Long-term carbon sink in Borneo’s forests halted by drought and vulnerable to edge effects

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Less than half of anthropogenic carbon dioxide emissions remain in the atmosphere. While carbon balance models imply large carbon uptake in tropical forests, direct on-the-ground observations are still lacking in Southeast Asia. Here, using long-term plot monitoring records of up to half a century, we find that intact forests in Borneo gained 0.43 Mg C ha\(^{-1}\) per year (95% CI 0.14–0.72, mean period 1988–2010) in above-ground live biomass carbon. These results closely match those from African and Amazonian plot networks, suggesting that the world’s remaining intact tropical forests are now en masse out-of-equilibrium. Although both pan-tropical and long-term, the sink in remaining intact forests appears vulnerable to climate and land use changes. Across Borneo the 1997–1998 El Niño drought temporarily halted the carbon sink by increasing tree mortality, while fragmentation persistently offset the sink and turned many edge-affected forests into a carbon source to the atmosphere.
Over the past half-century land and ocean carbon sinks have removed ~55% of anthropogenic CO₂ emissions to the atmosphere¹. At least half this uptake is attributable to the terrestrial biosphere, with multiple independent lines of evidence pointing to the tropics in particular. These include remotely sensed observations of planetary greenness², global modelling studies³, analysis of spatially and temporally resolved aircraft measurements of atmospheric CO₂ concentrations, and regional and global transport models⁴⁻⁵. A further body of experimental, observational, and theoretical evidence suggests that a large fraction of these carbon sinks may be driven by rising atmospheric CO₂ concentrations⁶⁻⁸. Meanwhile, on-the-ground, net carbon gains have been documented in Amazonia and Africa based on long-term observations of nearly 400 ~1 ha plots in structurally intact forests⁹⁻¹², and in ten larger plots distributed across the tropics¹³. If these findings apply across the tropics, they imply a mean sink of ≈0.5 Mg C ha⁻¹ per year and the annual removal of ≈1.2 Pg C from the atmosphere by tropical forests between 1990 and 2007¹⁴.

Nevertheless, crucial evidence required to establish whether the forest sink is pan-tropical remains missing. Far from the other two large forest blocks in the Amazon and Congo basins, the forests of Southeast Asia are an independent expression of the tropical forest biome, with unique evolutionary history and biota¹⁵, ¹⁶. The largest equatorial rainforests in this region are found in Borneo, where they are typically dominated both in terms of stems and biomass by a single family (Dipterocarpaceae), and characterized by a largely aseasonal climate¹⁶. While the remaining forests here include the tallest¹⁷, most carbon-dense¹⁹, productive²⁰ and diverse¹⁵, ¹⁹ tropical forests in the world, remarkably little is known about their long-term biomass balance. Trends based on ground measurements have been reported in two studies, but with too few locations monitored—one using eight plots²¹, the other three¹³—to draw wider conclusions. Bottom-up estimates of the pan-tropical forest carbon budget either rely on these limited data⁶, ²², ²³ or simply apply a mean rate from other tropical regions to Asia¹⁴. Micrometeorological studies using flux towers above the forest canopy suggest Asian...
tropical terrestrial ecosystems are a significant, but highly variable, carbon sink. Meanwhile, top-down assessments based on atmospheric inversions are inconsistent, showing SE Asia to be either a carbon source, a sink, or carbon neutral. Such top-down assessments estimate net fluxes from all processes, so dis-aggregation of fluxes to net ecosystem productivity and land use changes is challenging.

Tropical forests are subject to multiple global and regional environmental drivers of change. While a global CO₂ driver would favour a sink in the remaining intact forests, at least two other important processes could counteract it in SE Asia. First, SE Asia’s tropical forests are among the most fragmented in the world, and edge effects may negatively impact biomass accumulation. Neotropical studies show that fragmentation influences ecosystem processes linked to biomass dynamics, increasing tree mortality and recruitment, and altering forest structure and composition, with effects penetrating up to 400 m from forest edges. A pan-tropical remote sensing analysis found carbon stock within 500 m of forest edges was on average 25% lower, with reductions extending up to 1.5 km, although this likely integrated other anthropogenic effects. A higher-resolution analysis also suggests large, but highly variable, pan-tropical fragmentation emissions of 0.1–0.8 Pg C annually depending on assumptions made about edge loss rates (10–50%) and edge distance (100–300 m). These highlight the need for better quantification of edge-related losses from tropical landscapes based on long-term observations.

