Carbon flux and forest dynamics: increased deadwood decomposition in tropical rainforest tree-fall gaps

Running title: Faster deadwood decay in canopy gaps

Authors: H. M. Griffiths[1], P. Eggleton[2], N. Hemming-Schroeder[3], T. Swinfield[4,5], J. S. Woon[1, 2], S. D. Allison[3,6], D.A. Coomes[4], L. A. Ashton[7] & C. L. Parr[1,8,9]

Affiliations

[1] School of Environmental Sciences, University of Liverpool, Liverpool, L69 3GP, UK

[2] Department of Life Sciences, Natural History Museum, London, UK

[3] Department of Earth System Science, University of California, Irvine, CA 92697, USA

[4] Department of Plant Sciences, University of Cambridge Conservation Research Institute, Pembroke Street, Cambridge, CB2 3QZ, UK

[5] Centre for Conservation Science, Royal Society for the Protection of Birds, David Attenborough Building, Pembroke Street, Cambridge, CB2, 3QZ, UK

[6] Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697, USA

[7] School of Biological Sciences, The University of Hong Kong, Hong Kong SAR, China

[8] Department of Zoology & Entomology, University of Pretoria, Pretoria, South Africa

[9] School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits, South Africa

Hannah Griffiths ORCID: 0000-0002-4800-8031

Contact information

Email: Hannah.griffiths@liverpool.ac.uk; Tel: *+44 151 794 2000*

Abstract

Tree mortality rates are increasing within tropical rainforests as a result of global environmental change. When trees die, gaps are created in forest canopies and carbon is transferred from the living to deadwood pools. However, little is known about the effect of tree-fall canopy gaps on the activity of decomposer communities and the rate of deadwood decay in forests. This means that the accuracy of regional and global carbon budgets is uncertain, especially given ongoing changes to the structure of rainforest ecosystems. Therefore, to determine the effect of canopy openings on wood decay rates and regional carbon flux, we carried out the first assessment of deadwood mass loss within canopy gaps in old-growth rainforest. We used replicated canopy gaps paired with closed canopy sites in combination with macroinvertebrate accessible and inaccessible woodblocks to experimentally partition the relative contribution of microbes versus termites to decomposition within contrasting understory conditions. We show that over a 12-month period, wood mass loss increased by 63% in canopy gaps compared with closed canopy sites and that this increase was driven by termites. Using LiDAR data to quantify the proportion of canopy openings in the study region, we modelled the effect of observed changes in decomposition within gaps on regional carbon flux. Overall, we estimate that this accelerated decomposition increases regional wood decay rate by up to 18.2%, corresponding to a flux increase of 0.27 Mg C ha^{-1} yr^{-1} that is not currently accounted for in regional carbon budgets. These results provide the first insights into how small-scale disturbances in rainforests can generate

hotspots for decomposer activity and carbon fluxes. In doing so, we show that including canopy gap dynamics and their impacts on wood decomposition in forest ecosystems could help improve the predictive accuracy of the carbon cycle in land surface models.

Key words

Termites; Invertebrates; Carbon cycling; Carbon modelling; Canopy gap; Tree mortality; Disturbance; Global change

Introduction

Uncertainty in the behaviour of the carbon cycle is one of the biggest limiting factors in accurately predicting Earth's temperature into the 21st century (Bodman, Rayner, & Karoly, 2013). Tropical forests hold over half of global forest carbon stocks (471 ± 93 PgC), 56% of which is stored in biomass, and sequester 1.2 ± 0.4 PgC annually (Pan et al., 2011). Recent work has highlighted how human pressures affect rainforest carbon stocks in living and dead biomass, showing that selective logging and degradation increase the proportion of deadwood stocks relative to living biomass in African and Asian rainforests (Carlson, Koerner, Medjibe, White, & Poulsen, 2017; Pfeifer et al., 2015).

Decomposition is the process by which the carbon in dead plant material is assimilated into soil carbon stores, lost through leaching or released as CO_2 into the atmosphere through respiration (Cornwell et al., 2009; Swift, 1977). Yet, despite the fact that decomposition has far reaching implications for global carbon budgets (Hubau et al., 2020), it remains poorly understood compared with other key ecosystem processes such as primary production (Harmon, Bond-Lamberty, Tang, & Vargas, 2011). Furthermore, what is known about the factors controlling deadwood decay is geographically biased towards temperate regions, with tropical forest decomposition studies representing just 14% of the published literature (Harmon et al., 2020). This bias means we lack a basic understanding of

the factors that mediate the rate and fate of carbon turnover through globally important deadwood stocks in tropical rainforests.

The effect of canopy openness represents an important source of uncertainty in our understanding of the factors that affect the decomposition of deadwood in forests (Harmon et al., 2020). This is a major gap in understanding given that tree mortality rates are rising in humid tropical forests (McDowell et al., 2018) as a result of increases in the frequency and severity of hurricanes and drought (Cai et al., 2014); continued selective logging and degradation (Baccini et al., 2017); and increases in biotic agents of tree death (liana load, insect outbreaks and disease; Allen, Breshears & McDowell 2015). Consequently, it is likely that the size and frequency of rainforest canopy gaps are increasing, along with concurrent changes in the volume and spatial distribution of deadwood stocks (Carlson et al., 2017; Pfeifer et al., 2015). However, because our knowledge of the effect of canopy gaps on deadwood decay rates is currently limited to just two studies in temperate and boreal forests (Janisch, Harmon, Chen, Fasth, & Sexton, 2005; Shorohova & Kapitsa, 2014), we lack an empirical evidence base from which to predict the consequences of ongoing changes to the structure of tropical rainforests for decomposition and carbon flux. Data shortages such as these limit the capacity to resolve carbon budget imbalances because information on how land-surface heterogeneity can affect carbon-cycling and land-atmosphere interactions is a key area of uncertainty in Earth system models (Lawrence *et al.* 2019). Therefore, there is a clear need to

111 improve our mechanistic understanding of the drivers of change in
112 rainforest carbon budgets and thus increase the accuracy and predictive
113 power of the land surface models included in Earth system models.
114
115 There is mounting evidence that termites along with microbes are the
116 major agents of deadwood decomposition in rainforest ecosystems (da
117 Costa, Hu, Li, & Poulsen, 2019; Griffiths, Ashton, Evans, Parr, & Eggleton,
118 2019; Liu et al., 2015). It is possible that treefall canopy gaps could
119 negatively or positively affect the activity of both groups. Habitat
120 disturbance and degradation reduces termite abundance and diversity
121 (Dibog, Eggleton, Norgrove, Bignell, & Hauser, 1999; Eggleton et al.,
122 1995; Ewers et al., 2015; Luke, Fayle, Eggleton, Turner, & Davies, 2014;
123 Tuma et al., 2019) while microbial-mediated nutrient mineralisation rates
124 decline in response to drought (Yavitt, Wright, & Wieder, 2004). Changes
125 to the structure of forests caused by removal of trees during selective
126 logging has been reported to increase microclimate heterogeneity and
127 create hotter and drier conditions in the forest understory (Blonder et al.,
128 2018; Hardwick et al., 2015). Therefore, the changes in understory
129 conditions caused by openings in the canopy when a tree dies could have
130 major negative effects on both termite and microbial mediated
131 decomposition. If this is the case, we expect decay rates to slow in canopy
132 gaps as result of disturbance and unfavourable microclimatic conditions
133 for the decomposer community. However, an alternative possibility is that
134 the high concentration of foraging resource (i.e. dead plant matter) in
135 canopy gaps, that result from tree death, may positively affect

136 decomposition processes by attracting termites and/or stimulating a
137 positive priming effect within the microbial community (e.g. Lyu et al.,
138 2018). Under this scenario, we expect to see an increase in decay rates in
139 canopy gaps in response to elevated resource availability where a tree
140 has fallen.
141
142 The overarching aim of this investigation was to determine if deadwood
143 decay rates differ in canopy gaps compared with closed canopy sites in
144 tropical rainforest. Additionally, we partitioned the relative contribution of
145 microbes and termites in driving deadwood mass loss in canopy openings
146 and estimated the effect of any changes in decomposition rates within
147 canopy gaps on regional carbon flux. To achieve this aim, we used
148 macroinvertebrate-accessible and inaccessible woodblocks placed within
149 tree fall canopy gaps and closed canopy sites in an old growth rainforest
150 in Malaysian Borneo. Furthermore, we assessed the termite community
151 composition and soil microclimatic conditions within experimental sites
152 and estimated the volume of deadwood associated with canopy gaps
153 compared with closed canopy sites. This unique experimental design
154 allowed us to the test alternative hypotheses that deadwood
155 decomposition in canopy gaps could either: 1) decelerate due to a
156 negative effect of disturbance and a hotter, drier microclimate (e.g.
157 Blonder *et al.* 2018) leading to a reduction in the activity of the
158 decomposer community, or 2) accelerate in response to an influx of dead
159 plant material attracting termite foraging activity and/or stimulating a
160 microbial priming effect (e.g. Lyu *et al.* 2018). To scale up our results and

place them in a regional context, we used remote sensing (LiDAR) data to quantify the proportion of canopy openings in the study region and modelled the effect of observed changes in decomposition within gaps on regional carbon flux.

