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Lan Qie^{1,2,8} , Elizabeth M Telford^{1,6}, Mike R Massam^{1,7} , Hamzah Tangki³, Reuben Nilus⁴, Andy Hector⁵ and Robert M Ewers¹

¹ Department of Life Sciences, Silwood Park Campus, Imperial College London, Ascot, SL5 7PY, United Kingdom

² School of Life Sciences, University of Lincoln, Lincoln, LN6 7TS, United Kingdom

³ Conservation & Environmental Management Division, Yayasan Sabah, 88817 Kota Kinabalu, Sabah, Malaysia

⁴ Sabah Forestry Department Forest Research Centre, 90175 Sandakan, Sabah, Malaysia

⁵ Department of Plant Sciences, University of Oxford, Oxford, OX1 3RB, United Kingdom

⁶ Current address: School of GeoSciences, University of Edinburgh, Edinburgh EH9 8XP, United Kingdom.

⁷ Current address: Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, United Kingdom.

⁸ Author to whom any correspondence should be addressed.

E-mail: qie.lan@gmail.com

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Supplementary material for this article is available [online](#)

Abstract

Logged tropical forests represent a major opportunity for preserving biodiversity and sequestering carbon, playing a large role in meeting global forest restoration targets. Left alone, these ecosystems have been expected to undergo natural regeneration and succession towards old growth forests, but extreme drought events may challenge this process. While old growth forests possess a certain level of resilience, we lack understanding as to how logging may affect forest responses to drought. This study examines the drought–logging interaction in seedling dynamics within a landscape of logged and unlogged forests in Sabah Malaysia, based on 73 plots monitored before and after the 2015–16 El Niño drought. Drought increased seedling mortality in all forests, but the magnitude of this impact was modulated by logging intensity, with forests with lower canopy leaf area index and above-ground biomass experiencing greater drought induced mortality. Moreover, community traits in more heavily logged forests shifted towards being more ruderal after drought, suggesting that the trajectory of forest succession had been reversed. These results indicate that with reoccurring strong droughts under a changing climate, logged forests that have had over half of their biomass removed may suffer permanently arrested succession. Targeted management interventions may therefore be necessary to lift the vulnerable forests above the biomass threshold.

Introduction

More than half of the world's tropical forests now exist in various disturbed states due to historical or ongoing human activities, such as logging and shifting agriculture. While old growth tropical forests are important in conserving species diversity (Gibson *et al* 2011) and helping to take CO₂ out of the atmosphere (Qie *et al* 2017), logged tropical forests are increasingly recognized as harbouring great potential for providing much of the same benefits, especially if they recover from past disturbance and progress towards older growth states. Regenerating tropical forests have the potential to provide carbon sinks on par with, or even greater than,

intact tropical forests (Rutishauser *et al* 2015). The political and public wills for greater and denser forest cover are also growing ever stronger, driven by global scale forest restoration goals (Pistorius and Freiberg 2014, Holl 2017). The field of tropical forest regeneration and restoration thus has gained tremendous momentum and become a priority research area.

Natural regeneration, in which species assembly and ecological processes progress towards pre-disturbance state through secondary succession, may be the most cost-effective route of forest regeneration (Chazdon and Guariguata 2016). The forest succession pathways, however, depend on land-use history, soil conditions, seed pool and dispersal processes often