Secondly, severe drought events may offset any sink in living biomass, if they kill enough trees. Two recent severe droughts temporarily reversed the long-term forest carbon sink in the Amazon, but this carbon sink is vulnerable to drought and edge effects. Here, we develop a temporally and spatially extensive forest dynamics dataset for Borneo. We quantify long-term changes in above-ground live biomass (AGB, dry mass), assess the scale and magnitude of edge effects on forest biomass dynamics, and examine the impact of recent El Niño droughts. Specifically, we hypothesize that: (1) Structurally intact lowland forests in Borneo are gaining AGB, since the most likely driver of the sink in the Amazon and Africa, increasing atmospheric CO₂, will also impact Bornean forests. (2) The edges of intact forests will be a reduced carbon sink or a net carbon source to the atmosphere; the greatest effects will be seen closest to the edge and will rapidly diminish with distance. (3) Biomass dynamics in structurally intact Bornean forests were impacted by recent El Niño droughts through increased mortality, but such impacts are short-term and insufficient to cause long-term net loss of biomass.

We assemble data from 71 long-term plots (mean size 1.3 ha) in Borneo’s lowland forests (Fig. 1). These have been censused 363 times over the monitoring period spanning 1958–2015 (mean period 1988–2010). Distance from the nearest anthropogenic forest edge was estimated using remotely sensed imagery and published logging road data. For each census and plot we estimated AGB using standard allometric equations based on tree diameters ≥10 cm, wood density, and estimated tree height based on locally derived height-diameter models. The mean AGB change that occurred throughout the entire census period was estimated using linear mixed effects (LME) models. We find that Borneo’s intact forests have been gaining biomass at a rate comparable to recent estimates for the Amazon and tropical Africa, but this carbon sink is vulnerable to drought and edge effects.

**Results**

**Intact forest carbon sink in Borneo.** We first needed to separate edge-affected plots to estimate the interior forest biomass trend. Excluding plots 100 m from the edge and proceeding in 100 m steps to 1000 m from the edge always gave a significant interior sink. The minimum increase in interior AGB was 0.67 Mg ha⁻¹ per year with an edge threshold set at 100 m, and generally increased as more edge plots were excluded (Supplementary Table 1). The relationship between anthropogenic edge distance and individual plot AGB change saturates with distance: it was

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**Fig. 2** Anthropogenic edge impact on plot above-ground live biomass change in structurally intact forests of Borneo. a A hockey-stick model (solid line; break-point at 448 m, 1.14 Mg ha⁻¹ per year) and asymptotic model (dashed line, asymptote 1.26 Mg ha⁻¹ per year) showing saturating edge effect on AGB change. b Histograms of plot AGB change, weighted by the cube root of monitoring length, in forest interior (≥448 m, n = 49; mean 1.01 Mg ha⁻¹ per year, green dashed line) and edge plots (<448 m, n = 22; mean −0.36 Mg ha⁻¹ per year, orange dashed line)
Edge offset to the carbon sink. In edge plots, AGB decreased, non-significantly, by −0.28 Mg ha⁻¹ per year (95% CI −1.19 to 0.64; n = 22), and this was significantly more negative than the interior plot trend (mean difference −1.19 Mg ha⁻¹ per year (−2.29 to −0.09)). The contrast between the forest interior and edge AGB changes was not caused by differences in the rate of production of woody material, which was largely unchanged (7.34 Mg ha⁻¹ per year in interior plots vs. 7.52 Mg ha⁻¹ per year in edge plots, Fig. 4a). However, the rate of biomass loss due to mortality was non-significantly higher in edge plots than in forest interior plots (7.50 vs. 6.30 Mg ha⁻¹ per year, Fig. 4b). Despite losing AGB, the edge plots had positive BA change, though not significantly so (Fig. 5a), but they differed markedly from the interior plots in showing a strong change in tree community floristic composition, with lower wood density taxa gaining (Fig. 5b). Furthermore, in terms of rates of stem dynamics, edge plots had substantially greater turnover than interior plots—both for mortality (2.3% per year in edge plots (2.0–2.5%) vs. 1.8% per year (1.6–2.0)) in interior plots; Fig. 4d), and for recruitment (2.3% per year (1.9–2.6) vs. 1.6% per year (1.4–1.8); Fig. 4c).