Materials and methods

Study site and gap selection

This study was carried out within an area of lowland, old growth dipterocarp rainforest in the Maliau Basin Conservation Area, Sabah, Malaysia (4° 44' 35" to 55" N and 116° 58' 10" to 30" E; mean annual rainfall 2838 mm ± 93 mm). On the 20th of July 2017, there was a storm at the study site, which generated winds speeds of 8.4 m/s (Fig. S1). These were among the strongest winds normally experienced in inland forests of the region, which placed extreme sheer stress on trees (Jackson et al., 2020). Consequently, a large number of trees fell within the same 24-hour period in the study location. Ten tree-fall gaps (mean length: 32 m ± 2.8, mean width: 24.5 m ± 3; see table S1 for gap characteristics) created during this event were selected for use in this investigation, along with ten adjacent closed canopy sites, located 20 m from the edge of each gap. We took 10 hemispherical photos in each gap and closed canopy sites to quantity canopy openness at each location (see below).

Decomposition assay

In October 2017, we established a wood decomposition assay. Using a termite suppression experiment combined with macroinvertebrate

accessible and inaccessible mesh bags, Griffiths *et al.* (2019) demonstrated that non-termite macroinvertebrates did not contribute significantly to the decomposition of a standardised wood substrate, *Pinus radiata* blocks*,* at this site. Therefore, to assess the rate of decomposition within these paired gap and closed canopy sites and determine the relative contributions of termites versus microbes to the process, we used the same assay of mass loss from untreated *P. radiata* wood within macroinvertebrate accessible and inaccessible bags. Wood blocks (9 x 9 x 5 cm, 161.2 ± 1.3 g; wood density of 0.40 g cm^{-3} [Zanne et al., 2009]; wood C:N ratio of 462 ± 48 [Ganjegunte, Condron, Clinton, Davis, & Mahieu, 2004]) were dried at 60 ºC until they reached a constant weight and placed inside “open” (accessible to macroinvertebrates, principally termites, and microbes), or “closed” (accessible to microbes only) bags, which were all made with 300 micron nylon mesh (Plastok™, Merseyside, UK). The open woodblocks had ten 1 cm holes cut into the top and bottom of the bags to avoid confounding effects of using mesh of different sizes in decomposition assays (Stoklosa et al., 2016). The edges of the closed bags were folded several times and sealed with staples to prevent access by invertebrates. In each gap and closed canopy site, we ran a 50-m transect and randomly placed 5 open and 5 closed wood blocks 5 m apart along the transect (n = 10 per site; n = 200 woodblocks in total: 10 x forest sites x 2 canopy treatments [closed canopy or gap] x 2 mesh treatments [open or closed] x 5 replicates). Because the gaps were irregular in shape (Appendix table S1), we placed the transects along the longest axis of each gap. In all but one of the gap sites, we were unable to

establish a 50 m transect, therefore, we placed an additional line perpendicular to the first, ensuring that each block was always at least 5 m apart from its nearest neighbouring block (Fig. 1).

A hemispherical photograph was taken by placing an iPhone 6 with a fisheye lens attachment directly on top of each wood block. Photographs were analysed using the function *Hemiplot* in R to calculate canopy openness, which was twice as high within the gaps compared with closed canopy sites ($t = 9.67$, $P < 0.001$, mean openness in gap sites = 0.24 ± 0.03; mean openness in closed canopy sites = 0.12 ± 0.02; Fig. S2). When placing the woodblocks, the top layer of leaf litter was removed, and the blocks were put directly on the humus layer. Wood blocks were left on the forest floor for 12 months (October 2017 to October 2018), after which they were collected and dried at 60 ºC until they reached a constant weight. Once dried, wood material was separated from termite soil. The remaining deadwood and termite material (carton and soil) was then re-weighed separately to calculate the proportion of mass loss from each block and the mass of soil brought into the mesh bags by termites. Given that termites are the only invertebrates known to translocate soil into deadwood (Oberst, Lai, & Evans, 2016), the mass of soil moved into the experimental woodblocks provides additional information on the termite activity compared with non-termite wood-feeding invertebrates.

Soil conditions and termite communities

Every month for the 12-month duration of the study, soil moisture percentage and soil temperature were measured within 5 cm of each wood block using a Delta-T Devices HH2 moisture metre (precise to 0.01 %) and a digital soil thermometer. Measurements were taken in dry conditions, between 8 AM and 10 AM. To assess termite communities located within the gap and closed canopy sites, we carried out termite transects in September 2018 using the Jones and Eggleton transect method (Jones & Eggleton, 2000). This method uses a 100 m x 2 m belt transect which is divided into twenty 5 m x 1 m sections. Each section is sampled for 30 minutes by two trained collectors searching for termites in twelve 12 cm x 12 cm x 10 cm soil pits and examining all dead wood, leaf litter and trees for the presence of termites. When encountered, termite specimens were collected in 70% ethanol and taken to the laboratory for identification. Because our gap sites were not big enough to place a 100 m transect, we carried out the same method but two using smaller transects to equal a 50 m transect combined. Therefore the sampling effort was half that of the Jones & Eggleton (2000) method.

Quantifying regional gap area

To assess the size and frequency of gaps within Maliau Basin Conservation Area, we used LiDAR data collected from an airborne survey, which was carried out by the Natural Environment Research Council (NERC) Airborne Research Facility (ARF). In November 2014, a Dornier 228-201 was flown at 1,400-2,400 m a.s.l. with a ground-based Leica base station running simultaneously to allow sub-meter accuracy and georeferencing of the

data. Light detection and ranging data were collected using a Leica ALS50-II LiDAR sensor, which emits 120 kHz frequency pulses, has a 12° field of view and a footprint of approximately 40 cm. See Swinfield et al. (2019) for details of LiDAR data processing to generate canopy height and digital terrain models at a 0.5 m resolution. Using these data, we analysed canopy height models to identify gaps, defined as areas with a canopy height of less than 5 m. Gaps larger than 1 ha were filtered out to remove LiDAR artefacts, manmade clearances and the river running through Maliau Basin. We used the package *landscapemetrics* in R and the thresholds described above to detect gaps and to calculate the area of each. We then filtered these results to select only gaps that were between 0.025 and 0.16 ha, which is the area range of the gaps forming the basis of this investigation. This allowed us to assess the total area and percentage of the landscape likely to be subject to similar microclimatic conditions to our gap sites at the time of the airborne survey and to quantify the percentage of gaps that are similar in size to those in this study.

Dead wood surveys

To estimate the volume of deadwood found on the forest floor in areas affected by tree-fall, compared with undisturbed areas, we carried out deadwood surveys in December 2017. To avoid disturbing our decomposition assays, these surveys were carried out in areas within the forest surrounding experimental plots. We established eight 50 m transects, four of which were within 5 m of a tree that had fallen during

the storm in July 2017 and four that were in areas of forest at least 20 m from the nearest tree fall. Along each transect, we recorded the diameter of each piece of deadwood that intersected with the line, and these values were used to calculate the volume of dead wood using the following equation (Van Wagner 1968):

$$V = \frac{\pi^2}{8L} \sum d^2$$

Where V is the volume of deadwood (cm^3/50 m), d is the diameter of the deadwood item at the intersection and L is the length of the sample line.

Carbon Modelling

A bootstrapping scheme with a million simulations was implemented to estimate the carbon flux from dead wood and its uncertainty in Maliau Basin. We estimated carbon fluxes for a completely closed canopy scenario versus scenarios with observed changes in decay rate and deadwood volume in canopy openings as well as canopy gap percentages derived from the remote sensing analysis.

