectively logged and other degraded forests. However, sample size for field-based studies inevitably will be limited because of the immense time required to collect the measurements and difficulties in accessing degraded forests, which are often located in private land holdings. The recent advances in quantifying canopy forest traits in tropical forests using airborne imaging spectroscopy combined with airborne LiDAR (Asner *et al.*, 2015), and the multiple spaceborne missions aiming to

quantify structure, functioning and diversity of ecosystems (Stavros *et al.*, 2017) provide opportunities to greatly expand our understanding of the impacts of forest degradation in tropical ecosystems.

Selective logging is an important agent of disturbance and change in tropical forests along with understory fires, fragmentation, fuel wood harvesting, grazing, and hunting (Barlow *et al.*, 2016). In the face of these extensive changes to tropical forests, we can no longer rely only on studies of the remaining old-growth. Both *et al.* conducted an excellent, rigorous study showing the way forward. Their findings and data should encourage forest modelers to think about the importance of degradation and should stimulate empiricists to follow in their footsteps and extend their measurements outside the confines of the increasingly threatened realm of intact tropical forests.

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