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Large contribution of recent photosynthate to soil respiration in tropical dipterocarp forest revealed by girdling

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ABSTRACT

- Tropical forests are the most productive terrestrial ecosystems, fixing over 40 Pg of carbon from the atmosphere each year. A substantial portion of this carbon is allocated belowground to roots and root-associated microorganisms. However, there have been very few empirical studies on the dynamics of this below-ground transfer, especially in tropical forests where carbon allocation processes are mediated by high plant species diversity.
- We used a whole-stand girdling experiment to halt the belowground transfer of recent photosynthates in a lowland tropical forest in Borneo. By girdling 209 large trees in a 0.48 ha plot, we determined: i) the contribution of recent photosynthate to root-rhizosphere respiration and; ii) the relationships among the disruption of this belowground carbon supply, tree species composition and mortality.
- Mortality of the 209 trees was 62% after 370 days, with large variation among species and particularly high mortality within the Dipterocarpaceae (99%) and Fagacae (100%) families. We also observed a higher risk of mortality following girdling for species with lower wood density.
- Soil CO_2 emissions declined markedly (36 ± 5%) over ~50 days following girdling in three of six monitored subplots. In the other three subplots there was either a marginal decline or no response of soil CO_2 emissions to girdling. The decrease in soil CO_2 efflux was higher in subplots with dominance of Dipterocarpaceae.
- *Synthesis.* Our results indicate high spatial variation in the coupling of belowground carbon allocation and root-rhizosphere respiration in this tropical forest, with a closer coupling in forest dominated by Dipterocarpaceae. Our findings highlight the implications of tree species composition of tropical forests in affecting the dynamics of belowground carbon transfer and its release to the atmosphere.

Keywords: autotrophic respiration, belowground carbon allocation, global change ecology, heterotrophic respiration, plant-soil interactions, soil CO_2 efflux, SAFE project, terrestrial carbon cycle, tree mortality

RINGKASAN

- Hutan tropis adalah ekosistem terestrial yang paling produktif, menghasilkan sekitar 40 Pg karbon dari atmosfer setiap tahun. Sebilangan besar karbon ini diperuntukkan di bawah tanah untuk akar dan mikroorganisma yang berkaitan dengan akar. Walau bagaimanapun, terdapat sedikit kajian empirik mengenai dinamika pemindahan bawah tanah ini, terutama di hutan tropika di mana proses peruntukan karbon dimediasi oleh kepelbagaian spesies tumbuhan yang tinggi.
- Kami menggunakan eksperimen girdling utuh untuk menghentikan pemindahan fotosintesis baru-baru ini di hutan tropika dataran rendah di Borneo. Dengan merangkai 209 pokok besar di sebidang 0.48 ha, kami menentukan: i) sumbangan fotosintesis baru-baru ini untuk pernafasan akar-rizosfera dan; ii) hubungan antara gangguan bekalan karbon bawah tanah ini, komposisi spesies pokok dan kematian.
- Kematian 209 pokok adalah 62% selepas 370 hari, dengan variasi yang besar di antara spesies dan terutamanya kematian yang tinggi dalam keluarga Dipterocarpaceae (99%) dan Fagacae (100%). Kami juga mengamati risiko kematian yang lebih tinggi berikutan menyikat spesies dengan kepadatan kayu yang lebih rendah.
- Pelepasan CO_2 tanah menurun dengan ketara (36 ± 5%) selama ~ 50 hari berikutan menggelecek di tiga daripada enam subplot yang dipantau. Di tiga subplot yang lain terdapat penurunan marjinal atau tidak ada tindak balas pelepasan CO_2 tanah terhadap girdling. Penurunan aliran masuk CO_2 tanah lebih tinggi di subplot dengan dominasi Dipterocarpaceae.
- Sintesis. Hasil kajian kami menunjukkan variasi spasial yang tinggi dalam penggabungan alokasi karbon di bawah tanah dan respirasi akar-rizosfera di hutan tropika ini, dengan gandingan lebih dekat di hutan yang dikuasai oleh Dipterocarpaceae. Hasil kajian kami menunjukkan implikasi komposisi spesies pokok hutan tropika dalam mempengaruhi dinamika pemindahan karbon di bawah tanah dan pembebasannya ke atmosfera.

1. INTRODUCTION

Tropical forests dominate the terrestrial carbon (C) cycle, accounting for 34% of global gross primary production (GPP) (Beer et al., 2010). The total C stored in tropical forest vegetation is determined by its net primary production (NPP): the sum of C-fixation by photosynthesis (i.e. GPP) minus C-release by above and belowground components of plant-derived respiration. There is increasing evidence from extra-tropical studies that the belowground respiration component, arising from the activity of roots and rhizosphere- dwelling microorganisms ('root-rhizosphere respiration'), is driven by the supply of recent photosynthate (Irvine et al., 2005, Högberg et al., 2001, Savage et al., 2013), which is in turn related to plant species and/or community traits (Wright et al., 2004, Santiago et al., 2004). However, we have little understanding of the relationship between root-rhizosphere respiration and the species composition and productivity in tropical forests.

Root-rhizosphere respiration is often assumed to make a large contribution to the CO_2 efflux from tropical forests given their high productivity (Malhi, 2012) and because a lower proportion of C from GPP is allocated to NPP in tropical forests compared to ecosystems at higher latitudes (Chambers et al., 2004, Metcalfe et al., 2010). This pattern of a low proportion of GPP allocated to NPP in tropical forests has been explained by a combination of factors, including lower wood residence time due to conservative growth strategies, higher temperatures and lower soil fertility (Muller-Landau et al., 2021, Doughty et al., 2018), which may increase belowground C allocation to roots and root-associated microorganisms. However, our understanding of the carbon balance of tropical forests is limited by a lack of empirical studies that estimate root-rhizosphere respiration, which would allow for more complete partitioning of the autotrophic component of forest respiration. Of the studies performed, root-rhizosphere respiration has ranged widely from 38 to 70% of total belowground respiration (Nottingham et al., 2010, Metcalfe et al., 2007, Sayer and Tanner, 2010, Girardin et al., 2014, Li et al., 2004), overlapping with estimates in forests globally (from 10 to 90%; Hanson and Gunderson (2009)). The large variation in these estimates reflects not only the result of differences among study sites, but also differences in methodology and associated bias (see below) and potentially higher spatial variation associated with the high diversity of plant communities and plant-microbial associations in tropical forests (LaManna et al., 2017, Steidinger et al., 2019).

Root-rhizosphere respiration in tropical forests may vary widely among diverse tree species assemblages with different growth-strategies. For example, higher root-rhizosphere respiration may be associated with faster growing trees with related traits (e.g. lower wood density; Santiago et al. (2004)), due to higher belowground C allocation to support rapid growth. Spatial heterogeneity of root-rhizosphere respiration may also increase with increased diversity of root-microbial associations that influence belowground C allocation, such as mycorrhizal fungi. The magnitude of the belowground C flux may vary widely with plant diversity and community composition according to differences in root-microbial associations. For example, field studies in temperate forest show that carbon allocation to mycorrhizal fungi can represent up to 35% of NPP (Ouimette et al., 2020, Allen and Kitajima, 2014) and controlled pot experiments demonstrate that 7 to 30% and 2 to 20% of NPP is allocated to ecto- and arbuscular-mycorrhizal fungal systems, respectively (Leake et al., 2004). Although there is considerable variation in the extent of the C allocation among different plant-mycorrhizal associations to consider (Tedersoo and Bahram, 2019). Despite the importance of high diversity of plants and plant-microbial interactions in the functioning of tropical forests (Fujii et al., 2018, LaManna et al., 2017, Steidinger et al., 2019), we know surprisingly little about the relationship between root-rhizosphere respiration and tropical plant communities.

There is large methodological uncertainty when quantifying the contribution to root-rhizosphere respiration from organisms using root-derived C, including mycorrhizal fungi and rhizosphere microbial communities (Kuzyakov and Gavrichkova, 2010, Hopkins et al., 2013). There are five general methods used to estimate root-rhizosphere respiration and all have associated sources of bias:

i) *indirect mass balance* approaches where root-rhizosphere respiration is the balance of total soil respiration minus litterfall inputs in ecosystems, assuming that soil C stocks are at steady state (Davidson et al., 2002) which may be incorrect at smaller scales and under recent global change (Bond-Lamberty et al., 2018);

ii) *physical partitioning by root-trenching*, which can result in under-estimation of the fractional contribution from root respiration because heterotrophic respiration is increased as dead roots are decomposed (Savage et al., 2013, Sayer and Tanner, 2010); iii) *physical partitioning by root exclusion*, which can result in over-estimation of the contribution from roots due to preferential ingrowth of fresh root tips into root-free soils (Girardin et al., 2014, Nottingham et al., 2010);

iv) *isotopic methods,* which circumvent the biases from these disturbances associated with physical partitioning. However, they are difficult to implement in large forest stands and are subject to bias associated with variation in fractionation effects and isotopic end-member uncertainty among tree species (Ogle and Pendall, 2015), which may be especially difficult to interpret in species-rich tropical forest;

v) *tree girdling*, whereby the phloem is removed to stop the transfer of C from above- to below-ground, providing a more accurate estimate of root-rhizosphere respiration without physical disturbance of the root-soil system (Högberg et al., 2001). The obvious drawback of the method is that it kills trees, and therefore has not been implemented in tropical field experiments given the challenges in gaining approval from land managers for this kind of invasive activity; in addition to the ethical consequences of killing trees in intact tropical forest.

