

- Rose F. 1992. Temperate forest management: its effects on bryophytes and lichen florals and habitats. In: Bates JW and Farmer AM (Eds). *Bryophytes and lichens in a changing environment*. Oxford, UK: Clarendon Press.
- Sillett SC, McCune B, Peck JE, *et al.* 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecol Appl* **10**: 789–99.
- Tibell L. 1992. Crustose lichens as indicators of forest continuity in boreal coniferous forests. *Nord J Bot* **12**: 427–50.
- Verheyen K, Honnay O, Motzkin G, *et al.* 2003. Response of forest plant species to land-use change: a life-history trait-based approach. *J Ecol* **91**: 563–77.

Supporting Information

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The giant trees of the Amazon basin

The tallest trees currently found on Earth have reached their great heights by persisting and growing for centuries in the face of multiple hazards (Lindenmayer and Laurance 2016). The tropical rainforests of South America are not traditionally thought to harbor trees as tall as those on other continents. However, we present new evidence of giant trees in the Amazon basin. The discovery of such trees is important in the context of the ongoing critical threats to biodiversity from deforestation, habitat degradation, and climate change (Laurance *et al.* 2000; Lindenmayer *et al.* 2012).

Physiological studies assign an absolute limit on tree height of about 120 m, beyond which supplying water to leaf cells becomes impossible. As trees become taller, several factors – including increased hydraulic resistance – start to limit growth in height (Ryan *et al.* 2006). In addition to physiological limitations, both the environmental and species-specific traits (often constrained by evolutionary history) strongly influence the chances of a given tree emerging above the crowns of its nearest

neighbors (Cramer 2011). Besides physiological and environmental constraints, disturbances such as windstorms, fires, pests, pathogens, and (increasingly) chain saws threaten the continued existence of giant trees. Tall trees are susceptible to uprooting and breakage by wind because they are more exposed and so experience higher wind load (Laurance *et al.* 2000).

Large trees are particularly important as a source of inspiration to the general public, often playing a key role in campaigns to conserve forests. Furthermore, their dynamics are important for the maintenance of plant and animal diversity (Lindenmayer and Laurance 2016), and they contribute disproportionately to biomass and productivity (Lutz *et al.* 2018). Given that Amazonia represents the world's largest tropical forest, covering 5.3 million km² (Ter Steege *et al.* 2013) and contributing 17% of the terrestrial vegetation carbon stock (Feldpausch *et al.* 2012), the discovery of giant trees improves our understanding of their effects on global carbon dynamics and on biodiversity.

Our analysis of 594 airborne laser transects (375 ha each; WebFigure 1) obtained from airborne laser scanning (ALS) surveys conducted within the Amazon basin led to the discovery of a tree with a height of 88.5 m (Figure 1). It is surrounded by seven other trees taller than 80 m and many more above 75 m (WebFigure 2). The tree is located in a remote region, between Pará and Amapá states, at a straight-line distance of 360 km from the Atlantic Ocean, 280 km from the Amazon River delta, and 220 km from the closest city; it lies approximately 220 m above sea level (WebFigure 3). Additional details about the ALS surveys and data processing are provided in WebPanel 1. The region is accessible only via military helicopters or in small boats up the Jari River, a rapidly flowing watercourse containing numerous waterfalls and carnivorous fish that make navigation dangerous and slow.

The tallest extant trees on Earth, greater than 90 m, are located in North America, Southeast Asia, and Australia, in regions with average annual temperatures of 7.0°–15.4°C in temperate forests, and 22°–29°C

