Canopy structure and forest understory conditions in a wet Amazonian forest—No change over the last 20 years

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Abstract
Climate change is altering forest dynamics in the tropics, with large potential impacts on forest structure and understory conditions. However, we found that canopy height distribution and openness remained stable over two decades in the western Amazon, and that gap creation rates would need to increase 300% before affecting equilibrium.

Abstract in Spanish is available with online material

KEYWORDS
Canopy openness, climate change impacts, equilibrium canopy height, forest dynamics, transition matrix model, understory light, Yasuní National Park, Ecuador

1 INTRODUCTION

The dynamics of the Amazon forest are being influenced by climate change, with higher temperatures, extended dry seasons, and rising levels of atmospheric CO₂ as potential key drivers of increased tree turnover (Brienen et al., 2015; McDowell et al., 2018; Vilanova et al., 2018). Such changes in tree turnover are expected to affect forest structure and composition by favoring light-demanding species (Baker et al., 2016; Chambers et al., 2004) and influencing the amount of carbon stored (Brienen et al., 2015; Esquivel-Muelbert et al., 2019; Olivares et al., 2015). In spite of that, long-term data sets on canopy dynamics have only rarely been used to predict how forest structure will develop in the future (e.g., Kellner et al., 2009).

There are several reasons why it is difficult to predict the future of tropical forest dynamics. One is that predictions must be based on representative data, and as tree turnover is influenced by variations in topography and wind velocity on small spatial scales (Fontes et al., 2018; Fortunel et al., 2018; Vilanova et al., 2018), there is a risk that the use of data from a single plot yields biased predictions. Such biases also arise if the increased turnover is too subtle to measure directly, for example, when canopy gaps appear and close again between two censuses. But even small canopy gaps can result in temporarily elevated understory light levels and increased sapling recruitment, which may influence the understory vegetation for some time after gaps close (Brokaw, 1985; Dupuy & Chazdon, 2006). Increased understory plant density may therefore be used as an indicator of change. When canopy dynamics can be measured directly, it can be used to predict the future structure of the canopy using a transition matrix approach (Liang & Picard, 2013; Silvertown & Valverde, 1997), which also allows for analyses of how resilient canopy structure is to increased tree turnover.

In this study, we investigate whether canopy dynamics and understory conditions have changed over the last 20 years across six plots in Amazonian Ecuador, and specifically whether the fraction of the forest with tall canopy, visible canopy gaps, or dense understory has changed. As the region has experienced increased water deficit...
(Esquivel-Muelbert et al., 2019), we expected a decline in the number of areas with tall canopy due to an increase in tree turnover over time. Thus, more areas with visible canopy gaps and dense understory would be expected under these conditions. We investigate how the observed changes in canopy height influence the steady-state height class distribution, and use a perturbation analysis to assess how resilient the forest structure would be to further increases in canopy dynamics and compare our results with observations from other parts of the Amazon.

2 | METHODS

2.1 | Study site

Data were collected in the western part of the Amazon basin in Yasuní National Park in Ecuador (0°40′29″ S, 76°23′51″ W). The area is characterized by low Piedmont hills at 100–300 m above sea level and periodically inundated floodplains along the main river (Olivares et al., 2017). It is crossed by a 25-year-old road that has allowed indigenous people to settle around certain locations, but the study plots were all located in mature stands with no evidence of anthropogenic disturbances.

The climate in Yasuní is perhumid, with a mean annual precipitation of c. 3,000 mm and a mean temperature of c. 28°C (Nabe-Nielsen, 2001). Total monthly rainfall and mean temperature have not changed over the last decade in Yasuní (Olivares et al., 2017). Soil nutrient availability varies considerably in Yasuní, which influences the spatial distribution of both ferns and trees (John et al., 2007; Tuomisto et al., 2002).