The estimates for tropical forests have thus been predominantly based on mass balance, root-trenching or root-exclusion methods, which result in different forms of physical disturbance of root systems and root-soil microbial associations. There is, therefore, a need for experiments using methods that possess fewer artefacts - using isotopic or girdling methods - to quantify root-rhizosphere respiration in tropical forests.

Here, we report on a whole-stand girdling experiment in tropical forest in Borneo to estimate the magnitude of belowground C allocation and root-rhizosphere respiration, and investigate whether these fluxes are related to tree community traits. The opportunity to conduct this experiment arose because the forest-stand under study was already designated for land conversion by a private landholder. In the context of on-going rapid land-use change in this region (Fisher et al., 2011), the experiment has far-reaching implications for how the degradation of dipterocarp forests (dominated by the family Dipterocarpaceae) affects the forest ecosystem and C cycle. This paper, focussed on the relationship between tree communities and C allocation to soil, is one of several studies to emerge from this whole-stand girdling experiment (e.g. Doughty et al. (2020)). We tested three main hypotheses: 1) tree mortality occurs following girdling, with greater mortality one year following girdling for tree species with traits associated with faster growth rates; 2) soil CO_2 efflux decreases following plot-scale girdling, where the magnitude and rate of decrease indicate the contribution of roots to the CO_2 efflux and the speed of belowground C allocation, respectively; and 3) there is a relationship between the effect of girdling on mortality among tree communities and on changes in soil CO_2 efflux, thereby providing evidence for a link between belowground C allocation and the community composition of plants and plant-microbial associations. We specifically hypothesised a stronger relationship between changes in soil CO_2 efflux and the effect of girdling on mortality for species with faster growth rates for which we also hypothesised greater below-ground C allocation. The experiment is the first whole-stand girdling experiment performed in tropical forest that we are aware of and provides a novel opportunity to address these hypotheses on above-belowground C transfer for tropical forests at this scale.

2. MATERIALS AND METHODS

2.1 Site description

The study was conducted in the Malaysian state of Sabah in north-eastern Borneo, as part of the long-term ecosystem monitoring at the Stability of Altered Forest Ecosystem (SAFE) Project. The SAFE landscape consists of a broad gradient of forest disturbance from unlogged tropical lowland forest through to heavily logged forest and oil palm plantations (Ewers et al., 2011) and is part of the Yayasan Sabah Forest Management Area of lowland dipterocarp rainforest characterized by high tree species richness. The 1 ha forest plot under study here is situated in the selectively logged area at Lat. = 4.7163 N, Lon. = 117.6101 E, and at an elevation of ~240 m. The area has been logged twice, with the first round in the mid-1970s and the subsequent round during 1990–2008. Over this period, approximately 150–179 m^3 ha^{-1} of timber was removed (Struebig et al., 2013), similar to the mean extraction volume across Sabah (152 m^3 ha^{-1}) (Fisher et al., 2011). The plot was destined to be entirely cleared and converted to oil palm plantation immediately following this experiment. The degraded tropical forest study site is representative of old-growth lowland tropical forest in Sabah in terms of species composition and NPP, although there is evidence for a slight increase in NPP allocation from leaf to woody biomass in degraded forest (Riutta et al., 2018). The site has a mean annual temperature of 26.7°C and an annual rainfall of 2,600–3,000 mm (Walsh and Newbery, 1999). For further details on the SAFE study site, see Ewers et al. (2011).

The experimental girdling site consisted of one-half (0.48 ha) of the 1 ha forest plot (SAF-05, intensive plot in the Global Ecosystems Monitoring network); for further details see Riutta et al. (2018) and Marthews et al. (2015). The experimental plot was split into 12 subplots each measuring 20 x 20 m (400 m^2). Of these twelve subplots, six were selected for the study of soil respiration (subplots 14, 15, 21, 22, 24 and 25; Fig. S1). Across the entire site there were 209 large trees (≥10 cm d.b.h.) representing 52 genera, drawn from 30 families (note: 10 stems could not be reliably identified). The dominant tree families (by stem number) were Dipterocarpaceae (59), Urticaceae (24), Euphorbiaceae (18), Malvaceae (14), and Sapindaceae (11). Total stem biomass carbon was estimated at 21.6 Mg C (i.e. 45.2 Mg C ha^{-1}), which is within the range reported for tropical forest in Sabah, Borneo (20-120 Mg C ha^{-1}, including degraded forest) (Asner et al., 2018). The six subplots selected for measurement of soil CO_2 efflux were representative of the twelve subplots overall (compare Fig. 1 and Fig. S2). However, the dominance of particular groups varied within the six subplots. For example, Dipterocarpaceae comprised 30% of total biomass in subplot 14, 56% in subplot 15 and 36% in subplot 21; while the Euphorbiaceae comprised 8% of total biomass in subplot 22, the Moraceae comprised 62% of total biomass in subplot 14 and the Urticaceae comprised 9% and 6% of total biomass in subplot 22 and 24, respectively.

2.2 Girdling experimental design

All trees in the study area with d.b.h. (stem diameter at breast height, i.e. 1.3 m above ground level) ≥2 cm were girdled during January/February 2016, and trees ≥10 cm d.b.h (n = 209) were then regularly monitored for up to one year post-girdling. Girdling was performed by removing a strip of bark (approximately 6 cm wide and 0.5 cm deep) including the cambium, phloem and periderm from around the trunk (see Fig. S1), at approximately 1.2 m height. All trees in the study area were effectively girdled. For very large trees with buttress roots, girdling was performed just above protruding buttresses if they were present. All other vegetation was cut back and removed from the plot, including herbaceous plants, grasses and saplings that were too small to be girdled. In addition, to eliminate edge-effects of roots growing into the girdled plot, around which there was a 10 m boundary where vegetation was similarly girdled or cut-back. Given the large effort and time required to girdle the subplots, they were girdled in three equal swathes of 4 subplots, every 4-days between 28/1/2016 and 5/2/2016 (each swathe containing one monitored subplot-pair: 14 and 15; 21 and 22; 24 and 25). For the year following girdling, any cambium regrowth and resprouts below the girdle were removed.

2.3 Measurements

Taxonomic identity, d.b.h. and height of all trees ≥10 cm d.b.h. within the twelve subplots were determined during the month prior to girdling. We also mapped the spatial positions of the stems and their horizonal crown projections (crown areas) using the Field-Map technology (IFER, Ltd., Jílové u Prahy, Czech Republic; Hedl et al. (2009)). Following girdling, tree mortality was determined by the absence of a visible canopy and by carefully scratching a small section of the outer bark of the defoliated trees to examine the cambium layer, both above and below the girdle, assessed in 18 inventories distributed throughout the following year (376 days). Species level functional traits including wood density was compiled by reference to the Global Wood Density Database, complemented with local datasets. Where available species level information was used, however if not available then genus level averages from SE Asia were substituted. In the case of trees that could not be identified beyond family (n = 5) or genus (n = 19), then family or genus level averages from the rest of the research plot were used while for five trees for which there was no definitive botanical identification then the plot average (0.51 g cm^{-3}) was used.

Soil CO_2 efflux was measured four days prior to and during the first 65 days following girdling in six subplots (in three swathes across subplot pairs 14 and 15; 21 and 22; 24 and 25) within the girdled forest plot (Fig. S1). Each subplot had four systematically distributed soil respiration measurement points (soil respiration collars), approximately 15 m apart and located > 2 m from large stems. Therefore, soil CO_2 efflux measurements represented the average value by subplot without major influence due to proximity to individual stems (in a study of root respiration gradients we found increased soil CO_2 efflux < 2 m from stems for certain species; see supporting information). We carried out staggered sampling to match the staggered girdling process: continuous hourly measurements for a 4-day period were collected in a subplot pair per swathe before rotating to the next subplot pair. For example, following pre-girdle measurements for all subplots, all large stems were girdled (within a 12-hour period) in subplot 14 and 15 and soil CO_2 efflux was continuously measured for the following 4-days. After 4 days of measurements, subplots 21 and 22 were girdled and measurements performed; and so forth for subplots 24 and 25. Thus, continuous soil CO_2 efflux responses were measured in 4-day periods: pre-girdle (‘phase 1’, for 4 days prior to the girdling treatment) and post-girdle days 0 to 4, days 12 to 16, days 24 to 28 and days 49 to 53 (‘phases 2 to 5’). For subplots 24 and 25, due to logistical circumstances phase 5 occurred earlier (days 36 to 39) and we therefore included an additional set of later measurements (days 61 to 65). Because there was no change in soil CO_2 efflux between these two measurement periods (days 36 to 39 and 61 to 65), to represent ‘phase 5’ for subplots 24 and 25 we included all measurements > 36 days.