Wood density

One species, *Pinus radiata*, was used for estimating wood mass loss in our experiment. Therefore, to account for diversity in wood traits of other species likely to occur at the study site, we used tree survey data from Newbery and Lingenfelder (2004) (collected from a lowland dipterocarp

309 forest site within 100 km of our study site). Our bootstrap analysis used
310 the tree species frequencies from Newbery and Lingenfelder (2004) and
311 selected a wood density for each species from the Global wood density
312 database (Zanne et al., 2009). Where wood density for a species was not
313 available, we randomly selected a wood density value from members of
314 the same genus within the same region category (South-East Asia
315 (tropical)). A histogram of the wood density distribution for this study is
316 shown in Fig. S3. Given that termite and microbial decay rate is negatively
317 associated with wood density in tropical systems (Liu et al., 2015; Mori et
318 al., 2014), this approach reduces the possibility that our model
319 overestimates overall decay rate as a result of the disparity between the
320 density of our decomposition substrate (*P. radiata:* wood density of 0.40 g
321 cm^{-3}) and the estimated median density of wood from trees in the study
322 region (0.54 g cm^{-3}). We note that the relationship between wood density
323 and decay rate is less clear in temperate forests (Hu et al., 2018; Kahl et
324 al., 2017). In addition to wood density, other traits, such as wood
325 stoichiometry and size of woody substrate (Hu et al., 2018; Kahl et al.,
326 2017; Oberle et al., 2020), are likely to influence decay rates. However,
327 information is lacking on how these other traits affect termite-mediate
328 decay, or wood decomposition more generally in tropical systems.
329 Therefore, we did not incorporate these factors into our models of regional
330 carbon fluxes.
331
332 *Scaling decay rates*

Liu et al. (2015) is the only study we know of that quantifies how termite-mediated decay rates depend on wood density. Therefore, we first built a model to represent wood decay rates under termite attack based on Liu et al. (2015). We scaled this model to represent wood decay in gaps using the *P. radiata* wood density and associated decay rate from our study. Then, we scaled the model again to represent these rates under the closed canopy. Wood decay rates in forest gaps were based on Liu *et al.* (2015) who measured wood traits and decay rates driven by microbes and termites for 66 species. We fitted an exponential model to decay rates as a function of wood density using an L1 scheme that minimizes the sum of the absolute value of the residuals (R package: *L1pack*) (Fig. S4). We used this scheme, rather than a least-squares approach, to avoid over-weighting outliers with high decay rates. To obtain a decay rate for each wood density value, we sampled from a normal distribution with the decay rate model prediction as the mean and the 68%-confidence interval of the model fit as the standard deviation (in log space). To avoid biologically unrealistic decay rates, we truncated the model to the middle 96% of the modelled decay rate estimates (Fig. S4). Because the model derived from Liu *et al.* (2015) predicted a much higher mean decay rate for *P. radiata* than found in our study (1.3 $year^{-1}$ compared with 0.49 $year^{-1}$), we scaled the model to reflect the *P. radiata* decay rates in the canopy gaps open to termite activity that we measured in the field. To predict decay rates under the closed canopy, we also scaled our gap model predictions to match the decay rates of *P. radiata* open to termite decomposition under closed canopy in our study. We accounted for random error in this scaling

process by sampling our decay rate dataset with N(μ=0.49, σ=0.05) for the forest gaps and N(μ=0.30, σ=0.04) for the closed canopy to obtain a distribution of scaling factors. These normal distributions were also truncated to the middle 96% quantile.

Carbon fluxes

To estimate the deadwood carbon pool at our study site, we used surveys from Pfeifer *et al.* (2015) from nearby Old Growth plot (OG2) of the Stability of Altered Forest Ecosystem (SAFE) project, located within Maliau Basin, <5 km kilometres from our study sites. Pfeifer et al. (2015) estimated there to be 10.2 ± 3.5 Mg C per hectare contained in deadwood at the OG2. For the bootstrapping scheme, we sampled $1x10^6$ times from a normal distribution of wood pools with the corresponding mean and standard deviation, truncated to the middle 96% quantile. We then estimated carbon fluxes, F, for the closed canopy baseline scenario using the equation

$$F = k_{canopy} C,$$

where k_{canopy} is the decay rate per year under the closed canopy and C is the closed canopy carbon pool estimate in megagrams of carbon per hectare. Because the percentage of canopy gaps is small, we assumed that the carbon pool estimates from Pfeifer et al. (2015) are representative of the closed canopy. We estimated the carbon flux for our study site, including canopy gaps, using the following equation:

$$F' = p k_{gaps} \alpha C + (1-p) k_{canopy} C,$$

where F' is the flux when gaps are included, p is the proportion of canopy gaps at the study site, k_{gaps}, is the decay rate (yr^{-1}) in the canopy gaps and α is the ratio of the volume of dead wood in the canopy gaps to the volume of dead wood under the closed canopy. Because the sample size was small (n = 4, each) for the volume of dead wood in the canopy gaps and under the closed canopy, a normal distribution computed from these data may not be reliable. Therefore, we sampled α directly from the dataset for the bootstrapping scheme. Fluxes are reported as geometric means with geometric standard deviation intervals to best represent the central tendency of the approximately log-normal bootstrapped distributions we obtained.

Statistical analysis

A linear mixed effect model (R package: *LmerTest*) was used to determine if wood block bag type (macroinvertebrate accessible vs. macroinvertebrate inaccessible), canopy type (closed canopy vs forest gap) and the interaction between the two factors affected proportion of mass lost from wood blocks. Mass loss was logit transformed, which allowed us to use standard Gaussian linear methods (Warton & Hui, 2011) and forest site was included as a random factor. To carry out multiple comparisons of means and identify any differences in wood block mass loss between bag types and canopy types, we used the *glht* function (R

408 package: *multcomp*) and Tukey contrasts. An Adonis test (package:
409 *vegan*) was used to assess if the community composition of termites
410 differed between the closed canopy and forest gap sites, and zero-inflated
411 generalised linear mixed effects models (R package: *glmmTBM*) were used
412 to test for differences in the encounter rate of each genus separately in
413 the closed canopy and forest sites. Linear mixed effects models were used
414 to test for differences in minimum, mean and maximum soil temperature
415 and moisture values in closed canopy and gap sites; forest site and
416 sampling date were included as random factors. Linear mixed models
417 were used to assess the differences in canopy openness between the
418 closed canopy and forest gaps, with site included as a random factor.
419
420 Finally, to model the relationship between termite-derived soil recovered
421 from the woodblocks and woodblock mass loss, while taking into
422 consideration the high proportion of zeros in the data (50% of open
423 woodblocks contained no termite-derived soil), we analysed the data in a
424 two-stage approach following Min & Agresti (2002). First, we created a
425 binomial variable for the termite soil mass, where woodblocks containing
426 no soil received a 0 and those with more than zero grams of soil received
427 a 1. We then fit the data to a generalised linear mixed effect model
428 (glmer) with site included as a random factor, to test if the proportion of
429 wood mass lost (logit transformed) had a significant effect on the
430 probability of a woodblock containing termite soil. Next, we removed the
431 zero soil values from the dataset and ran a linear mixed effects model
432 (lmer) on only woodblocks from which we recovered soil, to assess if logit

transformed wood mass loss was significantly associated with the mass of soil that was recovered from the woodblocks. Again, site was included as a random factor. This approach overcame the problem of modelling zero-inflated data (only invertebrate accessible bags were included in these models because no soil was recovered from closed bags).

Results

Decomposition

Significantly more mass was lost from open woodblocks (accessible to both microbes and macroinvertebrates) in forest gaps (mean mass loss over 12 months: 49% ± 5%) compared with open woodblocks in closed canopy sites (mean mass loss: 30% ± 4%; $z = 3.8$, $P < 0.001$). This is an increase in decomposition by a factor of 1.63 in forest where both microbes and macroinvertebrates have access to the woodblocks (Fig. 2). In both the closed canopy and gaps sites, the presence of macroinvertebrates significantly increased the proportion of mass lost, but the magnitude of this increase was greater in forest gaps, as indicated by significant interaction between woodblock bag type and canopy type (LRT = 4.18, $P = 0.04$): woodblock mass loss increased by a factor of 2 in open (mean mass loss: 30 ± 4%) compared with closed bags (mean mass loss: 15 ± 2%) in closed canopy sites ($z = 3.08$, $P = 0.01$), but increased by a factor of 2.58 within open (mean mass loss: 49 ± 5%) versus closed bags (19 ± 2%) in forest gaps ($z = 5.9$, $P < 0.001$). We found a significant positive relationship between woodblock mass loss and the likelihood that a wood block contained termite-derived soil and carton within the open

