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Drought cuts back regeneration in logged tropical forests

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3 **1 Drought cuts back regeneration in logged tropical forests**

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16 **8 Keywords**

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19 9 Forest disturbance, forest recovery, community assembly, leaf trait, plant strategy, plant functional
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21 10 types

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24 **11 Abstract**

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27 12 Logged tropical forests represent a major opportunity for preserving biodiversity and sequestering
28
29 13 carbon, playing a large role in meeting global forest restoration targets. Left alone, these ecosystems
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31 14 have been expected to undergo natural regeneration and succession towards old growth forests, but
32
33 15 extreme drought events may challenge this process. While old growth forests possess a certain level of
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35 16 resilience, we lack understanding as to how logging may affect forest responses to drought. This study
36
37 17 examines the drought–logging interaction in seedling dynamics within a landscape of logged and
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39 18 unlogged forests in Sabah Malaysia, based on 73 plots monitored before and after the 2015-16 El Niño
40
41 19 drought. Drought increased seedling mortality in all forests, but the magnitude of this impact was
42
43 20 modulated by logging intensity, with forests with lower canopy leaf area index (LAI) and above ground
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45 21 biomass (AGB) experiencing greater drought induced mortality. Moreover, community traits in more
46
47 22 heavily logged forests shifted towards being more ruderal after drought, suggesting that the trajectory
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3 23 of forest succession had been reversed. These results indicate that with reoccurring strong droughts
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5 24 under a changing climate, logged forests that have had over half of their biomass removed may suffer
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7 25 permanently arrested succession. Targeted management interventions may therefore be necessary to
8
9 26 lift the vulnerable forests above the biomass threshold.
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16 28 **Introduction**

17
18 29 More than half of the world's tropical forests now exist in various disturbed states due to historical or
19
20 30 ongoing human activities, such as logging and shifting agriculture. While old growth tropical forests are
21
22 31 important in conserving species diversity (Gibson *et al.*, 2011) and helping to take CO₂ out of the
23
24 32 atmosphere (Qie *et al.*, 2017), logged tropical forests are increasingly recognized as harbouring great
25
26 33 potential for providing much of the same benefits, especially if they recover from past disturbance and
27
28 34 progress towards older growth states. Regenerating tropical forests have the potential to provide
29
30 35 carbon sinks on par with, or even greater than, intact tropical forests (Rutishauser *et al.*, 2015). The
31
32 36 political and public wills for greater and denser forest cover are also growing ever stronger, driven by
33
34 37 global scale forest restoration goals (Holl, 2017; Pistorius and Freiberg, 2014). The field of tropical forest
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36 38 regeneration and restoration thus has gained tremendous momentum and become a priority research
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38 39 area.
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44 40 Natural regeneration, in which species assembly and ecological processes progress towards pre-
45
46 41 disturbance state through secondary succession, may be the most cost-effective route of forest
47
48 42 regeneration (Chazdon and Guariguata, 2016). The forest succession pathways, however, depend on
49
50 43 land-use history, soil conditions, seed pool and dispersal processes often mediated by animals (Arroyo -
51
52 44 Rodríguez *et al.*, 2015). Selectively logged forests represent better opportunities for regeneration
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54 45 compared to previously clear-cut forests, because of their greater resemblance of old growth forests in
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3 46 structure and species pools (Crouzeilles *et al.*, 2016; Gibson *et al.*, 2011; Lewis *et al.*, 2015). Importantly,
4
5 47 logged forests likely retain a seedling and sapling pool consisting of late succession species potentially
6
7 48 allowing for faster regeneration, which served as the basis for traditional silvicultural management (Van
8
9 49 Gardingen *et al.*, 1998). Indeed low impact logging combined with improved tropical production forest
10
11 50 management may achieve rapid carbon stock recovery (Sasaki *et al.*, 2016) and encourage forest
12
13 51 regeneration (O'Brien *et al.*, 2019). It has also been shown that a range of abiotic and biotic processes
14
15 52 may be sustained in logged forests at levels similar to unlogged forest (Ewers *et al.*, 2015), indicating
16
17 53 substantial ecosystem resilience and potentially facilitating natural regeneration. Biomass carbon
18
19 54 accumulation rate, a strong indicator of forest regeneration, can be two- to five- folds faster in logged
20
21 55 forests, as shown by multiple long-term studies in Borneo (Berry *et al.*, 2010; Sist and Nguyen-Thé,
22
23 56 2002), the Amazon (Rutishauser *et al.*, 2015) and tropical Africa (Gourlet-Fleury *et al.*, 2013), giving hope
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25 57 for the regeneration capacity of logged forests.