mediated by animals (Arroyo-Rodríguez *et al* 2015). Selectively logged forests represent better opportunities for regeneration compared to previously clear-cut forests, because of their greater resemblance of old growth forests in structure and species pools (Gibson *et al* 2011, Lewis *et al* 2015, Crouzeilles *et al* 2016). Importantly, logged forests likely retain a seedling and sapling pool consisting of late succession species potentially allowing for faster regeneration, which served as the basis for traditional silvicultural management (Van Gardingen *et al* 1998). Indeed low impact logging combined with improved tropical production forest management may achieve rapid carbon stock recovery (Sasaki *et al* 2016) and encourage forest regeneration (O'Brien *et al* 2019). It has also been shown that a range of abiotic and biotic processes may be sustained in logged forests at levels similar to unlogged forest (Ewers *et al* 2015), indicating substantial ecosystem resilience and potentially facilitating natural regeneration. Biomass carbon accumulation rate, a strong indicator of forest regeneration, can be two-to five- folds faster in logged forests, as shown by multiple long-term studies in Borneo (Sist and Nguyen-Thé, 2002, Berry *et al* 2010), the Amazon (Rutishauser *et al* 2015) and tropical Africa (Gourlet-Fleury *et al* 2013), giving hope for the regeneration capacity of logged forests.

Forest regeneration is nevertheless a lengthy process that even in the best cases can take multiple decades (Curran *et al* 2014), and climate change effects at this time scale could pose significant challenges for forests undergoing dynamic transition. Global warming is expected to increase the frequency of extreme drought events, particularly through intensified El Niño Southern Oscillation cycles (Wang *et al* 2017). El Niño is known to negatively impact forest ecosystem through increasing tree mortality, suppressing gross primary production, altering phenology and shifting species composition (Bonaf *et al* 2016, Corlett 2016). These effects could be exacerbated in logged forests, especially in the understorey and at ground level, where lower canopy cover in these forests provides less protection from water stress compared to closed canopy forests. The 1997–1998 El Niño drought caused high mortality in logged forests in Borneo and dramatically increased the dominance of pioneer species in post drought seedling and sapling population (Slik 2004). However, drought impact on logged forest dynamics and their regeneration process likely depend on the degree of historical logging intensity. Understanding this drought x logging interaction will allow us to identify potential threshold in the level of biomass harvest beyond which natural regeneration may become hindered by climate change.

We focus on seedlings as they provide us foresight on the trajectory of forest succession (or lack of). Seedlings represent a bottleneck stage of tree demographic dynamics, subjected to strong environmental selection pressure and sensitive to microclimatic changes. Both

the direction and magnitude of seedling dynamics in response to drought will serve as indicators of forest resilience. In addition to analysing stem level dynamics in terms of mortality and recruitment rates, we assess community level trait shifts. We used a set of simple and informative trait measures based on the CSR plant functional attributes (Pierce *et al* 2013). Competitors (C) are selected to survive in relatively stable, productive habitats and invest in continued vegetative growth; stress-tolerators (S) are favoured in resource-poor environments and are characterized by dense, persistent tissues; ruderalism (R) is a life strategy of investing a large proportion of resources in propagules to ensure regeneration in repeated severe environmental disturbances. This method allows effective positioning of a plant in a triangular CSR trait space representing its strategy trade-off based on three leaf trait measures: leaf dry matter content (LDMC; as an index of conservatism in life history), specific leaf area (SLA; indicative of acquisitive economics) and leaf area (LA; photosynthetic organ size) (Pierce *et al* 2013). We specifically assess the succession trajectories of these forests by tracking the community mean *R* metric. Pioneer vegetation is expected to exhibit an *R*-selected strategy, and as forest regeneration progresses the community mean *R* value should decrease. We hypothesized that drought increases both seedling mortality and ruderalism, and that these impacts are stronger in forests with greater historical logging intensity.

Methods

The Stability of Altered Forest Ecosystem (SAFE) experimental forest landscape

This study is part of the long-term ecosystem monitoring at the SAFE Project (4° 38' N to 4° 46' N, 116° 57' to 117° 42' E). The SAFE landscape consists of a broad gradient of forest disturbance from unlogged tropical lowland forest through to severely logged forest and oil palm plantations (Ewers *et al* 2011). Forests within the 80 000 ha logged forest landscape represent a range of historical harvest intensity, from once (lightly) logged, twice logged and salvage logged (prior to conversion to plantation therefore with no harvest restriction). Forests in unlogged control site are part of the 58 840 ha Maliau Basin Conservation Area. The region has a tropical climate with rainfall >2000 mm/year and varying terrain topography. Vegetation monitoring is carried out through a network of permanent tree plots measuring 25 × 25 m designed to systematically capture the appropriate spatial variation, with varying terrain topography and all below 800 m altitude.