458 bags (z = 4.19, P < 0.001; Fig S5), and a significant positive relationship
459 between the proportion of mass lost from a woodblock and the mass of
460 dry soil recovered from bags containing soil (z = 2.94, P = 0.005; Fig. S5);
461 indicating that termites, rather than other macro-invertebrates, were
462 responsible for this mass loss. There was no significant difference in mass
463 lost from closed woodblocks in the closed canopy compared with closed
464 woodblocks in forest gap sites (z = 0.86, *P* = 0.83), suggesting that
465 changes in microbial activity were not responsible for the increase
466 decomposition in the gaps (Fig. 2).
467
468 *Soil microclimate and termite communities*
469 We found small but significant differences in soil temperature and soil
470 moisture within closed canopy and forest gap sites. The soil in gaps
471 tended to be warmer and wetter. Minimum soil temperature was higher by
472 0.5ºC and mean soil temperature was 0.3ºC higher in gaps compared with
473 closed canopy sites. There was no significant difference in maximum soil
474 temperature. Minimum, mean and maximum soil moisture were higher in
475 canopy gaps compared with non-gap sites by 2, 1.5 and 3.5 percentage
476 points, respectively (Fig. 3; Table 1). We found no difference in the
477 composition of termite communities collected in the closed canopy
478 compared with forest gaps sites nor was there any difference in the
479 number of encounters of individual genera in the two canopy types (Fig.
480 S6).
481
482 *Gap area and carbon modelling*

Within the LiDAR surveyed area of 940 ha of lowland tropical rainforest, we detected a total of 20,928 gaps, with the centre of the cumulative distribution of gaps (i.e. the point where half of the gap area is comprised of smaller gaps and the remaining half by larger gaps) at 122 m^2 (0.01 ha) and covering a cumulative area of 24 ha, or 2.5% of the study site. Of these, 128 gaps were of comparable size to those used in this study (between 0.025 and 0.16 ha). These gaps covered a cumulative area of 6.5 ha, which is 0.7 % of the surveyed area and represents 27% of the total gap area in the study region (Fig. 4). In the forest matrix immediately surrounding our experimental plots, we found 187% more deadwood in areas affected by tree fall compared with undisturbed areas (average volume in areas more than 20 m from tree fall: 95.4 ± 36.6 cm^3 per 50 m transect; average volume in areas close to tree fall: 272.9 ± 98.7 cm^3 per 50 m transect; Fig. 5).

Our initial model applied the changes in decay rate and wood pools to canopy gaps covering 0.7% of the surveyed area, which is the cumulative area that includes gaps of the same size as those forming the basis of this investigation: 128 gaps in total, measuring between 0.025 and 0.16 ha. Under this assumption of gap area, deadwood carbon fluxes increased above baseline by a geometric mean value of 5.7% with a geometric SD interval of -3.1% to 15.2%, corresponding to a flux increase of 0.09 Mg C ha^{-1} yr^{-1} (Table 2). If we assumed changes in wood pools and decay rates applied to all gaps detected by LiDAR, i.e. 2.5% of the survey area, then the flux increase was 18.2% (geometric SD interval of -15.4% to 47.7%),

or 0.27 Mg C ha^{-1} yr^{-1}. Increases in both wood pool sizes and termite-driven decay rates in gaps contributed to the higher fluxes relative to the baseline scenario with no gaps (Fig. S10). At the scale of the 940 ha region of our LiDAR analysis, gap-driven fluxes increased from 1380 Mg C ha^{-1} yr^{-1} to 1460 Mg C yr^{-1} for the 0.7% gap scenario and to 1640 Mg C ha^{-1} yr^{-1} for the 2.5% gap scenario.

Discussion

We found that deadwood decomposition in a lowland tropical rainforest increased by approximately two thirds in tree-fall canopy gaps, compared with closed-canopy forest, and that this accelerated decomposition was driven by termites. These results add to a growing body of evidence showing that termites are major drivers of deadwood decomposition in tropical rainforests (Griffiths et al., 2019; Law et al., 2019) and that their importance for the maintenance of ecological processes can increase in response to environmental perturbations (Ashton et al., 2019). The functioning of canopy gaps as hotspots for carbon cycling has important implications for land-surface model development given that tree mortality is increasing in rainforests (Brienen et al., 2015; Hubau et al., 2020; McDowell et al., 2018), which will increase the number of gaps, and cumulative area of forest affected by canopy openings.

Drivers of increased decomposition

We hypothesized that changes in deadwood stocks and microclimate in gaps might alter wood decomposition fluxes. Deadwood stocks were three times higher in canopy gaps than in closed canopy sites. Microbial decomposition did not differ between contrasting canopy conditions while termite-mediated decay increased by almost two thirds in tree-fall gaps. The small but significant differences we detected in the soil microclimate of our gap and closed canopy sites had no effect on microbial decay but may have led to an increase in termite-mediated decay. Combined, these results point to an influx of deadwood foraging material for termites as a likely driver of the increased decomposition in gaps we detected. However, because this hypothesis needs further testing, this work serves as a platform from which the mechanisms behind the patterns we report can be rigorously tested and a starting point for incorporation of these patterns into global carbon models.

We found no support for our hypothesis that shifts in microclimate and/or disturbance caused by tree mortality are detrimental to the decomposer community. Neither termite nor microbial-mediated wood mass loss declined beneath canopy gaps. Soil conditions in our focal canopy gaps were not as we predicted: although slightly warmer, they were wetter, rather than drier than in the paired closed canopy sites. This result could, in part, explain the lack of disturbance/microclimate effect detected on the decomposer community because we have no *a priori* reason to believe that these small increases in soil moisture would negatively affect microbial or termite activity.

Our finding of increased termite-mediated decay in canopy gaps supports our alternative hypothesis that an increase in termite food sources (deadwood) in tree fall gaps attracts more termites to these areas, which leads to increased decomposition. We found almost three times more deadwood on the forest floor in areas close to tree fall (Fig. 5), and we propose that this influx of wood is likely to have led to an increase in termite foraging in the gap sites. This finding has important implications for the way in which decomposition models are parameterised in rainforest systems because our results suggest that carbon flux rates from deadwood are not only a function of the proportion of wood necromass in the system (Rice et al., 2004) but may also be mediated by the spatial clustering of the deadwood resource. Given that microbial decay rates did not change in the canopy gaps, we found no evidence to suggest the clustering/influx of dead plant resources had a comparable positive effect on the microbial decomposer community.

We are confident that termites were responsible for the invertebrate driven increase in decomposition because a previous study, which used macroinvertebrate accessible and inaccessible woodblock bags, in combination with a large-scale suppression of termite communities, demonstrated that non-termite macroinvertebrates do not contribute significantly to wood decay at this site Griffiths et al., (2019). Our present study exactly mimics the experimental design used to manipulate the macroinvertebrate community access to wood blocks in the previous

583 work. Therefore, we conclude that termites were responsible for the
584 elevated mass loss from wood within the macroinvertebrate accessible
585 bags. Moreover, we found a significant positive relationship between the
586 probability that a wood block contained termite-derived soil and
587 proportion wood mass loss, as well as a positive relationship between the
588 mass of soil brought into our open woodblock bags and wood block mass
589 loss (no soil was recovered from closed woodblocks; Fig. S5). This
590 relationship provides further evidence that termites are the main drivers
591 of the observed wood mass loss from the macroinvertebrate accessible
592 bags because termites are the only decomposer organism known to
593 move clay and soil around in this way (Oberst et al., 2016). Because our
594 sampling to assess the composition and biomass of termites within the
595 gap and closed canopy sites was carried out 15-months after the storm
596 that created the focal gaps and influx of deadwood material, it seems
597 likely that we missed the increase in termite activity within the gap sites
598 that we hypothesise led to the elevated decay rate within our gaps.
599 Further work is needed to conclusively disentangle the possible drivers of
600 the increased termite activity and wood decay rates in canopy gaps
601 (microclimate versus increased food supply). Our findings highlight the
602 need to explicitly test the influence of microclimate versus deadwood
603 volume on decay rates in field experiments. This would allow us to gain a
604 deeper understanding of the factors mediating decomposition and carbon
605 balance in rainforest ecosystems.
606
607 *Implications for rainforest carbon flux and sources of uncertainties*

We show that termite-mediated deadwood decay responds positively to small-scale disturbances within old-growth rainforest. This suggests that accelerated termite decomposition could be a key driver of observed elevated carbon fluxes caused by increased tree mortality and degradation within standing tropical forests (Baccini et al., 2017; Hubau et al., 2020). As such, these results add to our understanding of the biotic mechanisms underpinning ongoing changes to rainforest carbon budgets. However, the resilience of termite-mediated ecosystem processes to differing disturbance thresholds is largely unknown (but see Tuma *et al.* 2019). Recent work has shown that termites maintain leaf litter decomposition, nutrient heterogeneity and soil moisture retention in old growth forest during periods of drought (Ashton et al., 2019), indicating that they can provide ecosystem resilience to climate change. Understanding the extent to which the resilience provided by termites is maintained in degraded habitats is key to the on-going improvement of land-surface models as well the development of land-management practices aimed at increasing the resilience of tropical landscapes under ongoing environmental change