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30 58 Forest regeneration is nevertheless a lengthy process that even in the best cases can take multiple
31
32 59 decades (Curran *et al.*, 2014), and climate change effects at this time scale could pose significant
33
34 60 challenges for forests undergoing dynamic transition. Global warming is expected to increase the
35
36 61 frequency of extreme drought events, particularly through intensified El Niño Southern Oscillation cycles
37
38 62 (Wang *et al.*, 2017). El Niño is known to negatively impact forest ecosystem through increasing tree
39
40 63 mortality, suppressing gross primary production, altering phenology and shifting species composition
41
42 64 (Bonal *et al.*, 2016; Corlett, 2016). These effects could be exacerbated in logged forests, especially in the
43
44 65 understorey and at ground level, where lower canopy cover in these forests provides less protection
45
46 66 from water stress compared to closed canopy forests. The 1997-1998 El Niño drought caused high
47
48 67 mortality in logged forests in Borneo and dramatically increased the dominance of pioneer species in
49
50 68 post drought seedling and sapling population (Slik, 2004). However, drought impact on logged forest
51
52 69 dynamics and their regeneration process likely depend on the degree of historical logging intensity.

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3 70 Understanding this drought x logging interaction will allow us to identify potential threshold in the level
4
5 71 of biomass harvest beyond which natural regeneration may become hindered by climate change.
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8 72 We focus on seedlings as they provide us foresight on the trajectory of forest succession (or lack of).
9
10 73 Seedlings represent a bottleneck stage of tree demographic dynamics, subjected to strong
11
12 74 environmental selection pressure and sensitive to microclimatic changes. Both the direction and
13
14 75 magnitude of seedling dynamics in response to drought will serve as indicators of forest resilience. In
15
16 76 addition to analyzing stem level dynamics in terms of mortality and recruitment rates, we assess
17
18 77 community level trait shifts. We used a set of simple and informative trait measures based on the CSR
19
20 78 plant functional attributes (Pierce *et al.*, 2013). Competitors (C) are selected to survive in relatively
21
22 79 stable, productive habitats and invest in continued vegetative growth; stress-tolerators (S) are favoured
23
24 80 in resource-poor environments and are characterized by dense, persistent tissues; ruderalism (R) is a life
25
26 81 strategy of investing a large proportion of resources in propagules to ensure regeneration in repeated
27
28 82 severe environmental disturbances. This method allows effective positioning of a plant in a triangular
29
30 83 CSR trait space representing its strategy trade-off based on three leaf trait measures: leaf dry matter
31
32 84 content (LDMC; as an index of conservatism in life history), specific leaf area (SLA; indicative of
33
34 85 acquisitive economics) and leaf area (LA; photosynthetic organ size) (Pierce *et al.*, 2013). We specifically
35
36 86 assess the succession trajectories of these forests by tracking the community mean R metric. Pioneer
37
38 87 vegetation is expected to exhibit an R-selected strategy, and as forest regeneration progresses the
39
40 88 community mean R value should decrease. We hypothesized that drought increases both seedling
41
42 89 mortality and ruderalism, and that these impacts are stronger in forests with greater historical logging
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44 90 intensity.

91 **Methods**

92 *The SAFE experimental forest landscape*

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2
3 93 This study is part of the long-term ecosystem monitoring at the Stability of Altered Forest Ecosystem
4 (SAFE) Project (4° 38' N to 4° 46' N, 116° 57' to 117° 42' E). The SAFE landscape consists of a broad
5 94 (SAFE) Project (4° 38' N to 4° 46' N, 116° 57' to 117° 42' E). The SAFE landscape consists of a broad
6 94 (SAFE) Project (4° 38' N to 4° 46' N, 116° 57' to 117° 42' E). The SAFE landscape consists of a broad
7 95 gradient of forest disturbance from unlogged tropical lowland forest through to severely logged forest
8 95 gradient of forest disturbance from unlogged tropical lowland forest through to severely logged forest
9 95 gradient of forest disturbance from unlogged tropical lowland forest through to severely logged forest
10 96 and oil palm plantations (Ewers *et al.*, 2011). Forests within the 80,000 ha logged forest landscape
11 96 and oil palm plantations (Ewers *et al.*, 2011). Forests within the 80,000 ha logged forest landscape
12 97 represent a range of historical harvest intensity, from once (lightly) logged, twice logged and salvage
13 97 represent a range of historical harvest intensity, from once (lightly) logged, twice logged and salvage
14 98 logged (prior to conversion to plantation therefore with no harvest restriction). Forests in unlogged
15 98 logged (prior to conversion to plantation therefore with no harvest restriction). Forests in unlogged
16 99 control site are part of the 58,840 ha Maliau Basin Conservation Area. The region has a tropical climate
17 99 control site are part of the 58,840 ha Maliau Basin Conservation Area. The region has a tropical climate
18 100 with rainfall >2000 mm/year and varying terrain topography. Vegetation monitoring is carried out
19 100 with rainfall >2000 mm/year and varying terrain topography. Vegetation monitoring is carried out
20 101 through a network of permanent tree plots measuring 25 x 25 m designed to systematically capture the
21 101 through a network of permanent tree plots measuring 25 x 25 m designed to systematically capture the
22 102 appropriate spatial variation, with varying terrain topography and all below 800 m altitude.
23 102 appropriate spatial variation, with varying terrain topography and all below 800 m altitude.
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25