The initial response of soil CO_2 emissions following girdling is expected to be the result of reduced root-rhizosphere respiration, typically occurring within 7 to 60 days (Högberg et al., 2001). Therefore, to estimate root-rhizosphere respiration we compared the average soil CO_2 efflux during phase 1 (pre-treatment) with the efflux during phase 5, assuming that the decrease in CO_2 efflux during this period was attributable to decreased root-rhizosphere respiration because of halted supply of recent photosynthate. However, as dead roots decompose, soil CO_2 emissions can increase and obscure the reduction in emissions from halted root-rhizosphere respiration. We addressed this in our study by focussing on the first 40 to 60 days (Phase 5), although we would expect soil CO_2 emissions to increase over longer-time scales (i.e. >2 months) in subplots with high mortality as dead roots decompose. For example, an experiment in old-growth forest in Sarawak found about 20% mass loss during the first 4–5 months of root decomposition (Ohashi et al., 2019), which suggested negligible or very minor root decomposition rates within 2 months for our study. Soil CO_2 efflux was measured using a multiplexed (LI-8150) soil respiration system connecting eight soil chambers (8100-104C long-term chambers) to an infra-red gas analyser (IRGA Li-8100; LI-COR Biosciences, Nebraska, USA). Soil volumetric moisture and temperature were measured hourly at 0–10 cm soil depth using ECH2O EC-5 soil moisture probes and LI-COR soil temperature thermistors, integrated with the soil respiration system.

2.4 Calculations

Above-ground stem biomass was calculated using an allometric equation for moist tropical forests with d.b.h., height and wood density as inputs (Chave et al., 2005) and converted into carbon stock by assuming a wood C content of 47.7% (Martin and Thomas, 2011); consistent with Riutta et al., (2018).

To quantify the impact of girdling on soil CO_2 efflux, we used the slope parameter for the change in soil CO_2 efflux over time following girdling. To quantify the impact of girdling on tree mortality ('girdling impact') associated with each soil respiration collar, we used an index of tree biomass weighted by mortality:

$$GI = \sum \text{d.b.h.}_{\text{collar}} * M \qquad \text{(Eq. 1)}$$

where GI is girdling impact, $\text{d.b.h}_{\text{collar}}$ is the d.b.h. of stems within 10 m distance of the soil collar and M is the percentage tree mortality in the subplot where the collar is located, determined one year following girdling.

2.6 Statistical approaches

Tree mortality: To investigate the role of tree functional traits in determining the effect of girdling on tree mortality, we used non-parametric Kruskal-Wallis tests to determine whether tree death in the first year (376 days) after girdling was associated with tree identity within the dominant tree families (i.e. Dipterocarpaceae, Urticaceae, Euphorbiaceae, Malvaceae, Fagaceae, Sapindaceae), crown area, stem diameter, previous year's d.b.h. growth increment (cm year^{-1}) or wood density. We selected these traits because we predicted they will reflect the size of belowground C allocation and sensitivity to mortality by girdling, by representing growth rate (previous year's growth in DBH, wood density), biomass (stem diameter) and leaf area index and C uptake (crown area). To further investigate the impact of noted traits (i.e. wood density and either Dipterocarpaceae or Fagaceae identity, see results), we applied Cox proportional hazards regressions modelling in the R packages "*survival*" (Therneau, 2020) and "*survminer*" (Kassambara et al., 2020). We initially considered the impact of wood density and Dipterocarpaceae or Fagaceae identity as univariate factors and then, subsequently, in a multivariate analysis, to calculate hazard ratios associated with these factors.

Girdling effects on soil CO_2 efflux: To investigate the effect of girdling on soil CO_2 efflux we used linear models (soil CO_2 efflux vs. time following girdling) for all subplots together and for individual subplots. To test for responses across different spatial scales, we performed the analyses using the mean soil CO_2 efflux per day by subplot and by individual sampling points (i.e. including within-subplot variation, four replicates). To further understand the influence of other environmental factors (i.e. soil temperature and soil moisture) on soil CO_2 efflux, we used mixed modelling with fixed effects (time following girdling, soil temperature and soil moisture) and with space (subplot identity or position within the subplot) as a random effect. We performed the mixed-model analyses for all subplots together (including subplot identity as a random spatial effect) and for individual subplots (including soil collar location as a random spatial effect).

Above-belowground linkages: To investigate the effect of aboveground tree community on the soil CO_2 efflux change following girdling, the tree community properties (see below) were determined for the area within 10 m radius of each individual soil collar. We used this area around each collar to approximately account for belowground root projection for nearby species, given average crown projection and evidence that root respiration was greatest within <10 m of stem; Fig S7). This approach resulted in 4 soil collars x 6 subplots = 24 data points for analyses. To determine which aboveground properties best explained the effect of girdling on soil CO_2 efflux (slope parameter of soil CO_2 efflux change over time), linear mixed effects models were used. A random effect of 'space' was included (where space = 24 spatial observations). Thirteen fixed terms were used in the initial model, including tree characteristics (d.b.h., wood density, crown area and biomass), tree girdling responses (mortality after 1 year and a weighted mortality value of d.b.h.*mortality) and tree identity weighted by contribution to belowground C flux (estimated by calculating total crown area per subplot for each dominant species, grouped by family, Dipterocarpaceae, Urticaceae, Fagaceae and Rubiaceae; and given their abundance a further subset of Dipterocarpaceae grouped by genus: *Dryobalanops*, *Shorea*, *Parashorea*). To represent the influence of tree identity - weighted by the contribution to belowground C flux - on the effect of girdling on soil CO_2 efflux in the model, we used crown area (by family or genus), which approximately scales with leaf area (Doughty and Goulden, 2008, Fisher et al., 2007) and given evidence for a close allometric root-shoot relationship for tropical forest trees (Eshel and Grunzweig, 2013). All terms included in models are known to affect belowground carbon allocation and soil CO_2 efflux, and therefore may determine the overall effect of girdling on soil CO_2 efflux.

Mixed effect modelling approaches: Mixed effects models were fitted by restricted maximum likelihood, validated for normal distribution of residuals and homogeneity of variance. For all cases we began with full models and removed terms which improved the model fit, using Akaike Information Criterion (AIC) to guide model selection, with full and reduced models compared using AIC likelihood ratio tests to assess the statistical significance of individual fixed effects (Zuur et al., 2009). To avoid co-linearity, we used correlation matrices to identify pairs of correlated terms (greater than 0.6 or less than -0.6) and removed the least significant of the correlated pair from the model. For all analyses, where necessary we used log-transformed variables as model parameters. All statistical analyses were performed in R (version 4.0.2; R Core Team, 2021).

3. RESULTS

3.1 The effect of girdling on tree mortality

Girdling resulted in substantial mortality within 1 year, although the effects varied among different taxonomic families, with a disproportionate impact for the Dipterocarpaceae and Fagaceae. Of the 59 individuals within the Dipterocarpaceae, the most abundant family across the twelve experimental sub plots, 58 died in response to girdling, which represented over 99% of total biomass (Fig. 1 for mortality among families; see Fig. S3 for total mortality over time). Among the other abundant families, there was 100% mortality (by total biomass) within the Fagaceae, 82% mortality within the Euphorbiaceae, and 19% within the Malvaceae. For the subplots included in the soil CO_2 efflux study, there was 100% mortality within the Dipterocarpaceae, 96% mortality within the Fagaceae, 64% mortality within the Malvaceae and 16% within the Euphorbiaceae (Fig. S2). Interestingly, of the 209 girdled trees, a total of 79 (38%) continued to survive after 376 days. When using Kruskal-Wallis test to compare monitored trees that died and survived over 376 days of intensive monitoring we found that taxonomic identity of

Dipterocarpaceae (Chi squared = 45.4, df =1, P <0.001) and Fagaceae (Chi squared = 3.1, df =1, P = 0.078) were associated with mortality. However, we did not find any differences in the crown area between trees that died and survived (Chi squared = 186, df =185, *P* = 0.48), d.b.h. (Chi squared = 124, df =123, *p* = 0.47), or previous year's growth, a metric for pre-girdling tree vitality (Chi squared =102, df=101, p=0.45). However, there was a significant difference between trees that died and survived for wood density (Chi squared = 118, df = 66, $P < 0.001$) with those that survived having on average a higher wood density (0.54 ± 0.10 g cm^{-3}) than those that died (0.50 ± 0.12 g cm^{-3}). Note that the average wood density for all large experimental trees was (0.51 ± 0.12 g cm^{-3}).

Cox proportional hazards regression modelling, which provides an estimate of the hazard ratio and its confidence interval when analysing time course survival data (Cox, 1972) was used to further explore predictors of mortality after girdling. An initial univariate analysis showed that while tree size (determined either by crown area or trunk diameter) had no influence on the risk of mortality (Table 1) both wood density and whether a tree was Dipterocarpaceae or Fagaceae (or neither) had a significant effect on an individual's hazard ratio (HR) ($P < 0.05$). Given the potential correlation between family identity and wood density, we further examined the influence of these two variables in concert, resulting in a highly significant model to predict tree survival (Likelihood ratio test 84.16, 2 d.f., $P < 0.001$). For the multivariate analysis we found a significantly ($P = 0.05$) negative regression coefficient for wood density with an HR of 0.998, indicating that for every increase of 1 mg cm^{-3} in wood density there was a reduction in the hazard of mortality by 0.002% (note the model was applied using wood density in units of mg cm^{-3} to aid interpretation). Conversely, while holding wood density constant we found a highly significant ($P < 0.001$) positive regression coefficient for being Dipterocarpaceae or Fagaceae (i.e. an increased hazard or mortality) with a substantial increase in the Hazard Ratio of 7.99 (799%) increase in risk relative to other taxa (Table 1, Fig. 2); this was exemplified by the modelled median survival probability for a Dipterocarpaceae or Fagaceae individual of 200 days compared to 372 days across all other families (Fig. 2, using plot average wood density; see Fig. S4 for wood density distribution among species).