Given the vast amounts of carbon contained within tropical forests (Lewis, Edwards, & Galbraith, 2015; Pan et al., 2011), even a relatively small change in C flux due to termite-mediated decomposition in canopy gaps may scale up to large differences over tropical biomes. For example, our estimated flux increase of 0.27 Mg C ha^{-1} yr^{-1} represents 2% of total net primary productivity (13.5 Mg C ha^{-1} yr^{-1}) measured in lowland rainforests

633 of Malaysian Borneo (Riutta et al., 2018). This timely finding is of
634 particular relevance given that the Community Land Model version 6
635 (CLM6) is currently under development, which will include additional
636 parameterisation of ecosystem processes that influence the cycling of C
637 through terrestrial ecosystems and build upon progress made in CLM5
638 (Lawrence et al., 2019). However, although our analysis indicated the
639 potential for substantial increases in carbon flux due to changes in termite
640 activity in canopy gaps, the variance around the estimated magnitude of
641 this change in flux remains high due to a number of potential sources of
642 uncertainty in our model.
643
644 Lack of data on how climate mediates the relationship between termite-
645 driven decay and wood density represents an area of uncertainty in our
646 model estimates and contributes to the large confidence intervals
647 associated with our C-flux estimates. Our estimate of termite-mediated
648 decay associated with the varying wood densities is reliant on an
649 empirical model we fitted to a single dataset of decay rates from a distant
650 study site in Yunnan Province, China (Liu et al., 2015). While both are
651 Asian tropical rainforests, the climate differs between the two regions:
652 mean annual rainfall of 1463 mm versus 2838 mm and average monthly
653 temperatures of 21.7°C versus 24.9°C in Yunan (Li et al., 2012) and Maliau
654 (Law et al., 2019), respectively. These climatic differences could be
655 important because while some studies suggest that wood traits are key
656 drivers of deadwood decay (Hu et al., 2018; Zanne et al., 2015), others
657 have found stronger relationships with climate (Chambers, Higuchi,

Schimel, Ferreira, & Melack, 2000; Pietsch et al., 2019). Consequently, it is possible that the effect of wood density on rate of termite mediated decay could differ between the two regions.

Wood density is not the only trait known to influence decay rates. Results from studies focussed on microbial wood decomposition in temperate regions show that a range of other traits can also significantly effect wood decay, either positively (e.g. phosphorous, nitrogen) or negatively (e.g. bark ratio, lignin concentration [Kahl et al., 2017; Oberle et al., 2019]). Furthermore, a recent meta-analysis (Hu et al., 2018), highlighted the importance of wood size (diameter) and nitrogen concentration in controlling wood decay globally. We acknowledge that termite-mediated decay rates could also be influenced by these wood traits and our models may be improved if more data were available on the effect of wood stoichiometry on termite attack rate in our system. However, data on wood chemical traits within our study region are currently unavailable, but Martin, Erickson, Kress, & Thomas (2014) provide an overview of wood nitrogen concentration and correlations between nitrogen and other wood traits for 59 Panamanian tree species. This work reveals a mean wood C:N ratio for these neo-tropical tree species of 278 ± 32, with values ranging from 84.7 to 1360.8, and a positive relationship between wood density and wood nitrogen concentration. Our wood decomposition substrate (*Pinus radiata*) falls within this range with a C:N of 462 (Ganjegunte et al., 2004).

We are aware of no study that has interrogated the influence of wood chemical traits on termite mediated decomposition; therefore, we are unable to speculate as to how these factors could influence our flux estimate. However, Ulyshen, Müller, & Seibold (2016) show that termite-mediated wood mass loss increased significantly where bark was present, which is in contrast to the findings presented by Kahl et al., (2017) who show that higher bark ratio negatively affected microbial decay rates. It is important to note that our use of wood blocks of a uniform (small) size and lacking in bark could have resulted in elevated mass loss compared to larger woody substrates with intact bark. However, our wood substrate was chosen to allow for standardization and to facilitate comparison across our experimental sites and treatments. Therefore, we highlight the need for additional work to partition the contributions of microbes versus termites in the decomposition of deadwood with a range of traits and in a range of ecosystems to facilitate the development of more precise models of wood decomposition and carbon cycling.

Possible inaccuracies in our estimates of deadwood on the forest floor are another potential source of error in our model estimates. We reported that the volume of deadwood was 187% higher in areas affected by treefall compared with those unaffected, using field transects 5-months after the storm that created the canopy gaps. However, it is possible that termite-mediated wood removal in that 5-month period, in response to the influx of foraging material, removed deadwood disproportionately from the tree-fall sites. This would result in an underestimation of the difference in wood

volume in contrasting canopy environments, with potentially more deadwood in recently created gaps than we reported. Further, we used data from Pfeifer *et al.* (2015) to describe the deadwood carbon pool under closed canopy conditions. However, Pfeifer *et al.* (2015) reported different deadwood carbon estimates from two sites, both within 3.2 km of our study site ("OG1": 27.05 Mg C per ha, and "OG2": 10.24 Mg per ha). We used values from the site closest to our experimental plots (< 1km), OG 2, which was the lowest carbon pool value and thus avoids inflated estimates of the effect of termites on regional C flux. However, the higher deadwood carbon pool reported from Old Growth 1 combined with the possibility that we underestimated the proportional difference in deadwood volume in gaps versus closed canopy sites suggests that our modelling effort is a conservative estimate of the true effect of termite mediated C flux in canopy gaps.

Finally, difficulties in describing temporally and spatially representative forest canopy gap fractions may have contributed model inaccuracies. Using data from the aerial survey carried out in November 2014, we found the cumulative area of canopy gaps in the study region to be between 0.7 and 2.5%. This range is within the lower bounds of canopy gap fractions described by Hunter *et al.* (2015) in the Amazon rainforest (2-5%) and smaller than that reported by Yavitt *et al.* (1995) within a Panamanian forest (4%). Small canopy openings in rainforest ecosystems caused by isolated tree fall events rapidly become colonised by lateral canopy growth, meaning that their detectability using remote sensing quickly

733 decreases with time since gap creation (Asner, Keller, & Silva, 2004). The
734 aerial survey used in this investigation was not, as far as we are aware,
735 carried out soon after an intense storm similar to the storm that created
736 the focal gaps in this study. Therefore, our gap fraction estimate is likely
737 to be smaller than if it been carried out immediately following the storm
738 that formed the basis of this investigation. However, despite these
739 uncertainties, our analysis demonstrates that canopy gaps in rainforest
740 ecosystems function as hotspots of deadwood decay, which has far
741 reaching implications for regional and global budgeting.
742
743 *Conclusion*
744 To our knowledge, this is the first study to show that rainforest treefall
745 canopy gaps represent hotspots for deadwood decay and carbon cycling.
746 We provide insights into the relative importance of invertebrates
747 compared with microbes in driving the decomposition of deadwood,
748 adding to a growing body of literature showing that termites and their
749 mutualistic microbes are equally, if not more important than free-living
750 microorganisms for deadwood decay in rainforests (Griffiths et al., 2019;
751 Law et al., 2019). These results demonstrate that to improve the accuracy
752 of carbon modelling, a variable rate of decomposition should be included
753 in model parameters to account for accelerated termite-mediated decay
754 within tree fall canopy gaps. However, we urgently require information on
755 the effect of a variety of wood traits on termite-mediated decay rates, as
756 well as research efforts to quantify whether these patterns of accelerated
757 decomposition hold true in selectively logged forest or oil palm

plantations. Only through addressing these knowledge gaps will we be able to reduce model uncertainties and accurately predict how ongoing changes to tropical landscapes will affect global carbon cycling, climate and the functioning and maintenance of vitally important tropical rainforest ecosystems.

Acknowledgements

We are extremely grateful to our field assistants R. Binti Manber, Lawlina Mansul and Donny Banasib for their tireless hard work in the field, which made this study possible. We thank G. Reynolds, U. Jami and A. Karolus for coordinating fieldwork. This work was supported by the South East Asian Rainforest Research Partnership (SEARRP), with permission from Maliau Basin Management Committee and the Sabah Biodiversity Council. We thank the funding bodies that financially supported this work: The Leverhulme Trust, research grant: RPG-2017-271 awarded to KP; National Science Foundation, Research Traineeship 1633631 to NHS, and National Science Foundation, grant DEB-1655340 to SDA.