Seedling dynamics monitoring

Seedling monitoring was carried out in 84 selected tree plots in sites ranging from 1028 down to 0.22 Mg ha⁻¹ of AGB, reflecting a gradient from primary through to heavily logged forest (Pfeifer *et al* 2016). A seedling plot

of 5×5 m was established within each of the tree plots in June 2012. Woody seedlings, including both trees and lianas, with height >50 cm and diameter at breast height <1 cm were tagged and mapped. Within a 2×2 m subplot in the centre of the seedling plot smaller woody seedlings with height >10 cm were also included in measurement. Species identification was assisted by local botanical experts, with 84.3% of stems identified to genus level. Three re-measurements of the seedling plots were carried out since establishment, with mean dates in December 2012, May 2015 (before drought) and June 2017 (after drought). In this study we compared seedling dynamics before and after drought using the last two census intervals of similar length, 2.4 and 2.1 years respectively. We excluded 11 plots that were disturbed by logging roads, landslide, or had too few stems (<3) alive pre-drought, and therefore based our analysis on 73 seedling plots.

We derived seedlings dynamics separately for all woody seedlings and all tree seedlings following Delisio and Primack (2003). Seedling mortality rate r_m and recruitment rate r_r were estimated as:

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

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

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

Leaf trait measurement

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

Seedling CSR values were calculated at stem level using LA (mm^2), LFW (mg) and LDW (mg) using the CSR calculator tool, 'StrateFy', produced by Pierce *et al* (2017), available online in Microsoft Excel format in the paper's Supporting Information. The StrateFy

tool converts LA, LFW and LDW to three standard leaf traits, LA, LDMC and SLA, then derives the CSR values using automatic formulae. For stems with no leaf collected, including those which died before the 2017 census, we applied mean CSR values at genus level where possible. We then derived community mean CSR value for each plot, each census. One plot had no available CSR data for at least one census and was excluded from the trait analysis.

Data analysis

We tested the difference in seedling mortality and recruitment rates before and after drought using Wilcoxon signed-rank test. Change in mortality rate from pre-drought period was termed 'drought mortality'. When there was significant drought induced change, we tested how different forest habitat variables influenced the magnitude of the drought impact using a linear mixed effects (LME) modeling framework and multi-model inference with information theoretic approaches. We first constructed a global model which included as predictors two measures of forest structural conditions likely to have causal effects on seedling dynamics: (1) aboveground live tree biomass (AGB) which reflects the historical logging intensity and overall forest quality, and (2) canopy leaf area index (LAI), i.e. total leaf surface area projected on the local horizontal datum, which relates closely to microclimatic conditions, especially daily maximum temperature and daily minimum humidity (Hardwick *et al* 2015). Both were measured at the vegetation plot level across the SAFE landscape, with AGB showing greater heterogeneity within unlogged forests compared to the canopy measure (Pfeifer *et al* 2016). As the latter resulted in a strong positively skewed distribution of the variable we applied log10-transformation on AGB values. Additional predictors consisted of plot mean slope and pre-drought mortality, and for the latter, including both its linear and squared terms. Pre-drought mortality rate was included because initial data exploration revealed a negative, nonlinear dependence of post-drought mortality change on pre-drought mortality. This was likely related to the highly dynamic nature of disturbed forests and the fundamental central limit theorem: if the initial observed value for a plot represented a large departure from the mean, subsequent observations were therefore more likely to move towards the mean than further away from it. Because mortality rate is bounded at zero, extreme large pre-drought mortality values had stronger effects, hence the nonlinear pattern. We included forest block (eight blocks in total) as a random effect to account for the spatially nested variance structure. We generated all nested models of the maximum model described above using the *dredge* function in the *R* package MuMIn, then evaluated the subset of models that meet the principle of marginality, i.e. the squared term of pre-drought mortality is allowed only if its

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 $\Delta\text{AIC} < 2$. 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 $\Delta\text{AIC} < 2$. 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

linear term is present. We then based our inference on the top model set with $\Delta\text{AIC} < 2$ (Grueber *et al* 2011). All analyses were conducted in the *R* statistical computing environment (R Core Team 2016).