3.2 The effect of girdling on soil CO_2 efflux

In the two months following girdling the soil CO_2 efflux decreased (Figs. 3, 4). Although there was a decrease for all six of the measured subplots (negative coefficient soil CO_2 efflux change with time for all subplots; Table S1), there was large variation in the response and rate of decrease among subplots. The decrease in soil CO_2 efflux following girdling was significant in half of the subplots (14, 15 and 21) but there were either no effects or only marginal effects in the other half (no effect subplots 22 and 24; marginal effect subplot 25) (Fig. 3). See Table S1 for model outputs including subplot-average response by day (DF = 23) and including within-subplot spatial variation (DF = 98–118).

Based on the girdling effect on soil CO_2 efflux over 60 days and comparing the average soil CO_2 efflux during phase 1 (pre-girdling) and phase 5 (>40 days after girdling) (see Fig. 4), estimates of root-rhizosphere respiration varied by subplot: from a reduction of 28.8% of the pre-girdling value (P14; 5.69 to 4.09 μmol CO_2 m^{-2} s^{-1}, average fluxes during phase 1 and 5, respectively), 44.4% (P15; 5.61 to 3.14 μmol CO_2 m^{-2} s^{-1}), 36.0% (P21; 5.68 to 3.63 μmol CO_2 m^{-2} s^{-1}), 11% (P22; 2.52 to 2.24 μmol CO_2 m^{-2} s^{-1}), to negligible (P24, P25; e.g. P25, 4.83 to 4.82 μmol CO_2 m^{-2} s^{-1}).

3.3 The effect of other environmental factors on soil CO_2 efflux

Soil temperature and moisture varied during the experimental period (Fig. 4, Fig. S5), with changes over time likely reflecting the onset of the 2016 El Niño event (Doughty et al., 2020). Soil temperature varied diurnally by approximately 2°C (Fig. 4) and mean values slightly increased during the 60-day measurement period by about 0.5–1°C (Fig. S5). Soil moisture did not vary diurnally (Fig. 4) but slightly decreased over time in subplots 21, 22, 25; increased in subplot 14 and was constant in subplots 15 and 25 (Fig. S5).

To assess whether the changes in soil temperature and moisture affected the soil CO_2 efflux we used mixed-effects models. Across all subplots there was a large influence of the girdling treatment on the soil CO_2 efflux (negative effect of time following girdling and decreased CO_2 efflux, $P < 0.001$), in addition to positive effects of temperature ($P < 0.001$) and soil moisture ($P < 0.001$), together suggesting temperature-stimulation of respiration and moisture limitation of respiration (Table 2A). The relative importance of girdling, soil temperature and moisture in explaining patterns in soil CO_2 efflux varied among subplots (Table 2B). For subplot 15, girdling was the only effect ($P < 0.001$), suggesting a dominant influence of halted supply of photosynthates in influencing in soil CO_2 emissions for this subplot, which over-rode any other environmental driver. For subplots 14, 21 and 25, there were effects of girdling (negative effect, $P < 0.001$), temperature (negative effect, $P < 0.001$), soil moisture (negative effect, $P < 0.001$) and space (soil collar location, $P < 0.001$). For subplot 22, soil moisture was the dominant effect (positive effect, $P < 0.001$), although there were also significant effects of girdling (negative effect, $P < 0.05$) and temperature (positive effect, $P < 0.05$). Similarly, soil temperature and moisture were more important in explaining soil CO_2 emissions for subplot 24 (temperature, moisture and space, $P < 0.001$), with a minor influence of girdling (negative effect, $P < 0.05$).

Further analyses of the polynomial relationships with soil CO_2 efflux showed a negligible effect of temperature and a moderate positive effect of soil moisture with a parabolic increase to maximum at around ~0.3 m^3 H_2O m^{-3} soil, and most soil moisture values below this maximum (Fig. S6).

3.4 The effect of tree community properties on soil CO_2 efflux response following girdling

Tree community properties had a large effect on the rate and magnitude of the transfer of C allocated belowground and released as soil CO_2 efflux, and explained a significant portion of the variation (39%) in the change in soil CO_2 efflux over 60 days following girdling (Table 3). The most significant variable was the index of girdling on aboveground biomass mortality (mortality × sum of d.b.h.), and there were significant effects related to two specific tree genera: the sum of crown area for Dipterocarpaceae *(Dryobalanops* and *Shorea*); other tree families were not retained in the final model. There was also a significant effect of space (within subplot soil collar location), pointing to large spatial variation in the response of soil CO_2 efflux to girdling.

Given our above findings of: 1) high mortality among the Dipterocarpaceae; 2) significant effects of the presence (within 10 m) of Dipterocarpaceae *(Dryobalanops* and *Shorea)*, in explaining the decrease in soil CO_2 efflux following girdling; we further explored whether there was a direct relationship between root-rhizosphere respiration and the relative abundance of Dipterocarpaceae. The relationship was significant, with higher root-rhizosphere respiration (i.e. larger CO_2 efflux reduction following girdling) for plots with greater dominance of Dipterocarpaceae ($P = 0.018$, $R^2 = 0.79$; Fig. 5).

4. DISCUSSION

4.1 The effect of girdling on mortality

The substantial mortality following girdling (62% of total biomass after 1 year) is unsurprising as girdling halted the supply of photosynthates to roots. The physiological responses preceding mortality were shown in another study of the same experiment and included a reduction in the leaf carbon balance: reduced light-saturated photosynthesis and increased dark respiration during the 50 days preceding death (Doughty et al., 2020). Results from this first whole-stand tropical forest girdling study contrast with studies of single-species of tropical trees, which found lower impacts on mortality (Nottingham et al., 2010, Binkley et al., 2006) likely because carbohydrate reserves maintained metabolic activity during cambium growth (Aubrey and Teskey, 2018). The high rate of mortality in our study may be related to the continuous removal of any cambium re-growth (see methods), although the mechanism by which the 38% biomass that survived one year following girdling requires further investigation. Our hypothesis of a greater effect of girdling on mortality for species with higher growth rates was supported but the effect was small (0.002% increased risk of mortality for every decrease of 1 mg cm^{-3} in wood density, assuming a relationship between growth and wood density as shown elsewhere (Santiago et al., 2004); Table 1). In contrast, we found a large and unexpected result associated with tree species identity, with a 799% increased risk of mortality for the Dipterocarpaceae or Fagaceae, for which there was 99% and 100% mortality following girdling respectively (Table 1; Figs. 1, 2). Thus, we propose that the high sensitivity of the Dipterocarpaceae or Fagaceae to girdling is related to taxon-specific traits that govern the supply and demand of photosynthate C from above to belowground.

4.2 The effect of girdling on soil CO_2 efflux

Considerable spatial variability was observed in the effect on soil respiration rates of halted supply of photosynthate by girdling (Fig. 3), which we hypothesise was attributable to taxon-specific differences in photosynthate use by roots. Root-rhizosphere respiration, defined by the decrease in total soil CO_2 efflux by 29–44% (36 ± 5%; mean ± 1 standard error) in the three subplots that were strongly affected by girdling, overlaps the range of estimates of root-rhizosphere respiration from different tropical forests (34–70%) (Nottingham et al., 2010, Metcalfe et al., 2007, Sayer and Tanner, 2010, Girardin et al., 2014, Li et al., 2004, Hanpattanakit et al., 2015), including a dipterocarp forest in Thailand (34 ± 4%) (Hanpattanakit et al., 2015). However, soil CO_2 efflux was largely unaffected by girdling in half of the subplots, indicating a weaker coupling of photosynthesis and root-rhizosphere respiration. For these generally unresponsive subplots, root-respiration may have been maintained if the trees had large belowground carbohydrate reserves (Aubrey and Teskey, 2018), which is consistent with the lower observed tree mortality rates for these subplots. The mechanism by which root-rhizosphere respiration was apparently unaffected by girdling for these subplots requires further investigation, including study of the presence and dynamics of non-structural carbohydrate stores within plant tissues. Overall, the high spatial variability in the effect of girdling on soil CO_2 efflux points towards diverse physiological responses to girdling and allocation of C to roots and root-rhizosphere microorganisms by different tree species. This result has important implications for the quantification and generalisation of tropical forest NPP and GPP (Doughty et al., 2018), pointing towards large spatial variation in C allocation where belowground C-transfer may differ with tree community composition.