Data Sharing and Accessibility

The data that support the findings of this study are openly available in Dryad data repository at http://doi.org/[doi], reference number [reference number].

References

Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On

783 underestimation of global vulnerability to tree mortality and forest die-
784 off from hotter drought in the Anthropocene. *Ecosphere*, *6*(8), 1–55.
785 https://doi.org/10.1890/ES15-00203.1
786 Ashton, L. A., Griffiths, H. M., Parr, C. L., Evans, T. A., Didham, R. K.,
787 Hasan, F., … Eggleton, P. (2019). Termites mitigate the effects of
788 drought in tropical rainforest. *Science*, *177*(January), 174–177.
789 Asner, G. P., Keller, M., & Silva, J. N. M. (2004). Spatial and temporal
790 dynamics of forest canopy gaps following selective logging in the
791 eastern Amazon. *Global Change Biology*, *10*(5), 765–783.
792 https://doi.org/10.1111/j.1529-8817.2003.00756.x
793 Baccini, A., Walker, W., Carvalho, L., Farina, M., Sulla-Menashe, D., &
794 Houghton, R. A. (2017). Tropical forests are a net carbon source based
795 on aboveground measurements of gain and loss. *Science*,
796 *358*(October), 230–234.
797 Blonder, B., Both, S., Coomes, D. A., Elias, D., Jucker, T., Kvasnica, J., …
798 Svátek, M. (2018). Extreme and Highly Heterogeneous Microclimates
799 in Selectively Logged Tropical Forests. *Frontiers in Forests and Global*
800 *Change*, *1*(October), 1–14. https://doi.org/10.3389/ffgc.2018.00005
801 Bodman, R. W., Rayner, P. J., & Karoly, D. J. (2013). Uncertainty in
802 temperature projections reduced using carbon cycle and climate
803 observations. *Nature Climate Change*, *3*(8), 725–729.
804 https://doi.org/10.1038/nclimate1903
805 Brienen, R. J. W., Phillips, O. L., Feldpausch, T. R., Gloor, E., Baker, T. R.,
806 Lloyd, J., … Zagt, R. J. (2015). Long-term decline of the Amazon carbon
807 sink. *Nature*, *519*(7543), 344–348.

https://doi.org/10.1038/nature14283

Cai, W., Borlace, S., Lengaigne, M., Van Rensch, P., Collins, M., Vecchi, G., … Jin, F. F. (2014). Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature Climate Change*, *4*(2), 111–116. https://doi.org/10.1038/nclimate2100

Carlson, B. S., Koerner, S. E., Medjibe, V. P., White, L. J. T., & Poulsen, J. R. (2017). Deadwood stocks increase with selective logging and large tree frequency in Gabon. *Global Change Biology*, *23*(4), 1648–1660. https://doi.org/10.1111/gcb.13453

Chambers, J. Q., Higuchi, N., Schimel, J. P., Ferreira, L. V, & Melack, J. M. (2000). Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia*, *122*(3), 380–388. https://doi.org/10.1007/s004420050044

Cornwell, W. K., Cornelissen, J. H. C., Allison, S. D., Bauhus, J., Eggleton, P., Preston, C. M., … Zanne, A. E. (2009). Plant traits and wood fates across the globe: Rotted, burned, or consumed? *Global Change Biology*, *15*(10), 2431–2449. https://doi.org/10.1111/j.1365-2486.2009.01916.x

da Costa, R. R., Hu, H., Li, H., & Poulsen, M. (2019). Symbiotic plant biomass decomposition in Fungus-Growing termites. *Insects*, *10*(4), 1–15. https://doi.org/10.3390/insects10040087

Dibog, L., Eggleton, P., Norgrove, L., Bignell, D. E., & Hauser, S. (1999). Impacts of canopy cover on soil termite assemblages in an agrisilvicultural system in southern Cameroon. *Bulletin of Entomological Research*, *89*(02), 125–132.

https://doi.org/10.1017/S0007485399000206

Eggleton, P., Bignell, D. E., Sands, W. A., Waite, B., Wood, T. G., & Lawton, J. H. (1995). The species richness of termites (isoptera) under differing levels of forest disturbance in the mbalmayo forest reserve, southern cameroon. *Journal of Tropical Ecology*, *11*(1), 85–98. https://doi.org/10.1017/S0266467400008439

Ewers, R. M., Boyle, M. J. W., Gleave, R. A., Plowman, N. S., Benedick, S., Bernard, H., … Turner, E. C. (2015). Logging cuts the functional importance of invertebrates in tropical rainforest. *Nature Communications*, *6*, 6836. https://doi.org/10.1038/ncomms7836

Ganjegunte, G. K., Condron, L. M., Clinton, P. W., Davis, M. R., & Mahieu, N. (2004). Decomposition and nutrient release from radiata pine (Pinus radiata) coarse woody debris. *Forest Ecology and Management*, *187*(2–3), 197–211. https://doi.org/10.1016/S0378-1127(03)00332-3

Griffiths, H. M., Ashton, L. A., Evans, T. A., Parr, C. L., & Eggleton, P. (2019). Termites can decompose more than half of deadwood in tropcal rainforest. *Current Biology*, *29*, 118–119. https://doi.org/10.1016/j.cub.2019.01.012

Hardwick, S. R., Toumi, R., Pfeifer, M., Turner, E. C., Nilus, R., & Ewers, R. M. (2015). The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology*, *201*, 187–195. https://doi.org/10.1016/j.agrformet.2014.11.010

Harmon, M. E., Bond-Lamberty, B., Tang, J., & Vargas, R. (2011). Heterotrophic respiration in disturbed forests: A review with examples

from North America. *Journal of Geophysical Research: Biogeosciences*, *116*(2), 1–17. https://doi.org/10.1029/2010JG001495

Harmon, M. E., Fasth, B. G., Yatskov, M., Kastendick, D., Rock, J., & Woodall, C. W. (2020). Release of coarse woody detritus - related carbon : a synthesis across forest biomes. *Carbon Balance and Management*, 1–21. https://doi.org/10.1186/s13021-019-0136-6

Hu, Z., Michaletz, S. T., Johnson, D. J., McDowell, N. G., Huang, Z., Zhou, X., & Xu, C. (2018). Traits drive global wood decomposition rates more than climate. *Global Change Biology*, *24*(11), 5259–5269. https://doi.org/10.1111/gcb.14357

Hubau, W., Lewis, S. L., Phillips, O. L., Affum-Baffoe, K., Beeckman, H., Cuní-Sanchez, A., … Zemagho, L. (2020). Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature*, *579*(7797), 80–87. https://doi.org/10.1038/s41586-020-2035-0

Hunter, M. O., Keller, M., Morton, D., Cook, B., Lefsky, M., Ducey, M., … Zang, R. (2015). Structural dynamics of tropical moist forest gaps. *PLoS ONE*, *10*(7), 1–19. https://doi.org/10.1371/journal.pone.0132144

Jackson, T. ., Shenkin, A. ., Majalap, N., Jami, J. ., Sailim, A. B., Reynolds, G., … Disney, M. (2020). The mechanical stability of the world's tallest broadleaf trees. *The Mechanical Stability of the World's Tallest Broadleaf Trees*, *00*, 1–11. https://doi.org/10.1101/664292

Janisch, J. E., Harmon, M. E., Chen, H., Fasth, B., & Sexton, J. (2005). Decomposition of coarse woody debris originating by clearcutting of an old-growth conifer forest. *Écoscience*, *12*(2), 151–160. https://doi.org/10.2980/i1195-6860-12-2-151.1

Jones, D. T., & Eggleton, P. (2000). Sampling termite assemblages in tropical forests: Testing a rapid biodiversity assessment protocol. *Journal of Applied Ecology*, *37*(1), 191–203. https://doi.org/10.1046/j.1365-2664.2000.00464.x

Kahl, T., Arnstadt, T., Baber, K., Bässler, C., Bauhus, J., Borken, W., … Gossner, M. M. (2017). Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. *Forest Ecology and Management*, *391*, 86–95. https://doi.org/10.1016/j.foreco.2017.02.012

Law, S., Eggleton, P., Griffiths, H., Ashton, L., & Parr, C. (2019). Suspended Dead Wood Decomposes Slowly in the Tropics , with Microbial Decay Greater than Termite Decay. *Ecosystems*, (June). https://doi.org/10.1007/s10021-018-0331-4

Lawrence, D. M., Fisher, R. A., Koven, C. D., Oleson, K. W., Swenson, S. C., Bonan, G., … Zeng, X. (2019). The Community Land Model Version 5: Description of New Features, Benchmarking, and Impact of Forcing Uncertainty. *Journal of Advances in Modeling Earth Systems*, *11*(12), 4245–4287. https://doi.org/10.1029/2018MS001583

Lewis, S. L., Edwards, D. P., & Galbraith, D. (2015). Increasing human dominance of tropical forests. *Science*, *349*, 827–832.