26 103 *Seedling dynamics monitoring*

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29 104 Seedling monitoring was carried out in 84 selected tree plots in sites ranging from 1028 down to 0.22
30 104 Seedling monitoring was carried out in 84 selected tree plots in sites ranging from 1028 down to 0.22
31 105 Mg ha⁻¹ of AGB, reflecting a gradient from primary through to heavily logged forest (Pfeifer *et al.*, 2016).
32 105 Mg ha⁻¹ of AGB, reflecting a gradient from primary through to heavily logged forest (Pfeifer *et al.*, 2016).
33 106 A seedling plot of 5 x 5 m was established within each of the tree plots in June 2012. Woody seedlings,
34 106 A seedling plot of 5 x 5 m was established within each of the tree plots in June 2012. Woody seedlings,
35 107 including both trees and lianas, with height > 50 cm and diameter at breast height < 1 cm were tagged
36 107 including both trees and lianas, with height > 50 cm and diameter at breast height < 1 cm were tagged
37 108 and mapped. Within a 2 x 2 m subplot in the centre of the seedling plot smaller woody seedlings with
38 108 and mapped. Within a 2 x 2 m subplot in the centre of the seedling plot smaller woody seedlings with
39 109 height > 10 cm were also included in measurement. Species identification was assisted by local botanical
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41 110 experts, with 84.3 % of stems identified to genus level. Three re-measurements of the seedling plots
42 110 experts, with 84.3 % of stems identified to genus level. Three re-measurements of the seedling plots
43 111 were carried out since establishment, with mean dates in December 2012, May 2015 (before drought)
44 111 were carried out since establishment, with mean dates in December 2012, May 2015 (before drought)
45 112 and June 2017 (after drought). In this study we compared seedling dynamics before and after drought
46 112 and June 2017 (after drought). In this study we compared seedling dynamics before and after drought
47 113 using the last two census intervals of similar length, 2.4 and 2.1 years respectively. We excluded 11 plots
48 113 using the last two census intervals of similar length, 2.4 and 2.1 years respectively. We excluded 11 plots
49 114 that were disturbed by logging roads, landslide, or had too few stems (< 3) alive pre-drought, and
50 114 that were disturbed by logging roads, landslide, or had too few stems (< 3) alive pre-drought, and
51 115 therefore based our analysis on 73 seedling plots.
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3 116 We derived seedlings dynamics separately for all woody seedlings and all tree seedlings following
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5 117 Delissio and Primack (2003). Seedling mortality rate r_m and recruitment rate r_r were estimated as:

$$r_m = 1 - \left(\frac{N_s}{N_0}\right)^{\frac{1}{t}} \quad (1)$$

$$r_r = \left(\frac{N_r}{N_0}\right)^{\frac{1}{t}} - 1 \quad (2)$$

15 118 where N_s is the number of seedlings that survived over the census interval, N_r is the number of
16
17 119 recruited seedlings, N_0 is the number of seedlings at the start of the interval and t is interval length
18
19 120 measured in decimal years. During the 2015 and 2017 censuses, we conducted additional rapid counts
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21 121 of newly germinated seedlings < 10 cm in height within the 2 x 2 m subplot, with no tagging, mapping or
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23 122 identification. These were used as proxies for seedling germination rates before and after drought.

24 123 *Leaf trait measurement*

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27 124 Measurement of three leaf traits, leaf area (LA), leaf fresh weight (LFW) and leaf dry weight (LDW), were
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29 125 collected during the 2017 census. For seedlings with more than five leaves on the main stem, we
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31 126 collected the fifth youngest leaf counting from the apical meristem. If the leaf was damaged (e.g. by
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33 127 herbivory), we took the nearest alternative. We stored leaves in sealed plastic bags for LFW
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35 128 measurement within 24 hours. Fresh leaves were photographed during the same period with a white
36
37 129 background and a calibration scale. Leaves were then oven dried at 80°C till constant weight and
38
39 130 measured for LDW. Both LFW and LDW were measured to 1 mg. Leaf area was measured using the
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41 131 ImageJ software (Schneider *et al.*, 2012).

42
43 132 Seedling CSR values were calculated at stem level using LA (mm²), LFW (mg) and LDW (mg) using the CSR
44
45 133 calculator tool, 'StrateFy', produced by Piece *et al.* (2017), available online in Microsoft Excel format in
46
47 134 the paper's Supporting Information. The StrateFy tool converts LA, LFW and LDW to three standard leaf
48
49 135 traits, LA, leaf dry matter content (LDMC) and specific leaf area (SLA), then derives the CSR values using
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3 136 automatic formulae. For stems with no leaf collected, including those which died before the 2017
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5 137 census, we applied mean CSR values at genus level where possible. We then derived community mean
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7 138 CSR value for each plot, each census. One plot had no available CSR data for at least one census and was
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9
10 139 excluded from the trait analysis.