El Niño drought impact. All plots experience largely aseasonal precipitation regimes, but are occasionally droughted during strong El Niño events. We could not detect any impact of the 1982–1983 El Niño event on the 17 plots monitored through the event. Notably, AGB mortality appeared unaffected (before 6.43 Mg ha⁻¹ per year (4.97–7.89), during 6.24 Mg ha⁻¹ per year (4.41–8.07), and after 6.05 Mg ha⁻¹ per year (4.71–7.38)). The 1997–1998 El Niño drought, however, significantly altered biomass dynamics of the 19 plots monitored through the event. Before the 1997–1998 drought plot AGB significantly increased (+1.15 Mg ha⁻¹ per year (0.10–2.20)), but during drought AGB declined (−2.07 Mg ha⁻¹ per year (−4.30 to 0.17)), and then recovered to provide a larger sink (+2.39 Mg ha⁻¹ per year (1.09–3.70)) (Fig. 6). Across the entire monitoring periods of these 19 plots, AGB increased by 0.87 Mg ha⁻¹ per year (0.03–1.71). The drought associated decline in AGB was driven by a sharp increase in mortality, with AGB mortality averaging 9.05 Mg ha⁻¹ per year (6.59–11.51) up from pre-drought levels of 5.49 Mg ha⁻¹ per year (4.56–6.42), and not by reductions in wood production, which did not change significantly (before 7.02 Mg ha⁻¹ per year (6.44–7.60); during 7.25 Mg ha⁻¹ per year (6.43–8.07)). After the 1997–1998 event, while mortality returned to pre-drought levels (5.92 Mg ha⁻¹ per year), above-ground wood productivity (AGWP) was significantly higher (8.33 Mg ha⁻¹ per year (7.72–8.95)) than pre-drought productivity.

Discussion

Our analysis of data from structurally intact forests across Borneo reveals an above-ground live biomass carbon sink of 0.43 Mg C ha⁻¹ per year during the late 20th and early 21st centuries (mean period 1988–2010). The sink value is not strongly dependent on the definition of edge distance, and edge effects rapidly diminish with distance (Fig. 2). Our estimate of the intact forest carbon sink is of similar magnitude to recent ground-based estimates for the Amazon⁹, 11, 12 and tropical Africa¹⁰ (Fig. 3), and broadly consistent with past results from two large plots in Malaysia¹³.

The similarity in both direction and magnitude of net biomass changes across three distinct tropical forest regions suggests that a common driver is causing each to behave in a similar, non-equilibrium way. The new finding from SE Asia contributes significantly to the body of evidence for such a global driver—⁸, 14 as it represents a geographically independent replicate of the ongoing global anthropogenic forcing of planetary atmosphere, climate, and primary productivity. Across the tropics, as...
Carbon dioxide is a key substrate for photosynthesis and the atmospheric carbon dioxide concentrations and in temperature. Carbon dioxide is a key substrate for photosynthesis and the increase in concentration is global and almost uniform geographically, so is hypothesized to lead to a pan-tropical increase in growth. Faster growth is expected to lead to a sink until losses percolate through the system and catch up. Thus, for example, modelling exercises show that a long slow 50-year increase in woody productivity can lead to a forest carbon sink for a century, until a new dynamic equilibrium at higher biomass is reached. Air temperatures have also increased globally, so could conceivably be an alternative driver of the pan-tropical sink. However, respiration increases with temperature, so all else being equal temperature increases are widely expected to decrease tropical tree growth, not increase it. Estimates of the net carbon impact of temperature changes at ecosystem-scale for tropical forests nevertheless remain poorly constrained because of substantial technical and practical challenges. How long the sink will continue is not known. Soil nutrients may limit future CO₂ fertilization, as seen in temperate zone experiments. N deposition, which has been increasing in the region may be beneficial to plants, or may increase soil acidity reducing the availability of limiting soil nutrients. Alternatively, if P is limiting, mechanisms may exist for availability to keep pace with demand.