Li, R., Luo, G., Meyers, P. A., Gu, Y., Wang, H., & Xie, S. (2012). Leaf wax n-alkane chemotaxonomy of bamboo from a tropical rain forest in Southwest China. *Plant Systematics and Evolution*, *298*(4), 731–738. https://doi.org/10.1007/s00606-011-0584-2

Liu, G., Cornwell, W. K., Cao, K., Hu, Y., Van, R. S. P., Yang, S., …

908 Cornelissen, J. H. C. (2015). Termites amplify the effects of wood traits
909 on decomposition rates among multiple bamboo and dicot woody
910 species. *Journal of Ecology*, *103*, 1214–1223.
911 https://doi.org/10.1111/1365-2745.12427
912 Luke, S. H., Fayle, T. M., Eggleton, P., Turner, E. C., & Davies, R. G. (2014).
913 Functional structure of ant and termite assemblages in old growth
914 forest, logged forest and oil palm plantation in Malaysian Borneo.
915 *Biodiversity and Conservation*, *23*(11), 2817–2832.
916 https://doi.org/10.1007/s10531-014-0750-2
917 Lyu, M., Xie, J., Vadeboncoeur, M. A., Wang, M., Qiu, X., Ren, Y., …
918 Kuzyakov, Y. (2018). Simulated leaf litter addition causes opposite
919 priming effects on natural forest and plantation soils. *Biology and*
920 *Fertility of Soils*, *54*(8), 925–934. https://doi.org/10.1007/s00374-018-
921 1314-5
922 Martin, A. R., Erickson, D. L., Kress, W. J., & Thomas, S. C. (2014). Wood
923 nitrogen concentrations in tropical trees: phylogenetic patterns and
924 ecological correlates. *New Phytologist*, *205*, 484–495.
925 McDowell, N., Allen, C. D., Anderson-Teixeira, K., Brando, P., Brienen, R.,
926 Chambers, J., … Xu, X. (2018). Drivers and mechanisms of tree
927 mortality in moist tropical forests. *New Phytologist*, *219*(3), 851–869.
928 https://doi.org/10.1111/nph.15027
929 Min, Y., & Agresti, A. (2002). Modeling Nonnegative Data with Clumping at
930 Zero : A Survey Models for Semicontinuous Data. *Jirss*, *1*(May), 7–33.
931 Mori, S., Itoh, A., Nanami, S., Tan, S., Chong, L., & Yamakura, T. (2014).
932 Effect of wood density and water permeability on wood decomposition

933 rates of 32 bornean rainforest trees. *Journal of Plant Ecology*, *7*(4),
934 356–363. https://doi.org/10.1093/jpe/rtt041
935 Newbery, D. M., & Lingenfelder, M. (2004). Resistance of a lowland rain
936 forest to increasing drought intensity in Sabah, Borneo. *Journal of*
937 *Tropical Ecology*, *20*(6), 613–624.
938 https://doi.org/10.1017/S0266467404001750
939 Oberle, B., Lee, M. R., Myers, J. A., Osazuwa-Peters, O. L., Spasojevic, M. J.,
940 Walton, M. L., … Zanne, A. E. (2020). Accurate forest projections
941 require long-term wood decay experiments because plant trait effects
942 change through time. *Global Change Biology*, *26*(2), 864–875. https://
943 doi.org/10.1111/gcb.14873
944 Oberle, B., Lee, M. R., Myers, J. A., Osazuwa-Peters, O. L., Spasojevic, M. J.,
945 Walton, M. L., … Zanne, A. E. (2019). Accurate forest projections
946 require long-term wood decay experiments because plant trait effects
947 change though time. *Global Change Biology*, (October), 1–12.
948 https://doi.org/10.1111/gcb.14873
949 Oberst, S., Lai, J. C. S., & Evans, T. A. (2016). Termites utilise clay to build
950 structural supports and so increase foraging resources. *Scientific*
951 *Reports*, *6*(September 2015), 1–11. https://doi.org/10.1038/srep20990
952 Pan, Y., Birdsey, R. a, Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. a, …
953 Hayes, D. (2011). A large and persistent carbon sink in the world's
954 forests. *Science, 333*(6045), 988–993.
955 https://doi.org/10.1126/science.1201609
956 Pfeifer, M., Lefebvre, V., Turner, E., Cusack, J., Khoo, M. S., Chey, V. K., …
957 Ewers, R. M. (2015). Deadwood biomass: An underestimated carbon

stock in degraded tropical forests? *Environmental Research Letters*, *10*(4). https://doi.org/10.1088/1748-9326/10/4/044019

Pietsch, K. A., Eichenberg, D., Nadrowski, K., Bauhus, J., Buscot, F., Purahong, W., … Wirth, C. (2019). Wood decomposition is more strongly controlled by temperature than by tree species and decomposer diversity in highly species rich subtropical forests. *Oikos*, *128*(5), 701–715. https://doi.org/10.1111/oik.04879

Rice, A. H., Pyle, E. H., Saleska, S. R., Hutyra, L., Palace, M., Keller, M., … Wofsy, S. C. (2004). Carbon balance and vegetation dynamics in an old-growth Amazonian forest. *Ecological Applications*, *14*(4), 55–71. https://doi.org/10.1890/02-6006

Riutta, T., Malhi, Y., Kho, L. K., Marthews, T. R., Huaraca Huasco, W., Khoo, M. S., … Ewers, R. M. (2018). Logging disturbance shifts net primary productivity and its allocation in Bornean tropical forests. *Global Change Biology*, *24*(7), 2913–2928. https://doi.org/10.1111/gcb.14068

Shorohova, E., & Kapitsa, E. (2014). Influence of the substrate and ecosystem attributes on the decomposition rates of coarse woody debris in European boreal forests. *Forest Ecology and Management*, *315*, 173–184. https://doi.org/10.1016/j.foreco.2013.12.025

Stoklosa, A. M., Ulyshen, M. D., Fan, Z., Varner, M., Seibold, S., & Müller, J. (2016). Effects of mesh bag enclosure and termites on fine woody debris decomposition in a subtropical forest. *Basic and Applied Ecology*, *17*(5), 463–470. https://doi.org/10.1016/j.baae.2016.03.001

Swift, M. J. (1977). The ecology of wood decomposition. *Science Progress*, *64*(254), 175–199. Retrieved from

http://www.bcin.ca/Interface/openbcin.cgi?submit=submit&Chinkey=35034

Swinfield, T., Both, S., Riutta, T., Bongalov, B., Elias, D., Majalap-Lee, N., … Coomes, D. (2019). Imaging spectroscopy reveals the effects of topography and logging on the leaf chemistry of tropical forest canopy trees. *Global Change Biology*, (October), 1–14. https://doi.org/10.1111/gcb.14903

Tuma, J., Fleiss, S., Eggleton, P., Frouz, J., Klimes, P., Lewis, O. T., … Fayle, T. M. (2019). Logging of rainforest and conversion to oil palm reduces bioturbator diversity but not levels of bioturbation. *Applied Soil Ecology*, *144*(August), 123–133. https://doi.org/10.1016/j.apsoil.2019.07.002

Ulyshen, M. D., Müller, J., & Seibold, S. (2016). Bark coverage and insects in fl uence wood decomposition : Direct and indirect effects. *Applied Soil Ecology*, *105*, 25–30. https://doi.org/10.1016/j.apsoil.2016.03.017

Van Wagner C.E. (1968). The Line Intersect Method in Forest Fuel Sampling. *Forest Science*, *14*(1), 20–26.

Warton, D. I., & Hui, F. K. C. (2011). The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, *92*(1), 3–10.

Yavitt, J. B., Battles, J. J., Lang, G. E., & Knight, D. H. (1995). The Canopy Gap Regime in a Secondary Neotropical Forest in Panama. *Journal of Tropical Ecology*, *11*(3), 391–402.

Yavitt, J. B., Wright, S. J., & Wieder, R. K. (2004). Seasonal drought and dry-season irrigation influence leaf-litter nutrients and soil enzymes in a moist, lowland forest in Panama. *Austral Ecology*, *29*(2), 177–188.

https://doi.org/10.1111/j.1442-9993.2004.01334.x

Zanne, A. E., Lopez-Gonzalez, G., Coomes, D. A., Llic, J., Jansen, S., Lewis, S. L., … Chave, J. (2009). Global wood density database. *Dryad*.