11 12 13 140 *Data analysis*

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15
16 141 We tested the difference in seedling mortality and recruitment rates before and after drought using
17
18 142 Wilcoxon signed-rank test. Change in mortality rate from pre-drought period was termed “drought
19
20 143 mortality”. When there was significant drought induced change, we tested how different forest habitat
21
22 144 variables influenced the magnitude of the drought impact using a linear mixed effects (LME) modeling
23
24 145 framework and multi-model inference with information theoretic approaches. We first constructed a
25
26 146 global model which included as predictors two measures of forest structural conditions likely to have
27
28 147 causal effects on seedling dynamics: 1) aboveground live tree biomass (AGB) which reflects the historical
29
30 148 logging intensity and overall forest quality, and 2) canopy leaf area index (LAI), i.e., total leaf surface
31
32 149 area projected on the local horizontal datum, which relates closely to microclimatic conditions,
33
34 150 especially daily maximum temperature and daily minimum humidity (Hardwick *et al.*, 2015). Both were
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36 151 measured at the vegetation plot level across the SAFE landscape, with AGB showing greater
37
38 152 heterogeneity within unlogged forests compared to the canopy measure (Pfeifer *et al.*, 2016). As the
39
40 153 latter resulted in a strong positively skewed distribution of the variable we applied log₁₀-transformation
41
42 154 on AGB values. Additional predictors consisted of plot mean slope and pre-drought mortality, and for
43
44 155 the latter, including both its linear and squared terms. Pre-drought mortality rate was included because
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46 156 initial data exploration revealed a negative, non-linear dependence of post-drought mortality change on
47
48 157 pre-drought mortality. This was likely related to the highly dynamic nature of disturbed forests and the
49
50 158 fundamental central limit theorem: if the initial observed value for a plot represented a large departure
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52 159 from the mean, subsequent observations were therefore more likely to move towards the mean than
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3 160 further away from it. Because mortality rate is bounded at zero, extreme pre-drought mortality values
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5 161 had strong effects, hence the non-linear pattern. We included forest block (8 blocks in total) as a
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7 162 random effect to account for the spatially nested variance structure. We generated all nested models of
8
9 163 the maximum model described above using the *dredge* function in the R package MuMIn, then
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11 164 evaluated the subset of models that meet the principle of marginality, i.e., the squared term of pre-
12
13 165 drought mortality is allowed only if its linear term is present. We then based our inference on the top
14
15 166 model set with $\Delta AIC < 2$ (Grueber *et al.*, 2011). All analyses were conducted in the R statistical computing
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17 167 environment (R Core Team, 2016).

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21 168 Community mean CSR values, as well as changes in these during pre-drought period 2012-2015 and
22
23 169 drought period 2015-2017, were tested against forest AGB (log₁₀-transformed) and LAI using linear
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25 170 models. We employed a ternary plot to visualize the positioning of community mean trait in the
26
27 171 triangular CSR trait space for all plots and the overall trajectory of trait shifts.

31 172 **Results**

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33
34 173 Across the study landscape woody seedling mortality rate over the drought interval during 2015-2017
35
36 174 was 26.0 % yr⁻¹ (bootstrapped confidence interval 23.2-29.3), on average 10.3 % yr⁻¹ higher compared to
37
38 175 the pre-drought interval 2012-2015 (15.7 % yr⁻¹, CI 13.7-18.1, $p < 0.001$). For tree seedlings (excluding
39
40 176 liana), mortality rate increased from the pre-drought level of 15.3 % yr⁻¹ (CI 13.1-18.2) to 23.8 % yr⁻¹ (CI
41
42 177 20.7-27.1) after drought. For drought mortality of all woody seedlings, the top model set with $\Delta AIC < 2$
43
44 178 consisted of four models (Supplementary Table S1) which did not include the variable LAI, and the effect
45
46 179 of plot mean AGB was relatively weak with low variable importance value (Table 1). For drought
47
48 180 mortality of tree seedlings, the top model set consisted of three models (Supplementary Table S2) and
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50 181 all variables except for slope had high variable importance values (Table 2). The best model contained
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182 LAI, pre-drought mortality and AGB, all with negative effects on the drought mortality of tree seedlings
183 (Figure 1).

184 Woody seedling recruitment rate was not significantly higher over the drought interval (11.1 % yr⁻¹, CI
185 8.1-15.8) compared to pre-drought interval (8.3 % yr⁻¹, CI 6.8-10.8). Increase in tree seedling recruitment
186 was similarly non-significant, from pre-drought 10.2 % yr⁻¹ (CI 7.7-15.1) to 10.7 % yr⁻¹ (CI 7.8-13.9) over
187 the drought interval. On the other hand, rate of new germinations significantly increased after drought
188 (before drought 16.1 % yr⁻¹, CI 12.5-21.2; after drought 36.2 % yr⁻¹, CI 28.6-48.8).