The spatially heterogenous response of soil CO_2 efflux to girdling among our subplots of varying tree community composition (ranging from negligible response to a 44% reduction; Fig. 3) contrasts with the lower spatial variation found in previous studies, performed across a range of low-diversity or monodominant forests. In a boreal forest in Sweden, girdling led to a broad-based reduction in soil CO_2 efflux, which was attributed to a reduced photosynthetic contribution to root and ectomycorrhizal (EM) fungal respiration (Högberg et al., 2001). The reduction in soil CO_2 efflux for this boreal forest, dominated by a single species (*Pinus sylvestris*), was 54% in two months and with only small spatial variation (Högberg et al., 2001); in comparison the soil CO_2 efflux decrease in our study for the subplot with greatest dominance of Dipterocarpaceae was 44% (P15, where dipterocarps represented 56% of total biomass; Fig. 3). In another high-latitude forest dominated by a single species (*Castanea sativa*), girdling 104 tree stems reduced soil CO_2 efflux by an average of 22% over 20 days, with low spatial variation (Frey et al., 2006). In both of these non-tropical studies, girdling also resulted in reduced root starch concentrations, supporting the conclusion that root respiration decreased in response to reduced replenishment of carbohydrate via photosynthate supply (Högberg et al., 2001, Frey et al., 2006).

Tropical tree girdling experiments have only been performed in single species plantations, with no studies performed in hyper-diverse tropical forest. For subtropical plantations in China, girdling reduced soil CO_2 efflux by 27% in *Acacia crassicarpa* and by only 14% in *Eucalyptus urophylla,* with the major decline within the first two months following girdling (Chen et al., 2010). For a tropical stand of *Eucalyptus grandis* × *urophylla* in Brazil, girdling reduced root respiration by 16 to 24% (after three months), and this relatively small effect was explained by large root non-structural carbohydrate reserves, which kept roots alive and maintained root respiration after the girdling treatment (Binkley et al., 2006). Similarly, in another study where potted tropical trees (*Pseudobombax septenata*) were girdled, little change in root respiration was observed, explained by maintenance of root respiration from carbohydrate reserves from within large root systems (Nottingham et al., 2010). Indeed, the mobilisation of stored root carbohydrates has been shown to maintain root respiration for up to 14 months following girdling in a temperate pine forest (Aubrey and Teskey, 2018) - a likely mechanism for the weaker coupling of photosynthesis and root-rhizosphere respiration for the non-responding plots in our study (see plots P22, P24; Fig. 3). Thus, the high variation in girdling responses among these studies of largely monodominant forest stands (Chen et al., 2010, Högberg et al., 2001, Binkley et al., 2006, Aubrey and Teskey, 2018) is consistent with our overall finding: girdling a diverse stand of tropical trees results in significant, but highly spatially variable, decrease in soil CO_2 emissions.

4.3 Linking the response of soil CO_2 efflux tree community properties

By analysing the spatial variation of girdling effects on soil CO_2 efflux, we were able to identify the tree community properties associated with the rate and magnitude of the coupling between photosynthesis, belowground C allocation and soil CO_2 release. First, girdling had the greatest impact on soil CO_2 efflux where tree mortality (weighted by biomass) was greatest (Table 3), indicating that the reduction in soil CO_2 efflux was the direct result of reduced belowground C allocation and root-rhizosphere respiration. Subsequently, our finding that the change in soil CO_2 was affected by the presence of Dipterocarpaceae (genera *Dryobalanops* and *Shorea*; Table 3), which also had increased soil CO_2 emissions with increased proximity to the trunk (in additional test data, Fig. S7), indicated a large influence of the presence of dipterocarps on the magnitude and rate of photosynthetic C allocation belowground. The relationship between Dipterocarpaceae presence and the change in soil CO_2 emissions following girdling was further confirmed by the high mortality rates for girdled dipterocarps; whether or not a tree was in the Dipterocarpaceae or Fagaceae, alongside having lower wood density, was the major determinant for tree mortality (Table 1). Indeed, the relative abundance of dipterocarps was strongly correlated with the magnitude of root-rhizosphere respiration, as estimated by girdling (Fig. 5). Unlike the Dipterocarpaceae, the Fagaceae did not strongly influence the impact of girdling on in soil CO_2 emissions but this may be due to the greater abundance and biomass of Dipterocarpaceae relative to the Fagaceae in the study area (Fig. 1; Fig S2).

Why might the dipterocarps be associated with such large belowground C allocation and release as soil CO_2 emission? We suggest that the relationship between the abundance of dipterocarps and girdling effect on soil CO_2 emissions can be explained by the strong associations Dipterocarpaceae (and Fagaceae) form with EM fungi (Tedersoo et al., 2010, McGuire et al., 2015, Smith et al., 2013, Maherali et al., 2016). Given these strong associations, EM fungi are abundant in tropical dipterocarp forests (Smith et al., 2013) and removal of Dipterocarpaceae results in a sharp decline in EM fungal biomass (McGuire et al., 2015). Indeed, a study of soil microbial communities in areas of logged dipterocarp forest found large declines in EM fungi abundance (Kerfahi et al., 2014), including in sites close to our experimental plots in Borneo, following logging and conversion to oil palm plantation (Robinson et al., 2020). Consistent results have been shown in boreal forests, where halted belowground C supply imposed by girdling or root exclusion resulted in reduced EM fungal abundance (Lindahl et al., 2010, Yarwood et al., 2009). Ectomycorrhizal fungi have a hyphal network an order of magnitude greater than arbuscular mycorrhizal (AM) fungi and are rich in recalcitrant C compounds (Smith and Read, 1997, Tedersoo and Bahram, 2019). They are, therefore, a large belowground sink for C - and source of soil CO_2 efflux (Heinemeyer et al., 2007) - and their dead biomass can significantly contribute to the accumulation of soil organic matter (Clemmensen et al., 2013, Averill et al., 2014).

The high mortality among Dipterocarpaceae and Fagaceae may also reflect a lack of stored root-carbohydrate for these species, shown to be important in maintaining root respiration following girdling elsewhere (Aubrey and Teskey, 2018), which may be further related to high belowground carbon demand for EM fungi. Considering this likely large C allocation to EM fungi, we predict an increase in soil CO_2 efflux would eventually occur as dead roots and EM hyphal residues are decomposed in girdled plots (e.g. after 5 months under moist conditions, Ohashi et al. (2019)), but it is very unlikely this process began during the first two months in our experiment where soils were relatively dry (see below). Further evidence showing that EM fungi are also important in facilitating C transfer between plants (Pickles et al., 2017) is consistent with the high mortality for all EM-forming Dipterocarpaceae and Fagaceae in this study (100% mortality within 10 months). Together, these observations point towards high root-rhizosphere respiration for EM fungal dominated forests. Moreover, they suggest that a large portion of the decline in soil CO_2 efflux following girdling in our study was related to reduced respiration from Dipterocarpaceae-associated EM fungi.

4.4 Linking the response of soil CO_2 efflux to other environmental factors

In addition to the effect of time following girdling on soil CO_2 emissions, there were minor effects of moisture and temperature (Table 2), which can affect both heterotrophic and root-derived sources of respiration. This experiment was undertaken during the 2016 El Niño event and the onset of these drought conditions resulted in minor warming and drying (e.g. 0.5–1°C warming and 0–20% moisture decrease among subplots; Fig. S5). In addition, the drought event may have accelerated mortality (Doughty et al., 2020) and, subsequently, accelerated the decrease in root respiration following girdling.

Soil respiration rates followed the typical parabolic relationship with volumetric moisture content, but moisture levels during the study were slightly below the optimal value for respiration (~0.3 m^3 m^{-3}) (Rubio and Detto, 2017), suggesting some moisture limitation (Fig. S6). Indeed, soil moisture had a positive effect on CO_2 emissions (Table 2) and explained some of soil CO_2 efflux variation for 5 of the 6 subplots (Table 2B), although mortality following girdling was the dominant overall driver (Table 2A). For example, decreased soil CO_2 efflux in subplot 15 was not related to soil moisture (Table 2; girdling effect only), which did not change over time (Fig. S5). Soil drying may have been alleviated by the girdling treatment causing a reduction in tree water use (e.g. reduced root hydraulic conductance), thus contributing to little soil moisture change in following girdling for some plots, in spite of low rainfall (see subplots 15, 24; Fig. S5).

Temperature is positively related to soil microbial respiration across ambient temperature ranges (Davidson and Janssens, 2006, Bååth, 2018). The positive effect of temperature on CO_2 emissions in our data (Table 2), would have predominantly resulted from the large diurnal variation in temperature (by about 2–3°C; Fig. 4), rather than the smaller increase in temperature over time, likely a consequence of the strengthening El Niño event (by about 0.5–1°C; Fig. S5). We suggest that a large portion of the effect of temperature on soil CO_2 emissions was the result of variation in root-rhizosphere respiration, because the diurnal signal in soil CO_2 emission diminished following girdling (Fig. 4: compare phase 1 and phase 5). The temperature sensitivity of respiration for roots has been shown to be generally higher than for (microbial) heterotrophs (Boone et al., 1998, Li et al., 2020), although not in all studies (Tan et al., 2013), which may be related to variation in photosynthetic C supply among studies given the observation of very high temperature sensitivity of root-rhizosphere respiration during the peak growing season (Ruehr and Buchmann, 2010). Thus, for these forest plots affected by girdling (dominated by dipterocarp genera *Dryobalanops* and *Shorea),* root respiration – and recently fixed photosynthetic C – may have contributed a significant portion of the diurnal variation in soil CO_2 emissions.