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

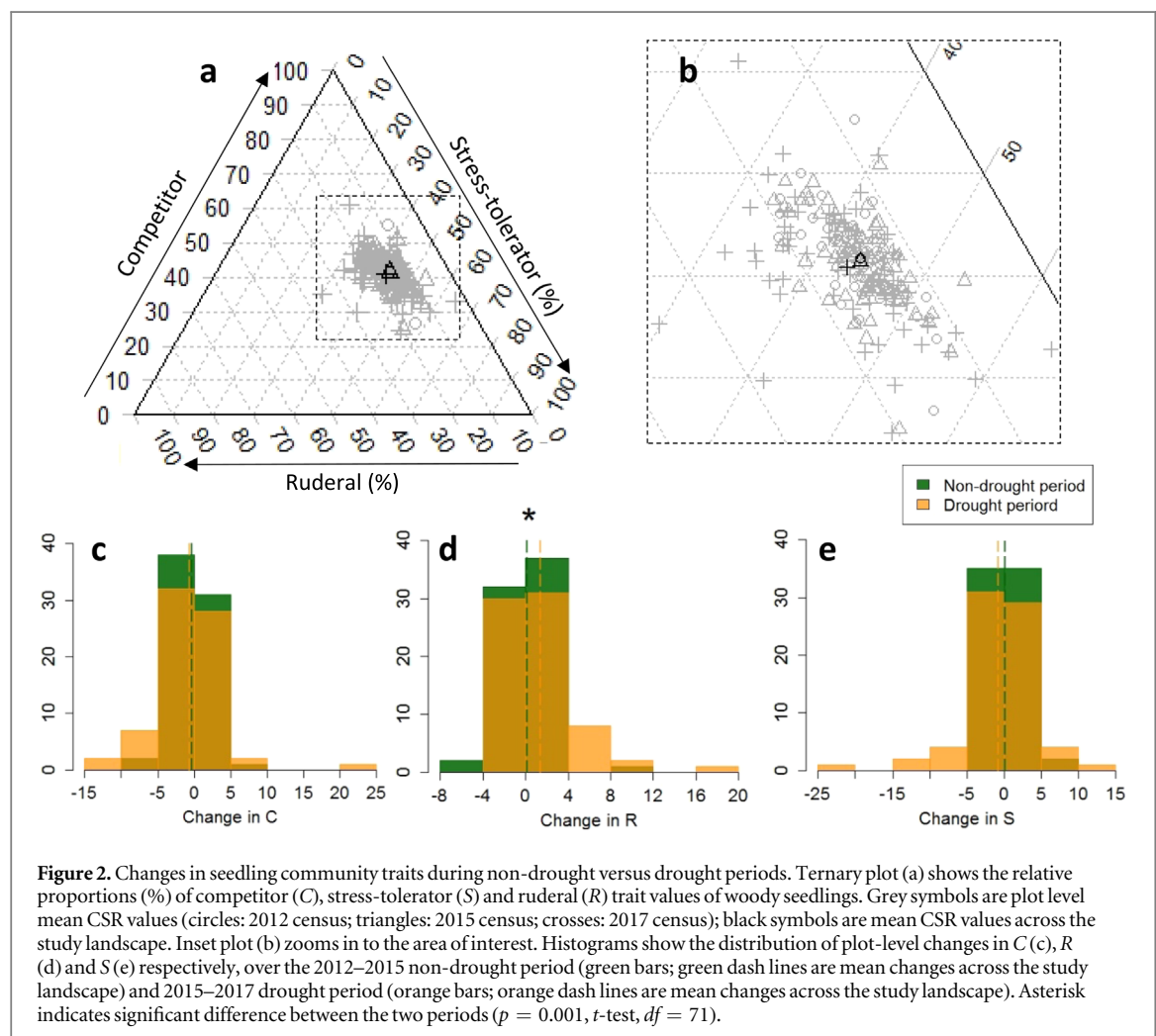
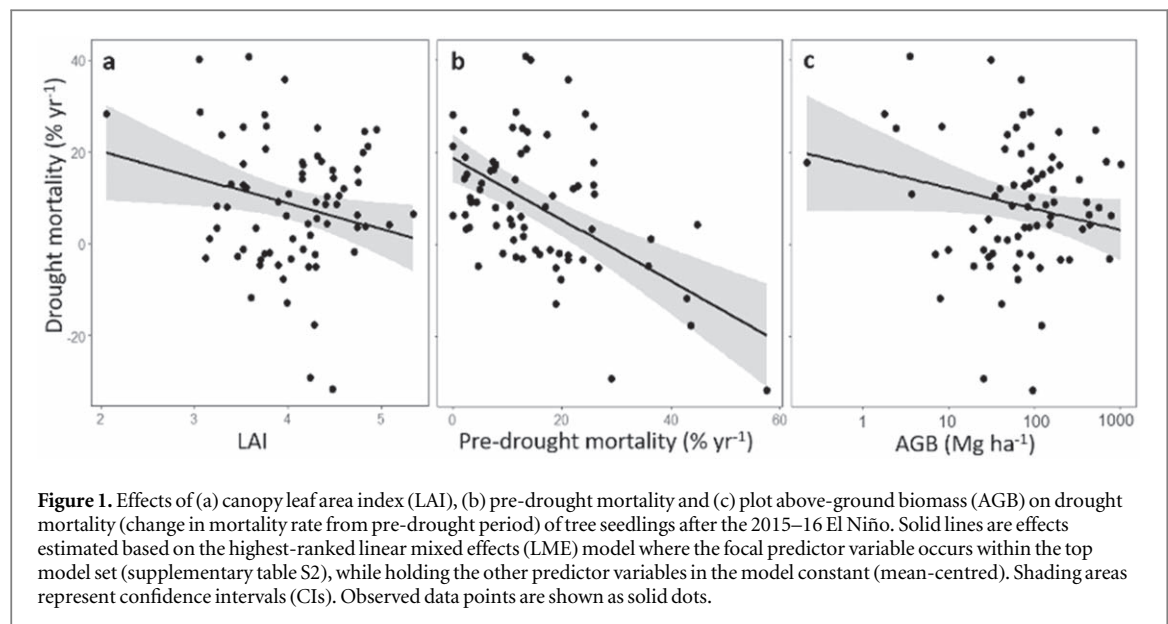
Results