189 During the non-drought interval between 2012 and 2015, across the study landscape seedling
190 community mean CSR values did not show significant changes. Variations in CSR values between plots
191 were not correlated with forest AGB or LAI. Over the drought interval between 2015 and 2017, however,
192 mean seeding community ruderalism (R value) across the landscape significantly increased ($p = 0.001$, t-
193 test, $df = 71$; Figure 2). This can be attributed to the fact that seedlings recruited over the drought
194 interval had significantly higher ruderalism values (mean 17.3, CI 15.7-19.0) compared to those that died
195 over the same period (mean 14.4, CI 13.9-15.0). Furthermore, ruderalism of recruited seedlings was
196 higher in forests with lower AGB, though not significantly so ($F_{1,53} = 3.75$, $p = 0.058$). Consequently, the
197 observed change in community ruderalism showed a significant dependency on forest AGB, with lower
198 AGB forests experiencing a greater shift towards ruderal species composition ($F_{1,70} = 17.28$, $p < 0.001$;
199 Figure 3). In 2012 and 2015, community ruderalism was not significantly correlated with forest AGB, but
200 this association became significant after drought in 2017 (Supplementary Figure S1). Our regression
201 model predicts, however, that in forests with AGB > 219 Mg ha⁻¹ (Figure 3; CI 137-644), woody seedling
202 communities are more likely to shift towards less ruderal species.

203 Discussion

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2
3 204 Understanding the response of woody seedling communities in tropical forests to climatic events can
4
5 205 provide us important insights on the climate resilience of these ecosystems (Whitmore, 1998). Studies
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7 206 monitoring seedlings over climate disturbances in their natural environment remain uncommon in
8
9
10 207 Southeast Asia, with many focusing on selected species, such as the dipterocarp trees (Bebber *et al.*,
11
12 208 2004; Delissio and Primack, 2003). Our study documented the dynamics of whole woody seedling
13
14 209 communities across a logging intensity gradient, before and after the strong 2015-16 El Niño drought.
15
16 210 We quantified functional changes at community level using the novel CSR leaf trait measure, providing a
17
18 211 new way to track the forest regeneration process and its sensitivity to supra-annual droughts.

21 212 *Drought cuts back natural regeneration in the most heavily logged forests*

23
24 213 The natural regeneration process of tropical forests critically depends on the seedling pool in the
25
26 214 understory. Seedlings of canopy tree species in Borneo's lowland rainforest typically need to survive a
27
28 215 long period of time, sometimes over ten years, to eventually emerge from the understory (Delissio *et*
29
30 216 *al.*, 2002). We show here that drought resulted in substantially higher mortality in all woody seedlings
31
32 217 than the pre-drought period across a logged forest landscape. The drought mortality of tree seedlings, in
33
34 218 particular, varied according to logging intensity. Forests with more canopy foliage (measured by canopy
35
36 219 leaf area index) and less historical logging (greater above ground biomass) experienced lower drought
37
38 220 mortality. Our model predicts that, other things being equal, increasing the forest canopy leaf area index
39
40 221 from 2 (representing the most heavily logged forests in the study landscape) to 4 (median value in the
41
42 222 study landscape) will reduce the drought mortality of tree seedlings from 20 % to 8 %. Similarly,
43
44 223 increasing plot AGB from severely logged state with 1 Mg ha⁻¹ to median level of forest AGB of 78 Mg ha⁻¹
45
46 224 ¹ is expected to reduce the drought mortality of tree seedlings from 17 % to 8 %. These results lend
47
48 225 further support to improved tropical production forest management recommendations (Sasaki *et al.*,
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50 226 2016), with reduced biomass impact harvesting being the key to achieving not only faster biomass
51
52 227 recovery, but also increased drought resilience of logged forests.

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3 228 When non-tree woody seedlings were considered, drought mortality was less sensitive to logging
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5 229 intensity (Table 1) compared to tree seedlings only (Table 2). This suggests the compounding impact of
6
7 230 logging and drought may provide a relative advantage for the regeneration of lianas over trees. Indeed
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9
10 231 liana cutting has been used as a management practice to encourage tree seedling regeneration in logged
11
12 232 tropical forests, but new evidence suggested that the benefits of lianas cutting were reduced during the
13
14 233 2015-16 El Niño drought (O'Brien *et al.*, 2019).

16
17 234 We found a negative effect of pre-drought mortality on drought mortality, and this was primarily driven
18
19 235 by the extreme high pre-drought mortality values in a few plots in logged forests (Figure 1b). This
20
21 236 reflects the temporally and spatially dynamic nature of disturbed forest – at any time there may be
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23 237 individual locations experiencing extreme mortality events, but the mortality rates over the subsequent
24
25 238 period are more likely to return closer to the mean level. Our results also suggest that drought mortality
26
27 239 may increase on steeper terrain. This may be an indirectly effect as steeper terrain can affect soil and
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29 240 microclimate conditions (Arroyo - Rodríguez *et al.*, 2015), and fallen trees and branches during drought
30
31 241 can lead to greater disturbance in the forest understorey in steep areas.