Other, regional and local, processes also shape forest dynamics and may also play a role. Many tropical forests have a long history of human use and individual plots are subject to disturbance and recovery. Our interior forest AGB results could potentially be the consequence of a recovery from a large Borneo-wide past disturbance, thereby leading to a long-term subsequent biomass carbon sink. Here, while we were unable to detect any impact of the 1982–1983 El Niño event, we show that the stronger 1997–1998 event was only responsible for net losses of <2% of total standing biomass and was insufficient to reverse the long-term sink (the 19 plots monitored through the event experienced long-term biomass gain of 0.87 Mg ha⁻¹ per year). Droughts exceeding the 1982–1983 and 1997–1998 episodes may have affected Eastern Borneo in the 19th century. However, to attribute the measured biomass increase to long-term recovery a century or more later, the hypothesized disturbance presumably needs to have caused widespread net biomass losses of at least 100 Mg ha⁻¹ which is more than an order of magnitude greater than observed in 1997–1998. As well as drought, other historical disturbances may have impacted individual plots. Our dataset includes natural disturbance-recovery dynamics, as all forests at all times are a mosaic of patches at different states of recovery from natural disturbance as an integral part of forest dynamics. While recovering forests become increasingly dominated by heavier-wooded species, during our observation window community average wood density did not change (Fig. 3b). Similarly, forests that are recovering substantially tend to start small and gain biomass, but our measured rates of net gain are insensitive to initial biomass, with the highest biomass forests having similar net gains to low biomass forests (Supplementary Fig. 2). Overall, the data available appear inconsistent with disturbance-recovery as a major driver of the measured carbon sink in Borneo’s intact forests. The close parallels with observations in Amazonia and elsewhere, there has been a persistent long-term increase in atmospheric carbon dioxide concentrations and in temperature.
A detailed analysis of Borneo's intact forest carbon sink further highlights the importance of protected forests in the region\textsuperscript{69}, which may attract Africa in terms of the magnitude, sign, and timing of change suggest that a single global driver provides a more parsimonious explanation.

We report changes in above-ground live biomass. However, larger trees, on average, have larger root systems, implying that the whole tree carbon sink is larger than we report. In turn, this might be expected to increase soil carbon storage, but data are lacking on below-ground changes in SE Asian tropical forests. Scaling up from our per-area above-ground carbon sink estimate for structurally intact forests to a wider region requires accurate and consistent land cover classifications. This however remains a challenge. Remaining forests are embedded in a relatively fine-grained mosaic of land uses, with selectively logged forests particularly difficult to distinguish from intact forests using remotely sensed datasets\textsuperscript{14, 59}, and definitions of ‘intact’ forest vary in such studies\textsuperscript{60, 61}. A detailed analysis of Borneo’s forest cover change reported that in 2010 there were 21 Mha of intact forest, defined as unlogged and >700 m from logging roads\textsuperscript{59} (Fig. 1). The analysis includes some forest types we lack data for (>1000 m in elevation, peat swamp, fresh water swamp and mangrove) but otherwise lies within our classification of structurally intact forest free from anthropogenic edge effects (Fig. 1). Assuming that all the 21 Mha of intact forest have the same carbon accumulation rate as forests in our study, our observations suggest a total above-ground intact forest carbon sink of \( \approx 9 \) Tg per year in Borneo.

Logged forest covered an additional 18 Mha of Borneo in 2010\textsuperscript{59}. If the drivers of intact forest sink also favour biomass gains in logged forests through similar underlying mechanisms, this would imply a total sink of \( \approx 17 \) Tg C per year provided by Borneo’s 39 Mha of logged and unlogged forest. Larger estimates are possible if logged forests are gaining biomass more rapidly as seen in studies showing rapid carbon stock recovery post logging in Asia\textsuperscript{62}, the Amazon\textsuperscript{63} and Africa\textsuperscript{64}. Conversely, any sink would be offset in areas undergoing forest degradation, e.g., adjacent to logging roads, loading yards and skid trails\textsuperscript{65}. Reducing this uncertainty requires both improved resolution in land cover monitoring and better understanding of the interplay between global drivers and local anthropogenic processes, for which our findings may serve to lay the groundwork.

Although we demonstrate that structurally intact forests far from edges in Borneo act as a carbon sink, we show two ways the carbon sink may reverse, one temporarily, due to extreme El Niño droughts, and one over the long-term, due to impacts of anthropogenic edges. We quantified the 1997–1998 drought offset to the biomass sink (\(-2.07 \) Mg ha\(^{-1}\) per year). More importantly, we find for the first time at the regional scale that there was rapid post-drought biomass recovery in Borneo’s forests in the following decade, which returned to being net sinks of similar or greater size than pre-drought, driven by accelerated growth and a return of mortality rate to pre-drought levels (Fig. 6). This demonstrates both the sensitivity (sharp increase in mortality)\textsuperscript{36} and resilience (ability to rebound)\textsuperscript{66} of the Bornean tropical forests to an extreme drought, similar to the responses observed in Amazonia to the 1997\textsuperscript{67} and the 2005\textsuperscript{11} droughts. However, recent evidence suggests that repeated droughts may have reduced the biomass recovery capacity in Amazonian forests\textsuperscript{34}, consistent with observations of a declining Amazon carbon sink\textsuperscript{68} so it is possible that the resilience of the Borneo sink may also be challenged in the future.