Across the study landscape woody seedling mortality rate over the drought interval during 2015–2017 was $26.0\% \text{ yr}^{-1}$ (bootstrapped confidence interval 23.2–29.3), on average $10.3\% \text{ yr}^{-1}$ higher compared to the pre-drought interval 2012–2015 ($15.7\% \text{ yr}^{-1}$, CI 13.7–18.1). For tree seedlings (excluding liana), mortality rate increased from the pre-drought level of $15.3\% \text{ yr}^{-1}$ (CI 13.1–18.2) to $23.8\% \text{ yr}^{-1}$ (CI 20.7–27.1) after drought. For drought mortality of all woody seedlings, the top model set with $\Delta\text{AIC} < 2$ consisted of four models (supplementary table S1 is available online at stacks.iop.org/ERL/14/045012/mmedia) which did not include the variable LAI, and the effect of plot mean AGB was relatively weak with low variable importance value (table 1). For drought mortality of tree seedlings, the top model set consisted of three models (supplementary table S2) and all variables except for slope had high variable importance values (table 2). The best model contained LAI,

pre-drought mortality and AGB, all with negative effects on the drought mortality of tree seedlings (figure 1).

Woody seedling recruitment rate was not significantly higher over the drought interval ($11.1\% \text{ yr}^{-1}$, CI 8.1–15.8) compared to pre-drought interval ($8.3\% \text{ yr}^{-1}$, CI 6.8–10.8). Change in tree seedling recruitment was similarly non-significant, from pre-drought $10.2\% \text{ yr}^{-1}$ (CI 7.7–15.1) to $10.7\% \text{ yr}^{-1}$ (CI 7.8–13.9) over the drought interval. On the other hand, rate of new germinations significantly increased after drought (before drought $16.1\% \text{ yr}^{-1}$, CI 12.5–21.2; after drought $36.2\% \text{ yr}^{-1}$, CI 28.6–48.8).

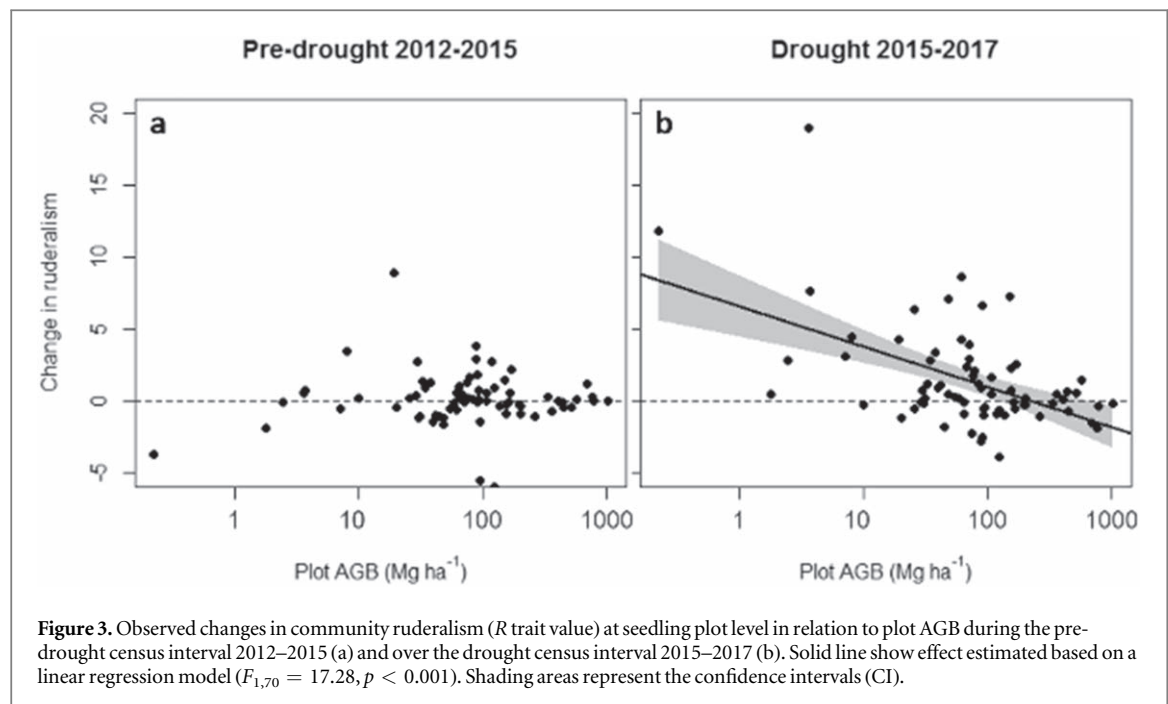
During the non-drought interval between 2012 and 2015, across the study landscape seedling community mean CSR values did not show significant changes. Variations in CSR values between plots were not correlated with forest AGB or LAI. Over the drought interval between 2015 and 2017, however, mean seedling community ruderalism (*R* value) across the landscape significantly increased ($p = 0.001$, *t*-test, $df = 71$; figure 2). This can be attributed to the fact that seedlings recruited over the drought interval had significantly higher ruderalism values (mean 17.3, CI 15.7–19.0) compared to those that died over the same period (mean 14.4, CI 13.9–15.0). Furthermore, ruderalism of recruited seedlings was likely higher in forests with lower AGB, though not significantly so ($F_{1,53} = 3.75$, $p = 0.058$). Consequently, the observed change in community ruderalism showed a significant dependency on forest AGB, with lower AGB forests experiencing a greater shift towards ruderal species composition ($F_{1,70} = 17.28$, $p < 0.001$; figure 3). In 2012 and 2015, community ruderalism was not significantly correlated with forest AGB, but this