2.2 | Data collection

Canopy height, canopy openness, and understory density data were recorded in six 10 × 250 m plots (1.5 ha in total) in 1998 and again in 2019. One of the plots was located in a seasonally inundated floodplain forest, and the five others covered ridge tops, slopes, and bottomland areas. The plots were established over an area of approx. 50 km² following the standard protocol of Balslev et al. (2010), ensuring that distances between plots were in the range of 0.1–12.5 km (Figure S1). Each plot was divided into a 5 × 5 m grid. For each grid square, we measured maximum canopy height and average height to the center of the tree crowns using a clinometer and measuring tape. Heights were assigned to the following classes: 0–5, 5–10, 10–20, and > 20 m. In the center of each square, we recorded canopy openness 1 m above the ground using crown illumination ellipses (CIE; Brown et al., 2000), where values > 1.0 indicated areas with visible gaps in the canopy and elevated light conditions (Figure S2). Following Nabe-Nielsen and Hall (2002), understory vegetation density was classified as either dense, herbaceous, liana-tangle, or sparse. Here “herbaceous” was used for areas covered with herbs (e.g., Marantaceae spp.), but with very few woody plants, and “liana-tangle” was used for areas where the ground was densely covered with lianas, but with only a few tree saplings.

2.3 | Statistical analyses

We used one-way analyses of variance (ANOVA) to test if number of squares per plot with tall canopy (maximum or average height > 20 m), open canopy (CIE > 1.0) or dense understory vegetation changed between the censuses in 1998 and 2019. Dependent variables were transformed $\log_{10}(x + 1)$ to attain normality, and Levene’s test was used to check that variances were homogeneous. All models were analyzed using R 3.6 (R Development Core Team, 2018).

2.4 | Transition matrix modeling

We constructed two different transition matrices $A$ to study the projected effects of changes in canopy dynamics, one for maximum and one for average canopy height (Table S1). The matrices were based on observed probabilities of transitions between height classes for all 600 grid squares between 1998 and 2019. We calculated the projected changes in height class distributions as $n(t + 1) = An(t)$, where the projection interval from $t$ to $t + 1$ was 20 years (Caswell et al., 2004). Here, $n(1)$ was the observed height class distribution in 1998 (Table S1). We used a bootstrap approach to calculate 95% confidence intervals for the projected distributions (Efron & Tibshirani, 1993). Matrix elasticity was calculated as $1/\lambda \cdot A \cdot S$, where the dominant eigenvalue $\lambda = 1$. Sensitivity $S$ was calculated as $V \cdot W^T$, the complex conjugate of the left and right eigenvectors of $A$ (Caswell, 2001). The steady-state equilibrium distribution of canopy height was obtained as the dominant right eigenvector of $A$ (Caswell, 2001).

To assess how increased creation of gaps would influence the asymptotic height class distribution, we used matrix modeling to conduct a perturbation experiment by gradually altering the number of squares with average height 10–20 m that were converted to gaps with 0–5 m tall canopy over a 20-year period. This influenced the probability that squares remained in the 10–20 m class ($[\text{row, col}] = [3,3]$ in the transition matrix, Table S1) and the probability that squares in this height class were converted to gaps ($[\text{entry } 1,3]$). In another experiment, we altered the number of squares with maximum height > 20 m that were converted to 0–5 m tall canopy. We used a bootstrap procedure to calculate the associated confidence intervals.

3 | RESULTS

3.1 | Changes in canopy height and understory conditions

Maximum canopy height was nearly the same in 1998 and 2019 (Figure 1a), and there was no change in the number of grid squares
with maximum height > 20 m ($p = .77, F_{1,10} = 0.089, R^2 = 0.009$). Average canopy height increased slightly from 1998 to 2019, but the trend was not consistent among plots (Figure S3), and the number of squares with average height > 20 m did not change significantly ($p = .11, F_{1,10} = 3.0, R^2 = 0.23$). The number of squares with open canopy (CIE > 1.0) decreased from 47 to 35 (Figure 1c), but the change was not significant ($p = .64, F_{1,10} = 0.23, R^2 = 0.02$). Finally, the number of squares with dense understory did not change significantly either ($p = .96, F_{1,10} = 0.002, R^2 < 0.001$).