The offset to Borneo’s intact forest carbon sink due to forest fragmentation, however, is clearly ongoing. In contrast to the long-term AGB increase in forest interior, forests closer to anthropogenic edges are more likely to have been a carbon source than a sink. Our data show that forests within 448 m from edges on average lost 0.13 Mg C ha\(^{-1}\) per year (0.28 Mg ha\(^{-1}\) per year biomass; though not significantly different from zero). The scale of edge effects supported by our data is broadly consistent with the maximum penetration distance of 400 m for a range of ecological processes reported by a comprehensive review of neotropical field studies\textsuperscript{32}. Of course edge types, the type of matrix next to the edge and edge age will all affect the temporal trajectories of individual edge forest plots, which require monitoring into the future.

Our analysis also revealed the mechanisms by which edge effects impact forest biomass dynamics. Edge forests may sequester less carbon than forest interior due to (1) lower above-ground wood productivity (AGWP), or (2) higher AGB mortality, or a combination of the two. We find that the biomass decline of edge forests was associated with elevated mortality (both the stem mortality rate and AGB mortality) but with no detectable change in AGWP (Fig. 4). However, elevated mortality in edge-affected forests was compensated for by recruitment, which is also significantly higher than forest interior (Fig. 4). This higher stem turnover near anthropogenic edge forests was accompanied by a significant decrease in stand level mean wood density, unlike in interior forests where WD was unchanged (Fig. 5). That is, near anthropogenic edges forests underwent a compositional shift towards lower wood density species, likely due to increased disturbance. We suspect that additional tree-falls and seed input from nearby disturbed areas have led to a greater probability of recruitment of earlier-successional lower wood density species, leading to the patterns we see.

Overall, our results provide new insight into the pan-tropical carbon sink, its driver(s), its sensitivity and resilience to drought, and the ways in which edge effects may degrade it. They also provide new baseline information to assist in regional carbon accounting, especially in light of the ambitious carbon emission cuts pledged by forest-rich nations such as Malaysia and Indonesia in the wake of the UNFCCC Paris Agreement. For example, the finding of an interior forest carbon sink further highlights the importance of protected forests in the region\textsuperscript{69}, which may attract
carbon financing. The high carbon density in SE Asia’s forests\(^2\) means that much is at stake. The contrasting biomass trajectories of plots near and far from anthropogenic forest edges indicate that overall biomass dynamics of forests in the region will depend, in part, on the landscape integrity of remaining forests. Based on our estimated rates of AGB change for forest interior vs. edge (0.91 vs. −0.28 Mg ha\(^{-1}\) per year) and the 448 m edge threshold, the minimum area required for a square forest fragment to maintain a carbon sink would be 302 ha (a \(1.7 \times 1.7\) km square). This estimate is likely to be sensitive to edge effect penetration and fragment shape. A worse-case scenario, corresponding to the lower CI (393 m) of our estimated edge threshold but steeper edge and fragment shape. A worse-case scenario, corresponding to the lower CI (393 m) of our estimated edge threshold but steeper edge