association became significant after drought in 2017 (supplementary figure S1). Our regression model predicts, however, that in forests with $AGB > 219 \text{ Mg ha}^{-1}$ (figure 3b; CI 137–644), woody seedling communities are more likely to shift towards less ruderal species.

Discussion

Understanding the response of woody seedling communities in tropical forests to climatic events can provide us important insights on the climate resilience of these ecosystems (Whitmore, 1998). Studies



monitoring seedlings over climate disturbances in their natural environment remain uncommon in Southeast Asia, with many focusing on selected species, such as the dipterocarp trees (Delissio and Primack, 2003, Bebbler *et al* 2004). Our study documented the dynamics of whole woody seedling communities across a logging intensity gradient, before and after the strong 2015–16 El Niño drought. We quantified functional changes at community level using the novel CSR leaf trait measure, providing a new way to track the forest regeneration process and its sensitivity to supra-annual droughts.

Drought cuts back natural regeneration in the most heavily logged forests

The natural regeneration process of tropical forests critically depends on the seedling pool in the understorey. Seedlings of canopy tree species in Borneo's lowland rainforest typically need to survive a long period of time, sometimes over ten years, to eventually emerge from the understorey (Delissio *et al* 2002). We show here that drought resulted in substantially higher mortality in all woody seedlings than the pre-drought period across a logged forest landscape. The drought mortality of tree seedlings, in particular, varied according to logging intensity. Forests with more canopy foliage (measured by canopy LAI) and less historical logging (greater above-ground biomass) experienced lower drought mortality. Our model predicts that, other things being equal, increasing the forest canopy LAI from 2 (representing the most heavily logged forests in the study landscape) to 4 (median value in the study landscape) will reduce the drought mortality of tree seedlings from 20% to 8%. Similarly, increasing plot AGB from severely logged

state with 1 Mg ha^{-1} to median level of forest AGB of 78 Mg ha^{-1} is expected to reduce the drought mortality of tree seedlings from 17% to 8%. These results lend further support to improved tropical production forest management recommendations (Sasaki *et al* 2016), with reduced biomass impact harvesting being the key to achieving not only faster biomass recovery, but also increased drought resilience of logged forests.

When non-tree woody seedlings were considered, drought mortality was less sensitive to logging intensity (table 1) compared to tree seedlings only (table 2). This suggests the compounding impact of logging and drought may provide a relative advantage for the regeneration of lianas over trees. Indeed liana cutting has been used as a management practice to encourage tree seedling regeneration in logged tropical forests, but new evidence suggested that the benefits of lianas cutting were reduced during the 2015–16 El Niño drought (O'Brien *et al* 2019).

We found a negative effect of pre-drought mortality on drought mortality, and this was primarily driven by the extreme high pre-drought mortality values in a few plots in logged forests (figure 1(b)). This reflects the temporally and spatially dynamic nature of disturbed forest—at any time there may be individual locations experiencing extreme mortality events, but the mortality rates over the subsequent period are more likely to return closer to the mean level. Our results also suggest that drought mortality may increase on steeper terrain. This may be an indirect effect as steeper terrain can affect soil and microclimate conditions (Arroyo-Rodríguez *et al* 2015), and fallen trees and branches during drought can lead to greater disturbance in the forest understorey in steep areas.