Overall, the positive effects of soil moisture and temperature on soil CO_2 efflux do not influence our conclusions based on the response following girdling, which remained a dominant influence through its impact on tree mortality. This observation is consistent with findings from a recent study conducted at the same site before girdling took place, showing that substrate supply rather than the soil abiotic environment was the main determinant of soil CO_2 efflux (Riutta et al., 2021). Furthermore, in our study the minor positive influence of moisture and temperature on respiration may have offset its decrease following girdling, resulting in an underestimation of root-rhizosphere respiration.

4.5 Conclusion

Our study provides the first data from a whole-stand girdling study in tropical forest, showing the rate and magnitude of photosynthetic C transfer belowground and release as CO_2 from soils. Furthermore, our results show high spatial variation in the rate and magnitude of this transfer, which was correlated with diverse physiological responses among tree species. This result highlights the role of tree species composition in affecting belowground C transfer in tropical forests, with important implications for the quantification and generalisation of the tropical forest C balance (Doughty et al., 2018, Anderson-Teixeira et al., 2016, Muller-Landau et al., 2021). In particular, we found a strong coupling between photosynthetic C supply belowground and soil CO_2 efflux for the Dipterocarpaceae, in addition to greater mortality for the Dipterocarpaceae and Fagaceae, which we hypothesise can be explained by a decline in C allocation to EM fungal symbionts. These results also have major implications for the impact of forest degradation on the global C budget: by demonstrating that the logging of large dominant dipterocarp trees in natural tropical rainforest – a commercially valuable timber and the major target for logging in SE Asia (Fisher et al., 2011) – is associated with a large and rapid decline in belowground C transfer to roots and root-symbionts (e.g. the decrease in root-derived CO_2 emissions by 44%, Fig. 3; equivalent to a decline of ~9 Mg C ha^{-1} $year^{-1}$). Indeed, the observation of persistent soil organic matter loss over time for logged forest in Borneo (4.2 Mg C ha^{-1} $year^{-1}$) (Riutta et al., 2021) can be explained by the disruption of this large C allocation to root-associated organisms and their subsequent death and degradation. Overall, our findings highlight the implications of the diverse species composition of tropical forests in affecting the dynamics of belowground C transfer and its subsequent release to the atmosphere.

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Data availability statement:

All data are openly available in Zenodo, within the SAFE community data https://doi.org/10.5281/zenodo.5519572. Additional data for the girdling plot (SAF-05) are available here: https://doi.org/10.5281/zenodo.3266770.

Conflict of interest statement:

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author contribution statement:

YT, YM, PM, TR, ATN, AWC and CED conceived the study. ATN, AWC, TR, CED, ET, WHH, MS, JK and NM performed the study. ATN and AWC analysed the data. ATN wrote the paper with input from all authors.

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TABLE 1

Results of univariate Cox proportional hazards regression modelling of mortality in the first 376 days post-girdling event. Univariate variables tested individually before examining possible correlation via examination of multivariate influence of wood density (mg cm^{-3}) and family identity as Dipterocarpaceae or Fagaceae on the risk of mortality.

Variable	Coefficient	Hazard Ratio (HR)		P-value
		exp(coef)	se(coef)	
Univariate				
Dipterocarpaceae (0,1)	1.73	5.628	0.199	< 0.001
Fagaceae *(0,1)*	1.1048	3.0185	0.4591	0.039
Wood Density (mg cm^{-3})	-0.0030	0.997	0.001	< 0.001
Crown Area (m^2)	-0.0002	1.000	0.006	0.97
Diameter (cm)	0.0044	1.000	0.006	0.50
Multivariate				
Dipterocarpaceae or Fagacea (0,1)	2.08	7.99	0.257	< 0.001
Wood Density (mg cm^{-3})	-0.0024	0.998	0.0010	0.0176

TABLE 2. The determinants of soil CO_2 efflux variation with time. The determinants of soil CO_2 efflux include time following girdling, soil temperature and soil moisture. Mixed-effects models were fitted using maximum likelihood, by beginning with full model (4 variables, time following girdling, soil temperature, soil moisture as fixed effects and space as a random effect) and step-wise parameter removal. The final model was determined by lowest AIC value. The significance of fixed effects was determined by AIC likelihood ratio tests comparing the full model against the model without the specified term. The analyses were performed for all data (A: all subplots; where space = subplot identity, n = 6) and for individual subplots (B: P14, P15, P21, P22, P24, P25; where space = within-subplot sampling location, n = 4).

A) All subplots	Parameter	SE	*P*-value
Fixed effects			
Time (relative day to girdling)	-4.517e-03	2.905e-04	< 2e-16 ***
Soil temperature	6.153e-01	1.820e-01	0.000728 ***
Soil moisture	1.819e-01	4.261e-02	1.99e-05 ***
Random effects			
Space (subplot)	-3.695e-01	6.023e-01	0.539630
AIC value			11854.46
B) Individual subplots			
P14	Parameter	SE	*P*-value
Fixed effects			
Time (relative day to girdling)	-7.081e-03	4.199e-04	< 2e-16 ***
Soil temperature	3.646	0.323	< 2e-16 ***
Soil moisture	-3.289e-01	8.249e-02	7.05e-05 ***
Random effects			
Space (soil collar location)	-1.054e+01	1.088e+00	< 2e-16 ***
AIC value			703.43

P15	Parameter	SE	*P*-value
Fixed effects			
Time (relative day to girdling)	-8.091e-03	5.076e-04	<2e-16 ***
Soil temperature	4.758e-01	3.535e-01	0.179
Random effects			
Space (soil collar location)	-3.553e-01	1.145e+00	0.756
AIC value			503.19

P21	Parameter	SE	*P*-value
Fixed effects			
Time (relative day to girdling)	-6.723e-03	7.122e-04	< 2e-16 ***
Soil temperature	2.011	0.2818	1.54e-12 ***
Soil moisture	8.074e-01	9.529e-02	< 2e-16 ***
Random effects			
Space (soil collar location)	-3.898	0.9763	0.000104 ***
AIC value			1533.418

P22	Parameter	SE	*P*-value
Fixed effects			
Time (relative day to girdling)	-0.001870	0.000792	0.0184 *
Soil temperature	0.725352	0.367786	0.0489 *
Soil moisture	0.54594	0.085829	3.11e-10 ***
Random effects			
Space (soil collar location)	-0.687127	1.194184	0.5652
AIC value			803.3323

P24	Parameter	SE	*P*-value
Fixed effects			

Time (relative day to girdling)	-9.843e-04	5.014e-04	0.0498 *
Soil temperature	-1.940	0.4002	1.36e-06 ***
Soil moisture	1.165	8.627e-02	< 2e-16 ***
Random effects			
Space (soil collar location)	9.170	1.298	2.31e-12 ***
AIC value			2711.232
P25	Parameter	SE	*P*-value
Fixed effects			
Time (relative day to girdling)	-2.143e-03	5.649e-04	0.000156 ***
Soil temperature	-1.215	3.603e-01	0.000773 ***
Soil moisture	-4.946e-01	8.475e-02	6.93e-09 ***
Random effects			
Space (soil collar location)	4.960	1.248	0.000114 ***
AIC value			1429.011

TABLE 3. The effect of tree community properties on the response of soil CO_2 efflux to girdling. The soil CO_2 efflux response to girdling was determined using the slope parameter of soil CO_2 efflux change over 50 days following girdling (see Table S1). To represent tree mortality in the model we used a 'tree mortality index' (Σ DBH*mortality), where Σ DBH was determined for all trees within a 10 m radius around each soil CO_2 sampling point (soil collar, n = 24) and where mortality was the proportion of dead stems within each area one year after girding. Mixed-effects models were fitted using maximum likelihood, by beginning with full model (13 variables) and step-wise parameter removal. The final model was determined by lowest AIC value. The significance of fixed effects was determined by AIC likelihood ratio tests comparing the full model against the model without the specified term.

	Coefficient	SE	*P*-value
Fixed effects			

Tree mortality index	0.030983	0.008894	0.0019**
Dipterocarpaceae *Dryobalanops*	-0.013114	0.005064	0.01608 *
Dipterocarpaceae *Shorea*	0.013362	0.004302	0.00482 **
Random effects			
Space (soil collar location)	-0.150684	0. 0.047454	0.00408 **
AIC value			-100.5726

Thirteen fixed terms were used in the initial model, including tree properties (d.b.h., biomass, wood density and total crown area), tree girdling responses (mortality after 1 year and a weighted mortality value of d.b.h.*mortality) and tree community properties (crown area for each dominant species grouped by family, Dipterocarpaceae, Urticaceae, Fagaceae and Rubiaceae. We used a random effect of space (soil collar location).

FIGURE 1

Tree community biomass and mortality following girdling. Tree species are grouped by family. Data are for all twelve subplots (total area of 0.48 ha): summed above-ground tree biomass (kg C) with the total number of individuals is listed at the end of each bar. Dark green shading represents the proportion of individuals that died within one year of girdling. See Fig. S2 for the same data for the six subplots for which soil CO_2 efflux was measured.