Methods

Long-term plot data. Borneo straddles the equator between 4.21°S and 7.04°N, and harbours the largest expanse of lowland rainforests in the Sundaland biogeographical region of SE Asia. All plots in this study were sampled within non-flooded lowland forests (below 1000 m a.s.l.; mixed dipterocarp and kerangas forests) and are geographically well dispersed across the region (Fig. 1, Supplementary Data 1). These forests are on mineral soils that vary in nutrient level\(^2\). All were mature, structurally intact forests, free from major direct human impacts including fire and logging (plots within logging concessions were in unlogged compartments). Plots had from 2 to 15 censuses (mean 5, median 5), and their monitoring period ranged from 3.8 to 55.8 years (mean 22.6, median 18.3). The combined sampling effort varied over time (Supplementary Fig. 3). Plot size was between 0.25 and 4.4 ha (area corrected for topography). Plots smaller than 0.4 ha that were within 1 km or less of one another were merged when censuses were synchronous, giving a total of 75 sampling units (referred to as plots hereafter), with a mean size of 1.3 ha (median 0.75). In total our dataset included 95 ha of forest with a combined monitoring effort of 1785 ha-years, containing 266,493 measurements on 67,319 individual stems \(210\) cm diameter. Of these individual stems, 96.7%, 94.7% and 78.7% were identified to family, genus and species level respectively, with 22% of the stems lacking species level identification belonging to the large and difficult genus Syzygium. All free-standing woody stems with diameter \(\geq 10\) cm were measured, at point of measurement (POM), mapped, and tagged except in seven plots where only trees \(\leq 15\) cm were included during census one to five. In these plots we used a minimum diameter of 15 cm throughout, given that in census six to eight, the biomass of 10–14.9 cm trees contributed only \(\approx 5\)% of total biomass. Plot metadata are summarized in Supplementary Data 1.

Standardized quality control procedures were carried out on diameter records at individual tree level following established protocols\(^2\),\(^7\),\(^3\). Thus, where potential errors were identified we corrected through extrapolation based on the best available information, i.e., where available, we applied mean growth rate of the same tree for those intervals with accepted measurements, else we applied the growth rate of the same diameter size class from that plot (median growth rate for size class 20–39 or >40 cm; mean growth rate for size class 10–19.9 cm). Median growth rate was used for larger size classes because it provides a more robust estimate when sample sizes are small and is more conservative than mean growth rate with respect to the hypothesis of net biomass gain\(^6\),\(^1\). While the standard POM for diameter was at 1.3 m from the base of the tree, for trees with buttress or deformity at 1.3 m, POM was above it. At censuses where buttress growth might reach existing POM before the next census, a new POM was located sufficiently high above the anticipated future top of buttress and diameter measured at both old and new POMs, providing a taper ratio between both POMs to compute complete diameter series standardized to the old and new POMs\(^3\). The mean of both diameter series corresponds to an invariant POM located between the old and new (final) POMs, so providing internal consistency over time while using available tree-level information and avoiding biases that result from not accounting for POM change\(^6\),\(^8\),\(^7\). In cases where a developing buttress already affected the existing POM making it unusable for measurement, a new POM was defined and measured following standard protocols and diameter at the old POM estimated by the quality control protocol. In total, diameter corrections were applied to 2.3% of tree measurements.

Above-ground live biomass calculation. Stem above-ground live biomass (AGB, dry mass) was calculated using the allometric equation \(\text{AGB} = 0.0673 \times (\rho D^2 H)^{0.976}\) for non-Monocots\(^6\) and \(\text{AGB} = \text{exp}(-3.3488 + (2.7483 \times \ln(D)))\) for Monocot families\(^4\), where \(D\) is stem diameter (in cm), \(H\) is height (in m), and \(\rho\) is stem wood density (WD, in g cm\(^{-3}\)) obtained from a global database\(^5\), applying appropriate genus or family-specific values if species level match was not available, and applying mean WD of all identified stems in the plot if no taxonomic information was available for a stem.
Height is an important parameter for estimating tree AGB with allometric equations\textsuperscript{18, 43}, but it is rarely measured directly in tropical inventory plots, and is often estimated from diameter using a H–D model parameterized at continental level\textsuperscript{14, 15}. Because this approach does not account for potentially important geographical variation in allometry within continents, we developed H–D models specific to the Sundaland bioregion and four lowland forest types (i.e., combinations of two climate types: ‘wet’ and ‘monsoon’, with 1 cm diameter per year; and a subsequent year following Chave et al.\textsuperscript{74}, and two edaphic types, ‘mixed dipterocarp’ and ‘kerangas’), using sub-samples of tree heights actually measured within our plots.

Tree heights (total height to tree top) were measured with either a clinometer or laser range finder in the field in 53 of the 71 plots (Supplementary Data 1), with a mean sample size of 100 stems per plot including the 10 largest trees in each plot. For each forest type we selected the best H–D model through comparing three equations, fitted using those trees with measured H and D. Firstly, we fitted a Weibull model, \( H = a \cdot b^{D \cdot D_{P}} \), where \( a \) and \( b \) are estimated parameters. Secondly, we fitted the same Weibull model, but using weights proportional to each tree’s height. Finally, a linear model was fitted using weights for each tree, more important in the stick during the census interval. Thirdly, we fitted a log-log model, \( \ln(H) = \beta \cdot \ln(D) \). We selected the model that minimized prediction error in AGB (i.e., the absolute difference between AGB estimated using measured heights and AGB estimated using heights predicted by the H–D model). In all cases one of the two Weibull models were selected (Supplementary Table 2). To assess the sensitivity of our AGB trend analysis to different H–D models we generated a second set of plot AGB estimates based on the widely used Weibull H–D equation for SE Asia parameterized by Feldpausch et al.\textsuperscript{44, 45}.