### 3.2 Long-term changes in canopy structure

Matrix projections indicated that the canopy height distribution was in steady-state in 2019 (Figure 2), and thus that no change in the canopy height distribution is expected after this point. The most abundant maximum canopy height class is > 20m (432 of 600 grid squares; Table S1), and dynamics are particularly sensitive to changes in the probability that squares remain in this class (i.e., the elasticity for this matrix entry is high; Table S1). The most abundant average canopy height class is 10–20 m (386 of 600 squares), and dynamics of average canopy height is most sensitive to squares remaining in this class. The perturbation experiment revealed the number of squares transitioning from 10–20 m to 0–5 m average height would have to increase from 7 (observed number) to approximately 28 (a 300% increase) before it would significantly affect the steady-state height class distribution, that is, before the predicted steady-state average canopy heights are no longer within the confidence interval based on observed data (Figure 2). Another experiment based on maximum canopy height revealed that the transition from > 20 m to 0–5 m had to increase approximately 250% before affecting the steady-state height class distribution.

### 4 DISCUSSION

The number of areas with tall canopy or open canopy was the same in 1998 and 2019 in Yasuní, so there is no direct evidence that canopy dynamics have changed. Even if canopy gaps close rapidly, a temporary increase in tree turnover at some point between the two censuses would presumably have led to increased light levels and areas with dense understory vegetation due to sapling recruitment (Dupuy & Chazdon, 2006; Montgomery & Chazdon, 2002). However, the number of areas with dense vegetation did not increase either. This suggests that Yasuní has been less affected by global climate change than many other parts of the Amazon forest.

The way future climate change will influence forest structure depends on how rates of regeneration and gap creation are affected. The transition matrix analyses indicated that the
FIGURE 2  Projected (a) maximum and (b) average canopy height based on observed transition probabilities. (c) Change in equilibrium average canopy height when increasing the probability that squares with 10–20 m tall canopy are converted to 0–5 m tall canopy. Error bands show ± 95% bootstrap confidence intervals [Color figure can be viewed at wileyonlinelibrary.com]
canopy structure has already reached steady-state after the mod- 
est changes in forest structure that have occurred until now, which 
mirrors the findings of Kellner et al. (2009) from La Selva, Costa 
Rica, where canopy height at the beginning of the study was close 
to the projected steady-state. Only if areas where the average 
height to the center of the tree crowns were converted to gaps 
approximately 300% more often than today would it have a signif-
icant impact on the steady-state canopy height class distribution. 
Similarly, the conversion of > 20 tall canopy (maximum height) to 
gaps would need to increase by approximately 250% before affect-
ing the height class distribution. This assumes that all other trans-
ition probabilities remain as in the period 1998–2019, which may 
not be the case if fast-growing species become increasingly abun-
dant. In that case the probability of transitions to higher canopy 
classes increases. But our results suggest that the conversion of tall 
canopy to gaps needs to increase substantially before the steady-
state height is altered.

The most likely reason why canopy height and canopy openness 
have not been affected by global climate change is that local precipi-
tation has remained relatively stable in Yasuní (Olivaere et al., 2017), 
and that the observed temperature increase (Figure S4) has not been 
sufficient to influence tree turnover. It is, however, possible that tree 
turnover and canopy openness have been higher at some point be-
tween the two censuses, which could influence forest composition. 
But the lack of changes in canopy height suggests that the impact 
of increasing atmospheric CO₂ (a 13% increase over the study pe-
riod) has been limited (GLOBALVIEW-CO2, 2019). In areas where 
CO₂ fertilization is important, we expect productivity to increase 
(Clark et al., 2013), which would presumably result in increased can-
opy heights. Although such increases may to some extent remain 
undetected when using coarse height intervals, there was no sign 
that tree heights increased in Yasuní.

Most parts of the central Amazon forests have experienced in-
creasing rates of tree turnover (Phillips et al., 2004), and changes 
have been particularly prominent in areas where the dry season has 
become more intense (Clark et al., 2013; Feldpausch et al., 2016; 
Phillips et al., 2009; Vlanova et al., 2018). In many areas, the species 
composition of newly recruited trees is being affected by increased 
turnover and longer dry seasons (Esquivel-Muelbert et al., 2019).

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DATA AVAILABILITY STATEMENT
Data available from the Dryad Digital Repository: https://doi. 
org/10.5061/dryad.612jm641x (Nabe-Nielsen & Valencia, 2020).

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Additional supporting information may be found online in the Supporting Information section.