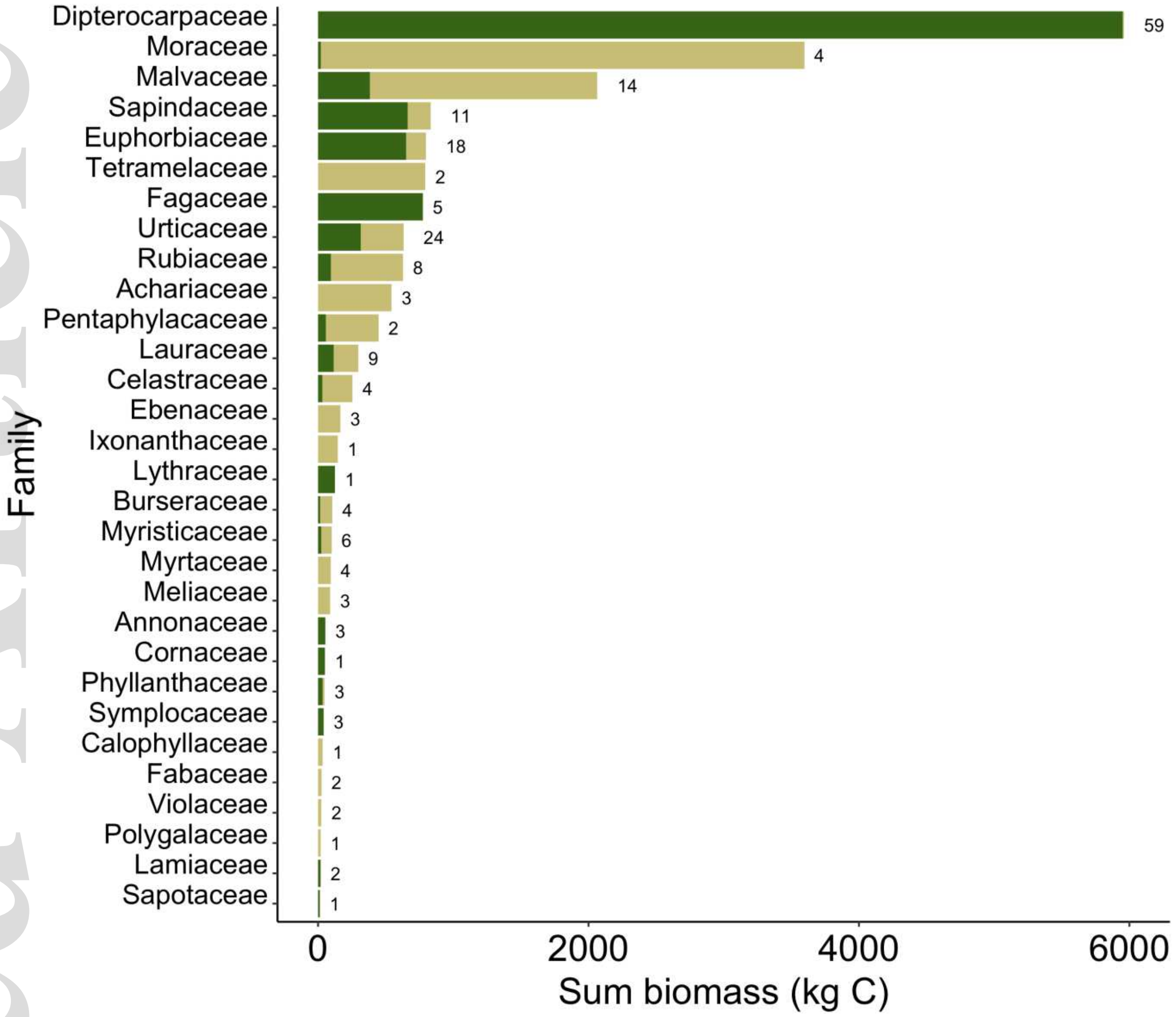


FIGURE 2

The modelled probability of tree survival over 376 days following girdling: (A) Including all tree species and (B) grouped by the families Dipterocarpaceae and Fagaceae versus others when assuming a plot-average for wood density, 0.52 g cm^{-3}. The probability of survival was determined for the 209 trees monitored 18 inventories using multivariate Cox proportional hazards regression modelling (see Table 1), examining the impact of wood density and family identity. See methods for further detail and information on how mortality was determined. We show that for every increase of 1 mg cm^{-3} in wood density there was a reduction in the hazard of mortality by a factor of 0.998 or 0.002%, while being Dipterocarpaceae or Fagaceae resulted in a substantial increase in the Hazard Ratio of 7.99, or 799%. For both plots the 95% confidence limits are shown.

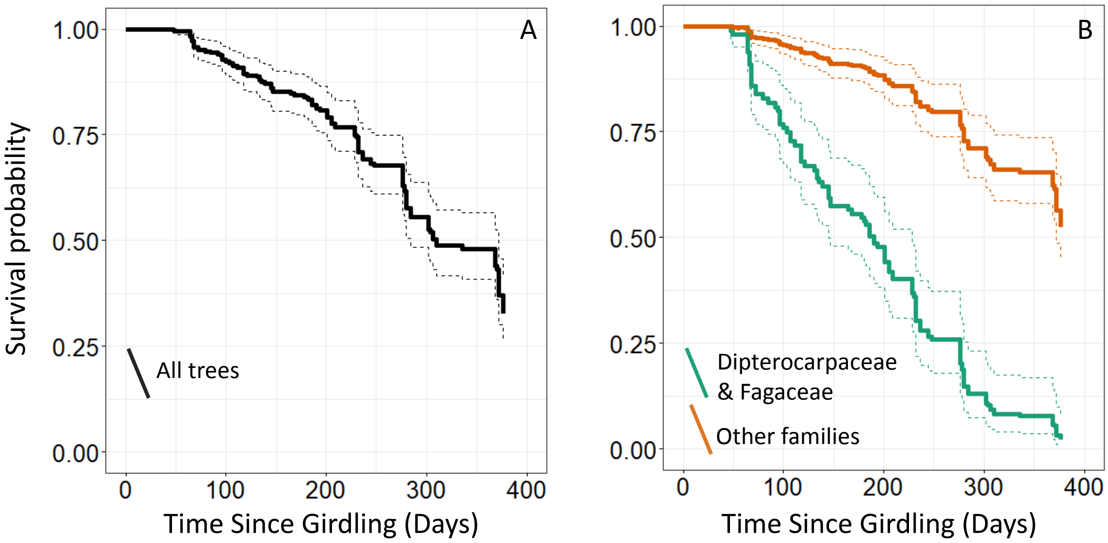


FIGURE 3

The average response of soil CO_2 efflux to girdling. Data points are daily averages for 12 diurnal measurements (soil CO_2 efflux measured every 2 hours for 24 hours) and for four spatial replicates for six subplots. Girdling occurred on day 0 (vertical stippled line) and measurements continued for up to 70 days following girdling. Subplot numbers are shown (P14, P15, P21, P22, P24, P25), including relative dominance of *Dipterocarpaceae* per subplot (% of total biomass). Significant relationships between CO_2 efflux and time are shown for 3 of the 6 plots (marginal effect in subplot 25). Linear model outputs are presented in Table S1. The results are supported by linear mixed models in Table 2, showing a dominant effect of time-following girdling for subplots 14-21, with greater effects of other environmental factors (temperature and moisture) for subplots 22-25.