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35
36 242 More importantly, species turnover driven by the drought resulted in a clear shift in the seedling
37
38 243 functional traits. During the non-drought period, seedling community composition represented in the
39
40 244 competitor/stress-tolerator/ruderal (CSR) trait space were relatively stable across the landscape, but
41
42 245 after drought there was a collective movement up the ruderal dimension. This change, albeit relatively
43
44 246 small (Figure 2), was driven by the most heavily logged forests (Figure 3b), suggesting that seedling
45
46 247 communities in these forests were more sensitive to the drought stressor. The drought itself has,
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48 248 therefore, acted as a climate filter favouring species with a more ruderal life strategy, typically pioneer
49
50 249 species (Pierce *et al.*, 2017). On the other hand, community level seedling traits were more stable in less
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52 250 intensely logged and old growth forests with AGB above 219 Mg ha⁻¹, where predicted trait shift in
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3 251 response to drought was close to zero (Figure 3b). This equates to logging having removed
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5 252 approximately 51 % of tree biomass (mean AGB = 449 Mg ha⁻¹ in unlogged forests). These results point
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7 253 to the alarming consequence of overharvesting compounded by climate change, that at least for the
8
9 254 short term, severe drought can reverse the successional trajectory of these heavily logged forests.

12 255 *Microclimate and recruitment pool*

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14
15 256 Microclimatic conditions such as light, temperature and moisture in the tropical forest understorey may
16
17 257 affect seedling establishment, survival and competition (Baraloto and Goldberg, 2004). Across our study
18
19 258 landscape, changes in microclimate due to forest disturbance were closely correlated with canopy leaf
20
21 259 area index (Hardwick *et al.*, 2015). Our results showed that drought induced seedling mortality was
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23 260 modulated by microclimatic conditions. On the other hand, drought induced seedling community trait
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25 261 shift was strongly associated with forest AGB, that is, historical logging intensity, but not with
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27 262 microclimatic conditions. This suggests that the maturity of the surrounding forests, in terms of number
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29 263 of big trees and presumably, the intactness of forest structure and composition, plays a central role in
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31 264 maintaining the trait stability of seedling communities.

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34 265 Drought conditions may present recruitment opportunities for pioneer species. It is likely that pioneer
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36 266 seed and seedling pools were more available in logged forests, and indeed post-drought seedling
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38 267 recruits were more strongly ruderal in these forests. This drought selection effect may be exacerbated
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40 268 by the fact that seed production of pioneer species is better sustained during El Niño drought than late
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42 269 succession species (O'Brien *et al.*, 2018), possibly creating a positive feedback that could further push
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44 270 these logged forests towards a reversal of the succession trajectory.

45 271 *Lifting logged forests out of arrested succession*

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47 272 It has long been recognized that forest management needs to plan for the interactive effect of
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49 273 anthropogenic disturbance and climate change, and efforts need to focus on the forest regeneration

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3 274 stage (Whitmore, 1998). Our results show that tropical seedling communities are sensitive to drought,
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5 275 rapidly responding with elevated mortality and a functional shift towards more pioneer-like
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7 276 composition. Given that natural regeneration of tropical forest requires decades even in the best cases,
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10 277 and strong El Niño drought is becoming more frequent with a return period of less than a decade (Wang
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12 278 *et al.*, 2017), it is a real concern that these drought-susceptible logged forests will remain in arrested
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14 279 succession or face further degradation. We also find, however, that seedling communities were more
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16 280 resilient to drought where surrounding forests have above ground biomass $>219 \text{ Mg ha}^{-1}$. This biomass
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18 281 density is around half that of intact forests in our study landscape and in this region (Avitabile *et al.*,
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20 282 2015), and not substantially higher than the average of $134.2 \pm 6.1 \text{ Mg ha}^{-1}$ estimated in severely
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22 283 degraded forests in Borneo (António *et al.*, 2018). Therefore efforts should be invested in active forest
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24 284 restoration aiming at lifting the biomass of the vulnerable forests above this threshold, at which point
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26 285 their succession trajectories should become self-sustaining and resilient to future drought events. Our
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28 286 knowledge is accumulating on how forest regeneration may be assisted (Chazdon and Guariguata, 2016)
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30 287 and practices such as enrichment planting and pioneer removal have shown some initial success in this
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32 288 region (Swinfield *et al.*, 2016).

37 289 **Conclusion**

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40 290 Our study show that tropical forest seedling communities are sensitive to drought. The 2015-16 strong
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42 291 El Niño drought not only increased seedling mortality rate but also resulted in a shift in community
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44 292 functional traits towards more ruderal, pioneer-like composition. The drought impact, however,
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46 293 interacted with logging intensity, and was buffered in areas with higher canopy leaf index and forest
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48 294 above ground biomass. We suggest that in order to increase the drought resilience of the most
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50 295 disturbed forests in a changing climate, active regeneration management should be considered in order
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52 296 to lift these forests out of arrested succession.
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Table 1. Model averaged estimates of effects of pre-drought mortality (mort), plot above-ground biomass (AGB, log10-transformed) and plot mean slope on the 2015-16 El Niño drought mortality of all woody seedlings. Estimates were based on the top model set with $\Delta AIC < 2$. The relative importance of a variable was calculated by summing the AIC weights across all the models in the set where the variable occurred.