Plot AGB per ha for each census was calculated using the total AGB of live trees. Stand basal area (BA; m\(^2\) ha\(^{-1}\)) and mean WD was weighted by stem BA (g cm\(^{-2}\)) were calculated for each census. At census interval level, above-ground wood productivity (AGWP) of a plot was calculated following Talbot et al.\textsuperscript{73} as the AGB change for individual plots, calculated as the slope from a linear regression of two successive censuses increases with interval length. Following Lewis et al.\textsuperscript{10, 11}, for plot area, we found no relation between individual plot AGB change rate from the population mean plotted against plot area and monitoring length respectively. For plot area, we found no relation between individual plot AGB change rate from the population mean plotted against plot area and monitoring length respectively. For plot area, we found no relation between individual plot AGB change rate from the population mean plotted against plot area and monitoring length respectively.

Establishing edge distance threshold. To investigate the impact of edge effects without having to define plots as ‘edge’ or ‘interior’, we first used an incremental edge effect threshold from 100 m, in 100 m steps, to 1000 m, to generate explorative AGB change estimates for ‘edge’ and ‘interior’ plots employing linear mixed effects (LME) models described below. We then calculated the number of individual plot AGB change as a function of distance to forest edge: a non-linear asymptotic model \( y = a \cdot b^{-r} \) and a hockey-stick model consisting of two linear segments, the second of which had a zero slope, implemented in the R package \texttt{Smer}". The asymptotic model is more ecologically meaningful whereas the hockey-stick model is more robust to outliers. We compared these with a simple linear model (non-asymptotic relationship) and an intercept-only model (no relationship) based on Akaike’s Information Criterion (AIC) to test if the hypothesized models better represent the relationship with the given data. We first limited this analysis to plots with edge distance ≤2,000 m (\( m = 0 \) and not all plots required the edge threshold). Then we repeated the analysis on all plots to test the robustness of the result. The edge distance threshold identified by the hockey-stick model was then used to divide all plots into two categories, interior and edge plots.

Modelling AGB dynamics for interior and edge forests. We used a linear mixed effects (LME) model of AGB observed at each census in each plot as a function of time, a categorical variable indicating whether plots were near an edge, and their interactions \( \times D \) and fixed effect per year, and time represents the estimate of AGB change for interior plots, and the time \( \times D \) interaction represents how edge effects influence the AGB change. This model formulation thus allows us to quantify the rate of AGB change in interior and edge plots, and test if these rates are different. Plot identity was included as a random effect, allowing us to include any idiosyncratic differences among plots, a random effect was better in identifying the optimal edge distance threshold. We compared these with a simple linear model (non-asymptotic relationship) and an intercept-only model (no relationship) based on Akaike’s Information Criterion (AIC) to test if the hypothesized models better represent the relationship with the given data. We first limited this analysis to plots with edge distance ≤2,000 m (\( m = 0 \) and not all plots required the edge threshold). Then we repeated the analysis on all plots to test the robustness of the result. The edge distance threshold identified by the hockey-stick model was then used to divide all plots into two categories, interior and edge plots.

Statistical significance was assessed using the t test statistic. We obtained the 95% CI’s of model parameter estimates using a normal approximation to the distribution of the restricted maximum likelihood estimators. Model explanatory power was assessed by calculating marginal R-squared\textsuperscript{89} using the MuIn R package\textsuperscript{80}. For AGB, the marginal R-squared was 0.11 (Supplementary Table 3). This value gives the proportion of variation in both space and time explained by model fixed effects; variation in AGB in space was larger than in time, and this spatial variation was primarily accounted for by the plot random effect (Supplementary Table 3). However, LME modelling implicitly assumes homogeneity of variance and normally distributed residuals and it is important to check if our model meets these assumptions. LME model validation was done with standard diagnostic plots including examining model standardized residuals against fitted values and plot area. Patterns in LME model residuals suggested that residual variance was correlated positively with fitted value and negatively with plot area. To remove this the model was refitted with weights inversely proportional to variance, where variance = \( \text{plot area}^{0.028} \times (\text{fitted value})^{0.767} \) (estimated using model fitting using the varFunc function in the nlme R package\textsuperscript{81}). The resulting model was then used again but before any interaction was made.