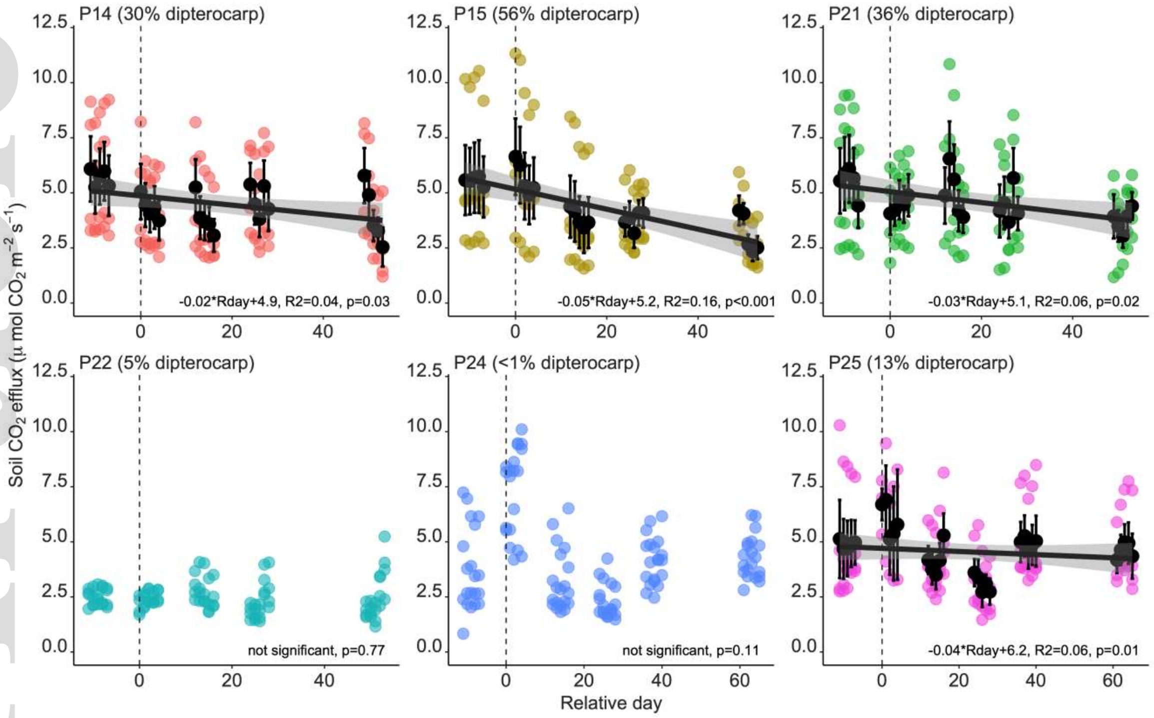


FIGURE 4

Soil CO_2 efflux, temperature and moisture over time following girdling. The figure shows the change in total soil CO_2 emissions over five four-day periods before and after the girdling treatment (A, subplot 14; B, subplot 15); and diurnal variation in soil temperature (C, subplot 15) and moisture (D, subplot 15) at 0-10cm depth. For average responses for all subplots, see Fig. 3 (soil CO_2 efflux) and Fig. S5 (temperature and moisture). Points are coloured dark yellow for measurements between 6:00 and 18:00 (day) and blue for between 18:00 and 6:00 (night). The mean trend line is shown in black with error bars representing one standard error of the mean (n = 4 per subplot). Time periods are phase 1 (pre-girdling; relative days -11 to -7) followed by phase 2 (relative days 0-4), phase 3 (relative days 12-16), phase 4 (relative days 24-28) and phase 5 (relative days 49-53). Average soil CO_2 emission before girdling (phase 1) was 5.69 and 5.61 µmol CO_2 m^{-2} s^{-1} for subplots 14 and 15, respectively, which decreased by 29% and 44%, to 4.09 and 3.14 µmol CO_2 m^{-2} s^{-1} after 49 days (phase 5).

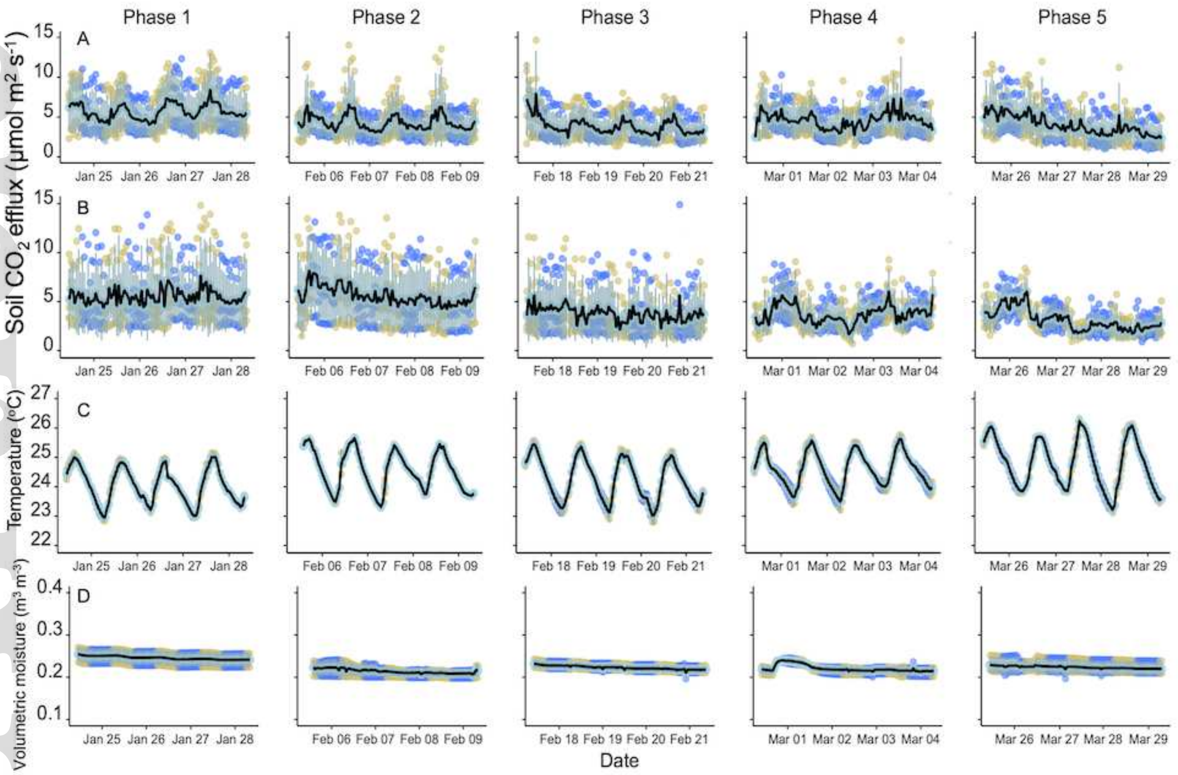
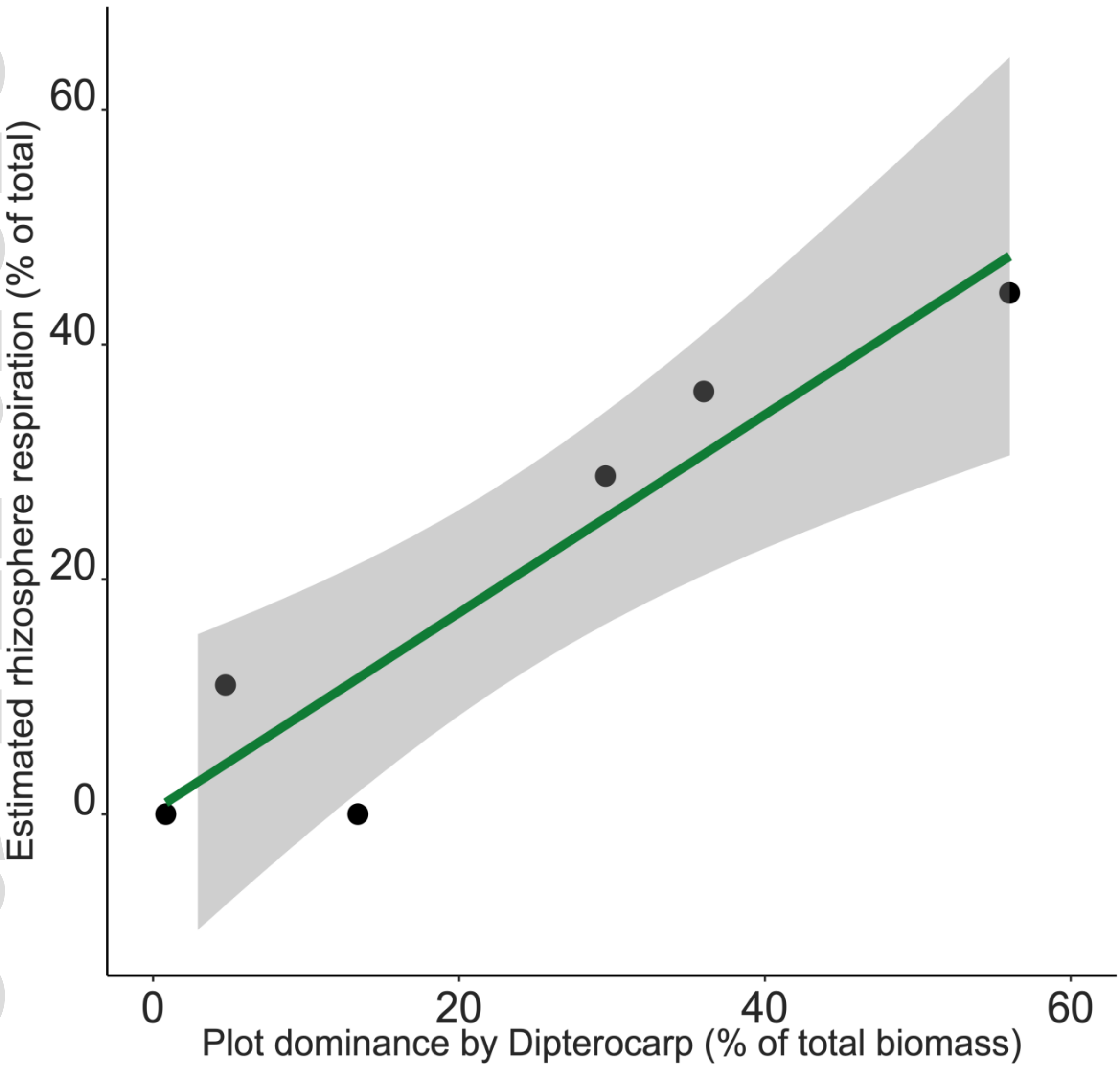


FIGURE 5

The relationship between root-rhizosphere respiration and the dominance of Dipterocarpaceae. Root-rhizosphere respiration was calculated according to the difference (reduction) in soil CO_2 efflux before girdling and 40-60 days following girdling, and is expressed at % of total soil CO_2 efflux. Points represent subplots. ($y = 0.84x + 0.3$; F = 27.3, DF = 4, p = 0.006, R^2 = 0.84).


Estimated rhizosphere respiration (% of total)
60
40
20
0
0
20
40
60
Plot dominance by Dipterocarp (% of total biomass)