Parameter	Estimate	SE	CI lower	CI upper	Relative importance
(Intercept)	6.90	9.22	-11.17	24.97	
mort	0.78	0.52	-0.23	1.80	1.00
mort ²	-0.03	0.01	-0.06	-0.01	1.00
slope	0.38	0.22	-0.05	0.81	0.57
log(AGB)	-3.13	2.60	-8.24	1.97	0.38

Table 2. Model averaged estimates of effects of canopy leaf area index (LAI), pre-drought mortality (mort), plot above-ground biomass (AGB, log10-transformed) and plot mean slope on the 2015-16 El Niño drought mortality of tree seedlings. Estimates were based on the top model set with $\Delta AIC < 2$. The relative importance of a variable was calculated by summing the AIC weights across all the models in the set where the variable occurred.

Parameter	Estimate	SE	CI lower	CI upper	Relative importance
(Intercept)	47.45	11.60	24.71	70.19	
LAI	-5.97	2.58	-11.02	-0.92	1.00
mort	-0.64	0.13	-0.90	-0.38	1.00
log(AGB)	-4.52	2.46	-9.35	0.31	0.68
slope	0.16	0.21	-0.25	0.58	0.19

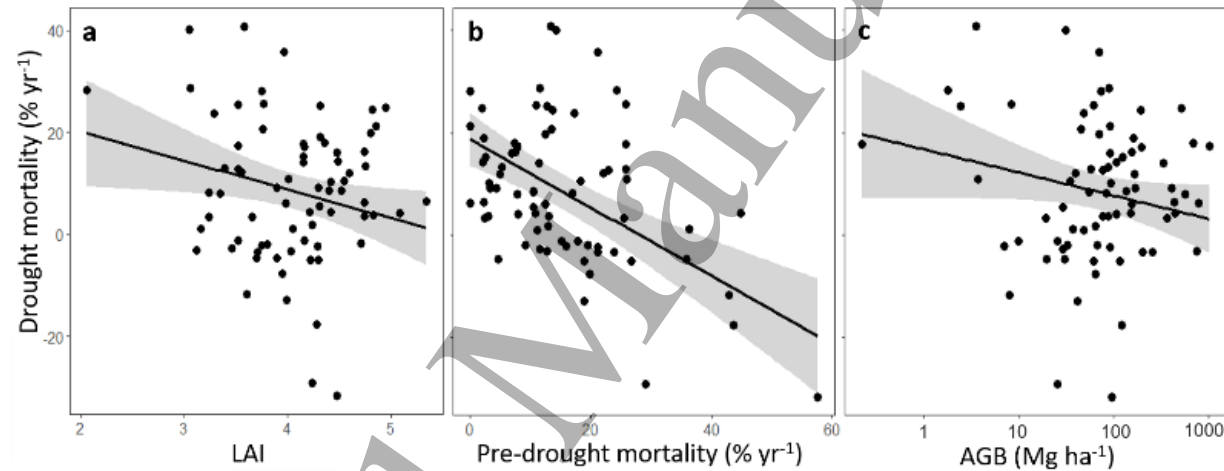


Figure 1. Effects of (a) canopy leaf area index (LAI), (b) pre-drought mortality and (c) plot above-ground biomass (AGB) on drought mortality (change in mortality rate from pre-drought period) of tree seedlings after the 2015-16 El Niño. Solid lines are effects estimated based on the highest-ranked linear mixed effects (LME) model where the focal predictor variable occurs within the top model set (Supplementary Table S2), while holding the other predictor variables in the model constant (mean-centred). Shading areas represent confidence intervals (CIs). Observed data points are shown as solid dots.