Individual AGB change estimates. We first generated simple estimates of AGB change for individual plots, calculated as the slope from a linear regression of AGB against time. Plots with greater sampling effort, in terms of plot area and monitoring length may better represent local AGB changes. Following Lewis et al.\textsuperscript{25, 27}, an appropriate weighting was determined by examining the deviation of individual plot AGB change rate from the population plot rate per plot area and monitoring length respectively. For plot area, we found no relationship (Supplementary Fig. 4c), while for monitoring length there was an inverse relationship (Supplementary Fig. 4a). We used cubic root of monitoring length as the weight which optimally removed this (Supplementary Fig. 4b, d). Subsequent use of each plot’s AGB change metric was based on weighted values.

Measuring edge distance. We defined forest edge as the interface of what we considered original forest vegetation and any anthropogenically modified habitat of minimum 1 ha, including active anthropogenic land uses such as inhabited areas, plantations, clear cut logging, as well as regenerating forests from past major anthropogenic disturbances. In selectively logged forests, the exact boundary between unlogged and logged forests was difficult to determine and we considered the selected logging forest to be edge forest. We used Google Earth Pro, Landsat imagery from http://earthexplorer.cr.usgs.gov/, and additional GIS data on Borneo’s logging roads\textsuperscript{89}. Because some plots were near to dynamic anthropogenic processes, we always selected historical Landsat imagery corresponding to the majority of the plot monitoring period. From each plot’s centre point, we searched for the nearest forest edge on remotely sensed imagery using the built-in circle tool of Google Earth Pro, the distance to which was then measured using the software’s built-in line tool.

Testing for drought impact. We tested for the potential short-term reversal of the long-term trend associated with impact of the 1982–1983 and 1997–1998 El Niño

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droughts on forest biomass using all forest interior plots that were all monitored before, during and after the El Niño events (17 plots for 1982–1983 and 19 plots for 1997–1998). The El Niño time window contained a single census interval from each plot spanning the drought episodes (mean start and end dates for the 1982–1983 window: 1981.4 and 1986.6, and for the 1997–1998 window: 1996.5 and 2000.0). The remaining intervals were assigned to the pre- or post-drought time windows. LME models as described above were then applied for each time window to estimate mean AGWP, AGM mortality, and AGM change. All analyses were conducted in the R statistical computing environment.

Among-site mean levels of AGM change are presented in the text with 95% CIs.

**Data availability** The plot level biomass dynamics data that support the findings of this study are given in Supplementary Data 1. Tree-by-tree data are curated at [www.forestplots.net](http://www.forestplots.net) and additional institutional databases (details given in Supplementary Data 1).

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Author contributions

O.L.P., Y.M. and S.L.L. conceived the T-FORCES forest monitoring network. O.L.P., S.L.L. and L.Q. conceived and designed the study. L.Q. led the 2013–2015 Borneo field campaigns with the help of O.L.P., Y.M., S.L.L., G.C.P., T.S., K.A.S., K.C.H., L.K.K., H.K., C.M., F.E., M.N., R.N., R.O., C.A.P., R.B.P., E.R., I.S., J.W.F.S., R.S.S., A.T., M.N., R.R.E. V., I.Y., M.F. and K.H.J. Data contribution was made by S.L.L., P.A., K.A.S., S.A., L.F.B., N.B., Q.F.B., D.B., M.D., S.J.D., G.F., R.H., L.K.K., S.I., S.L., C.M., E.M., L.N., R.N., C.A.P., A.D.P., R.B.P., E.R., I.S., J.W.F.S., R.S.S., M.S., S.T., M.N., R.R.E.V., I.Y., P.S.K., R.S., L.S.A.L. and M.S.S. O.L.P., S.L.L., M.J.P.S., G.L.G., G.C.P. and W.H. contributed tools to analyse and curate data. G.C.P produced the forest edge metrics and Fig. 1. L.Q. carried out data analysis. L.Q., S.L.L. and O.L.P. wrote the paper. All co-authors commented on or approved the manuscript.

Additional information

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