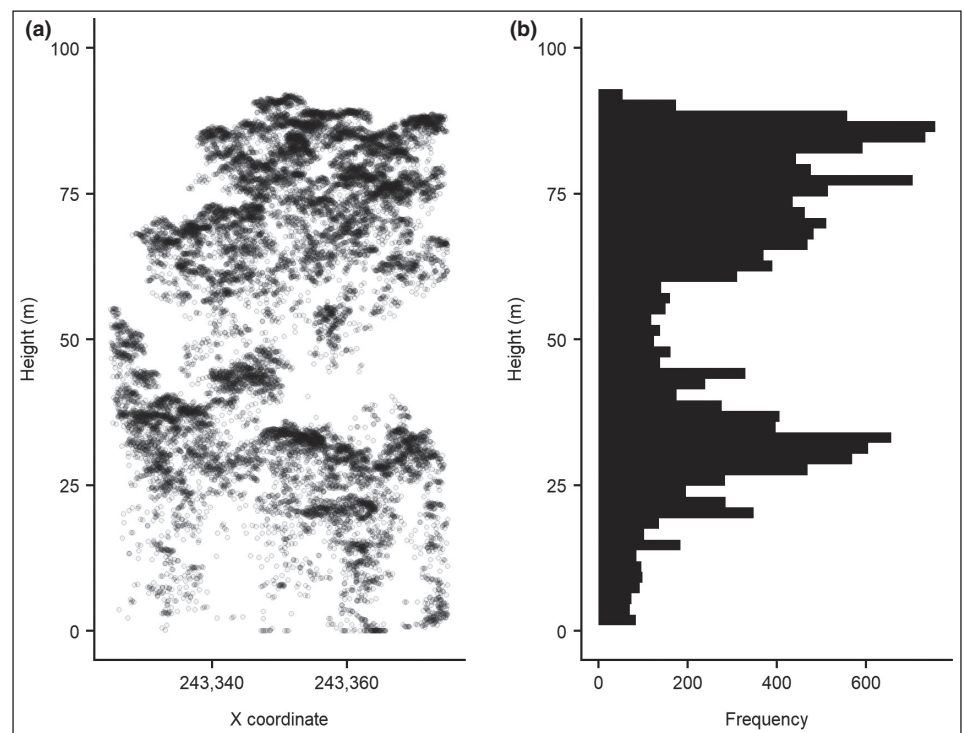


Figure 1. Two representations of the vertical profile of the tallest known tree in the Amazon basin: (a) a two-dimensional LiDAR cloud, where the x axis indicates longitude in meters and the y axis indicates height in meters; and (b) the canopy-height profile, where the x axis indicates the frequency of laser returns and y axis indicates the height classes.

in tropical forests (Larjavaara 2013). The tallest known tree on Earth (a redwood, *Sequoia sempervirens*) measures 115.6 m in height and is located in the wet temperate forests of northern California (Sillett *et al.* 2010). The tallest tropical tree is a yellow meranti (*Shorea faguuetiana*) measuring 100.8 m and is located in the Malaysian state of Sabah (Shenkin *et al.* 2019). Currently, there are no published records of trees of similar heights in the Amazon basin. Available studies indicate the existence of large specimens of the Brazil nut (*Bertholletia excelsa*), sumaúma (*Ceiba pentandra*), piquiá (*Caryocar villosum*), and angelim (*Dinizia excelsa*). The tallest known individuals from these species reach 50 to 60 m (Shultes 1990; Salomão 2009).

Recently, remotely sensed canopy-height maps identified a region with a canopy taller than others in the Amazon between Pará and Amapá states (Tao *et al.* 2016). However, those maps were limited in vertical resolution and so reported the tallest canopies as only a single group, greater than 50 m. Furthermore, the horizontal resolution of satellite-based LiDAR (Light Detection and Ranging) does not allow determination of individual tree heights. Previous studies have demonstrated that small-footprint airborne LiDAR systems – similar to the one used here – can help to accurately estimate individual tree heights of tropical hardwood species in leaf-on conditions (Jucker *et al.* 2017).

Our high-resolution ALS surveys across 222,750 ha provided unprecedented information on the existence of record-breaking tall trees in the Amazon basin. However, the detection of these emergent canopies has implications beyond merely documenting an ecological novelty. Given the sensitivity of trees in the Amazon to droughts, logging, and forest fragmentation, we urge the protection of these globally important forests.

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Cramer MD. 2011. Unravelling the limits to tree height: a major role for water and nutrient trade-offs. *Oecologia* **169**: 61–72.

Feldpausch TR, Lloyd J, Lewis SL, *et al.* 2012. Tree height integrated into pantropical forest biomass estimates. *Biogeosciences* **9**: 3381–403.

Jucker T, Caspersen J, Chave J, *et al.* 2017. Allometric equations for integrating remote sensing imagery into forest monitoring programmes. *Global Change Biol* **23**: 177–90.

Larjavaara M. 2013. The world's tallest trees grow in thermally similar climates. *New Phytol* **202**: 344–49.

Laurance WF, Delamônica P, Laurance SG, *et al.* 2000. Rainforest fragmentation kills big trees. *Nature* **404**: 836.

Lindenmayer DB and Laurance WF. 2016. The unique challenges of conserving large old trees. *Trends Ecol Evol* **31**: 416–18.

Lindenmayer DB, Laurance WF, and Franklin JF. 2012. Global decline in large old trees. *Science* **338**: 1305–06.

Lutz JA, Furniss TJ, Johnson DJ, *et al.* 2018. Global importance of large-diameter trees. *Global Ecol Biogeogr* **27**: 849–64.

Ryan MG, Phillips N, and Bond BJ. 2006. The hydraulic limitation hypothesis revisited. *Plant Cell Environ* **29**: 367–81.

Salomão RP. 2009. Densidade estrutura e distribuição espacial de castanheira-do-brasil (*Bertholletia excelsa* H & B) em dois platôs de floresta ombrófila densa na Amazônia setentrional brasileira. *Boletim do Museu Paraense Emílio Goeldi Ciências Naturais* **4**.

Shenkin A, Chandler C, Boyd D, *et al.* 2019. The world's tallest tropical tree in three dimensions. *Front Forests Glob Changes* **2**; doi.org/10.3389/ffgc.2019.00032.

Shultes RE. 1990. Gifts of the Amazon flora to the world. *Alnoldia* **50**: 21–34.

Sillett SC, Pelt RV, Koch GW, *et al.* 2010. Increasing wood production through old age in tall trees. *Forest Ecol Manage* **259**: 976–94.

Tao S, Guo Q, Li C, *et al.* 2016. Global patterns and determinants of forest canopy height. *Ecology* **97**: 3265–70.

Ter Steege H, Pitman NC, Sabatier D, *et al.* 2013. Hyperdominance in the Amazonian tree flora. *Science* **342**: 1243092.

■ Supporting Information

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