More importantly, species turnover driven by the drought resulted in a clear shift in the seedling functional traits. During the non-drought period, seedling community composition represented in the competitor/stress-tolerator/ruderal (CSR) trait space were relatively stable across the landscape, but after drought there was a collective movement up the ruderal dimension. This change, albeit relatively small (figure 2), was driven by the most heavily logged forests (figure 3(b)), suggesting that seedling communities in these forests were more sensitive to the drought stressor. The drought itself has, therefore, acted as a climate filter favouring species with a more ruderal life strategy, typically pioneer species (Pierce *et al* 2017). On the other hand, community level seedling traits were more stable in less intensely logged and old growth forests with AGB above 219 Mg ha⁻¹, where predicted trait shift in response to drought was close to zero (figure 3(b)). This equates to logging having removed approximately 51% of tree biomass (mean AGB = 449 Mg ha⁻¹ in unlogged forests). These results point to the alarming consequence of overharvesting compounded by climate change, that at least for the short term, severe drought can reverse the successional trajectory of these heavily logged forests.

Microclimate and recruitment pool

Microclimatic conditions such as light, temperature and moisture in the tropical forest understorey may affect seedling establishment, survival and competition (Baraloto and Goldberg 2004). Across our study landscape, changes in microclimate due to forest disturbance were closely correlated with canopy LAI (Hardwick *et al* 2015). Our results showed that drought induced seedling mortality was modulated by microclimatic conditions. On the other hand, drought induced seedling community trait shift was strongly associated with forest AGB, that is, historical logging intensity, but not with microclimatic conditions. This suggests that the maturity of the surrounding forests, in terms of number of big trees and presumably, the intactness of forest structure and composition, plays a central role in maintaining the trait stability of seedling communities.

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

Lifting logged forests out of arrested succession

It has long been recognized that forest management needs to plan for the interactive effect of anthropogenic

disturbance and climate change, and efforts need to focus on the forest regeneration stage (Whitmore 1998). Our results show that tropical seedling communities are sensitive to drought, rapidly responding with elevated mortality and a functional shift towards more pioneer-like composition. Given that natural regeneration of tropical forest requires decades even in the best cases, and strong El Niño drought is becoming more frequent with a return period of less than a decade (Wang *et al* 2017), it is a real concern that these drought-susceptible logged forests will remain in arrested succession or face further degradation. We also find, however, that seedling communities were more resilient to drought where surrounding forests have above-ground biomass >219 Mg ha⁻¹. This biomass density is around half that of intact forests in our study landscape and in this region (Avitabile *et al* 2015), and not substantially higher than the average of 134.2 ± 6.1 Mg ha⁻¹ estimated in severely degraded forests in Borneo (António *et al* 2018). Therefore efforts should be invested in active forest restoration aiming at lifting the biomass of the vulnerable forests above this threshold, at which point their succession trajectories should become self-sustaining and resilient to future drought events. Our knowledge is accumulating on how forest regeneration may be assisted (Chazdon and Guariguata 2016) and practices such as enrichment planting and pioneer removal have shown some initial success in this region (Swinfield *et al* 2016).

Conclusion

Our study show that tropical forest seedling communities are sensitive to drought. The 2015–16 strong El Niño drought not only increased seedling mortality rate but also resulted in a shift in community functional traits towards more ruderal, pioneer-like composition. The drought impact, however, interacted with logging intensity, and was buffered in areas with higher canopy leaf index and forest above-ground biomass. We suggest that in order to increase the drought resilience of the most disturbed forests in a changing climate, active regeneration management should be considered in order to lift these forests out of arrested succession.

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ORCID iDs

Lan Qie  <https://orcid.org/0000-0002-7309-7523>

Mike R Massam  <https://orcid.org/0000-0003-4591-0369>

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