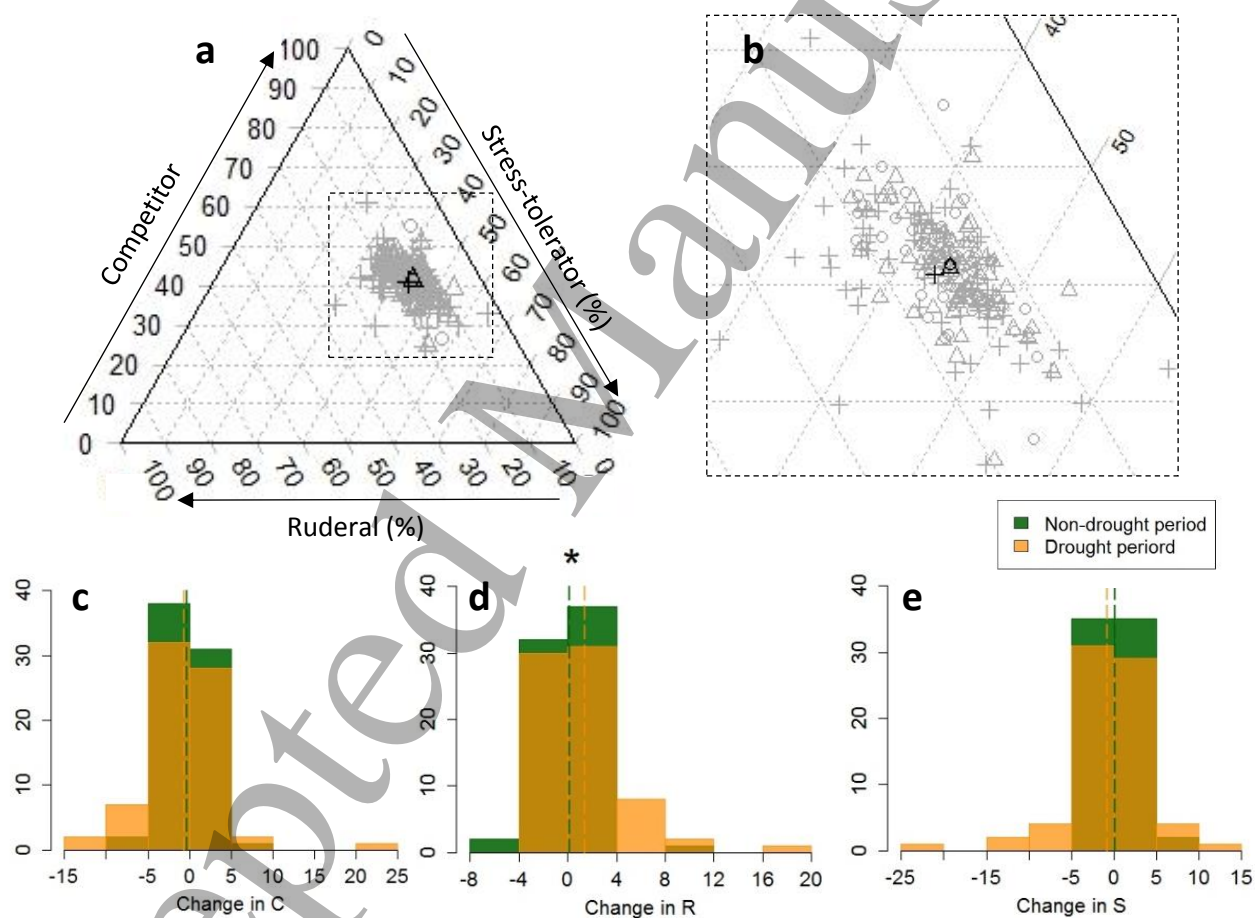


Figure 2. Changes in seedling community traits during non-drought vs drought periods. Ternary plot (a) shows the relative proportions (%) of competitor (C), stress-tolerator (S) and ruderal (R) trait values of woody seedlings. Grey symbols are plot level mean CSR values (circles: 2012 census; triangles: 2015 census; crosses: 2017 census); black symbols are mean CSR values across the study landscape. Inset plot (b) zooms in to the area of interest. Histograms show the distribution of plot-level changes in C (c), R (d) and S (e) respectively, over the 2012-2015 non-drought

period (green bars; green dash lines are mean changes across the study landscape) and 2015-2017 drought period (orange bars; orange dash lines are mean changes across the study landscape). Asterisk indicates significant difference between the two periods ($p = 0.001$, t-test, $df = 71$).

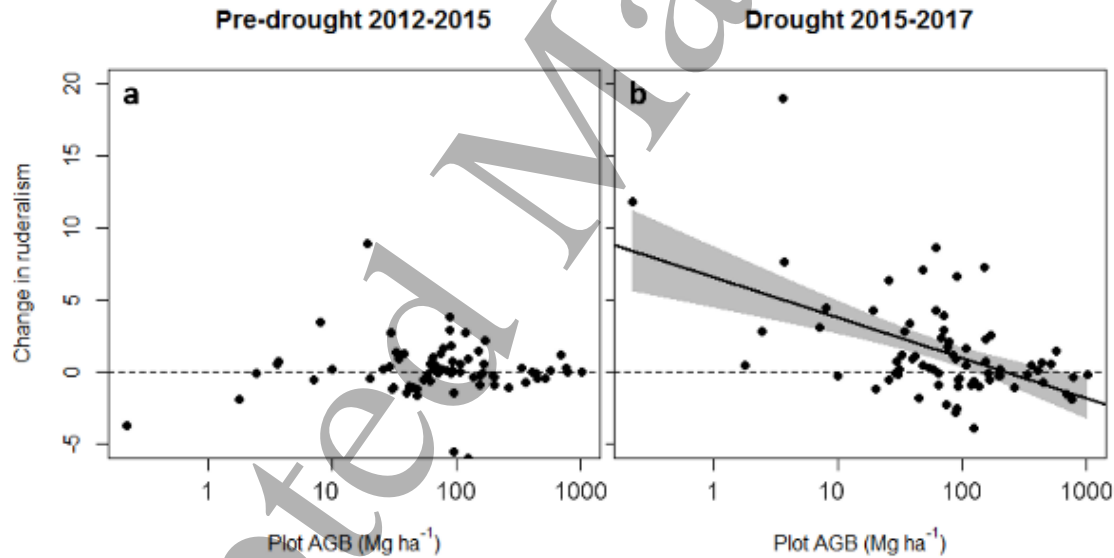


Figure 3. Observed changes in community ruderalism (R trait value) at seedling plot level in relation to plot AGB during the pre-drought census interval 2012-2015 (a) and over the drought census interval 2015-2017 (b). Solid line show effect estimated based on a linear regression model ($F_{1,70} = 17.28$, $p < 0.001$). Shading areas represent the confidence intervals (CI).