Zanne, A. E., Oberle, B., Dunham, K. M., Milo, A. M., Walton, M. L., & Young, D. F. (2015). A deteriorating state of affairs: How endogenous and exogenous factors determine plant decay rates. *Journal of Ecology*, *103*(6), 1421–1431. https://doi.org/10.1111/1365-2745.12474

Tables

Table 1. Mean soil temperature and moisture in closed canopy and forest gap sites and outputs from linear mixed effects models to assess the effect of gaps on soil conditions (asterisks indicate significant differences between closed canopy and gap sites).

Microclimate metric	**Mean value** Closed canopy		Forest gap		**t-value**	***P***
Min. soil temp. (ºC)	22.7 7	± 0.22	23.2 5	± 0.17	2.56	0.01*
Mean soil temp. (ºC)	24.0 9	± 0.07	24.4 0	± 0.07	3.22	0.001 **
Max soil temp. (ºC)	25.1 3	± 0.10	25.3 8	± 0.09	1.38	0.17
Min. soil moisture	12.9	± 0.39	14.0	± 0.24	2.28	0.02*

(%)			0		6			
Mean soil moisture			19.5		20.9			
(%)			0	± 0.44	5	± 0.48	2.65	0.01*
Max soil moisture			26.7		30.2			0.001
(%)			7	± 0.58	6	± 0.76	3.37	**

Table 2. Estimates of geometric mean carbon fluxes and standard deviation intervals (square brackets) based on $1x10^6$ simulations for the following scenarios: a closed canopy baseline; a scenario with 0.7% forest gap, which, based on the LiDAR data, is the cumulative percentage of forest area that is a gap of the same size as our focal experimental gaps (between 0.025 and 0.16 ha); and a scenario with 2.5% forest gap, which is the total (maximum) proportion of forest that was classified as a gap in the LiDAR survey.

	Baseline	**0.7% gaps**	**Forest**	**2.5% gaps**	**Forest**

Carbon flux ($Mg\ C\ ha^{-1}\ yr^{-1}$)	1.47 [0.57, 3.83]	1.56 [0.61, 3.96]	1.74 [0.70, 4.32]
Ratio to baseline	1.000	1.057 [0.969, 1.152]	1.182 [0.846, 1.477]
Carbon flux for LiDAR region ($Mg\ C\ yr^{-1}$)	1380 [530, 3600]	1460 [570, 3720]	1640 [660, 4060]

Figure legends

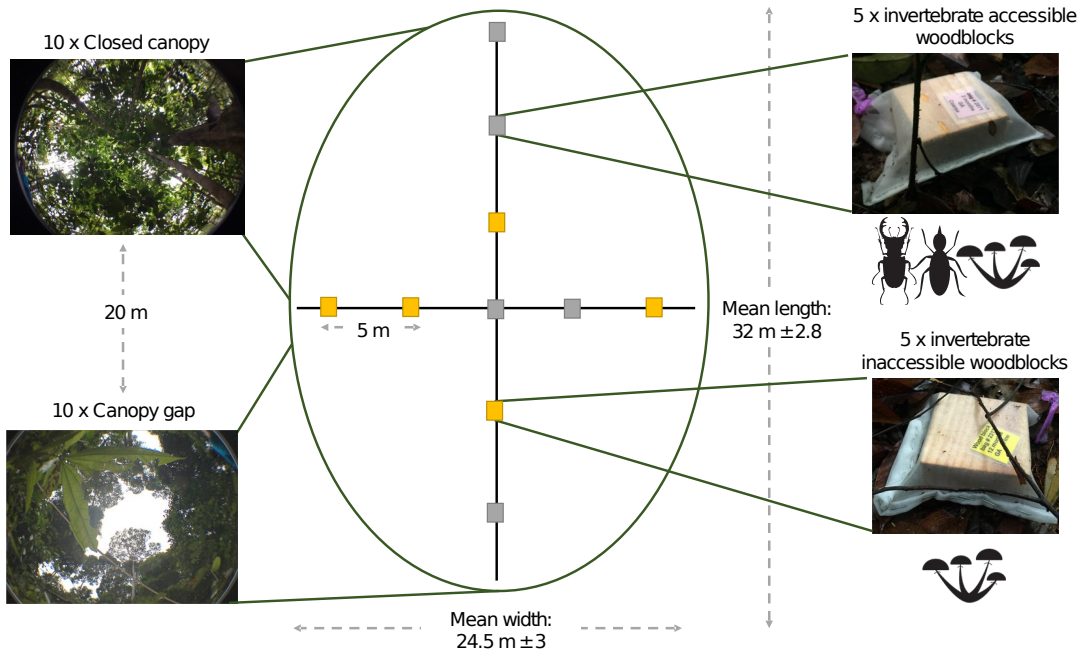
Figure 1. Schematic diagram of the study experimental design. In October 2017, we selected 10 canopy gaps (mean width 24.5 m, mean length 32 m), created by tree-fall during a storm even in July 217, and 10 paired closed canopy sites (located 20 m from the edge of each gap). Within each gap and closed canopy site, we randomly placed 5 x invertebrate accessible woodblocks (represented by the grey boxes) and 5 x invertebrate inaccessible woodblock (yellow boxes). Each woodblock was separated by at least 5 m and was left on the forest floor for 12-months.

Figure 2. Median plus interquartile range for mass loss from macroinvertebrate accessible (grey boxes) and macroinvertebrate inaccessible (yellow boxes) wood blocks within closed canopy and tree-fall gaps. Points are the raw data are displayed over the boxes.

Figure 3. Frequency distributions of minimum, mean and maximum soil temperature (panels a, c, e) and soil moisture (panels b, d, f) within closed canopy (grey ribbons) and forest gaps (yellow ribbons). Vertical dashed lines indicate significant differences between mean microclimate attributes in the different canopy types (closed canopy: grey lines, forest gaps: yellow lines).

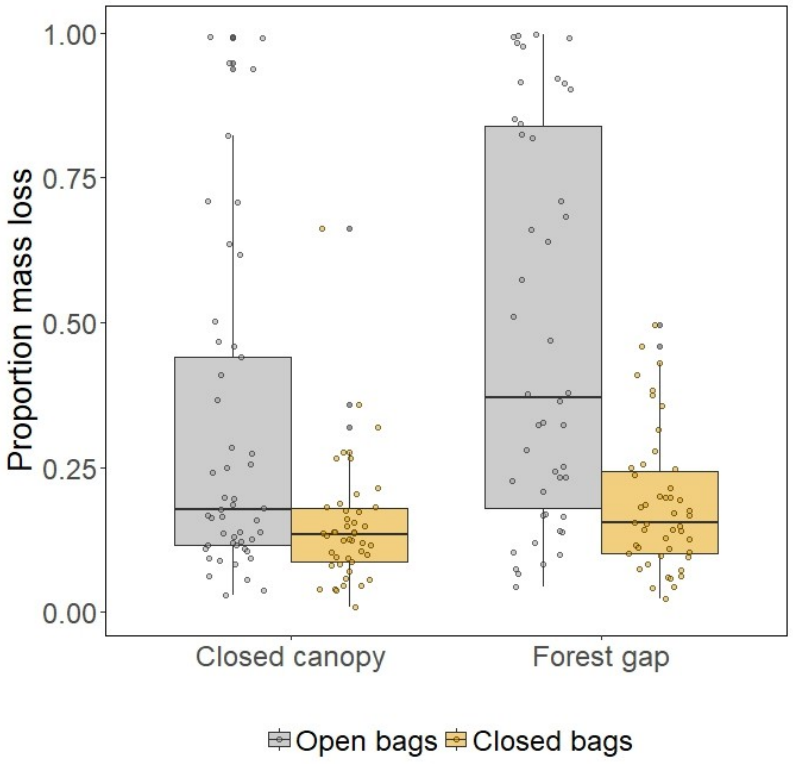
Figure 4. Cumulative distribution of canopy gap area. Gaps of the same area as those forming the basis of this investigation (128 gaps, between 0.025 and 0.16 ha) fall within the yellow rectangle. The total area represented by the yellow rectangle is 6.5 ha, which is 0.7 % of the surveyed area and represents 27% of the total gap area in the study region. The vertical dashed line at 122 m^2 (0.01 ha) represents the centre of the cumulative distribution function, where half of the gap area is comprised of smaller gaps and the remaining half by larger gaps.

Figure 5. Median (horizontal lines) plus 95% confidence intervals (whiskers) of the volume of deadwood on the forest floor beneath closed canopy (grey box) and sites within 5 m of a canopy gap.



1086

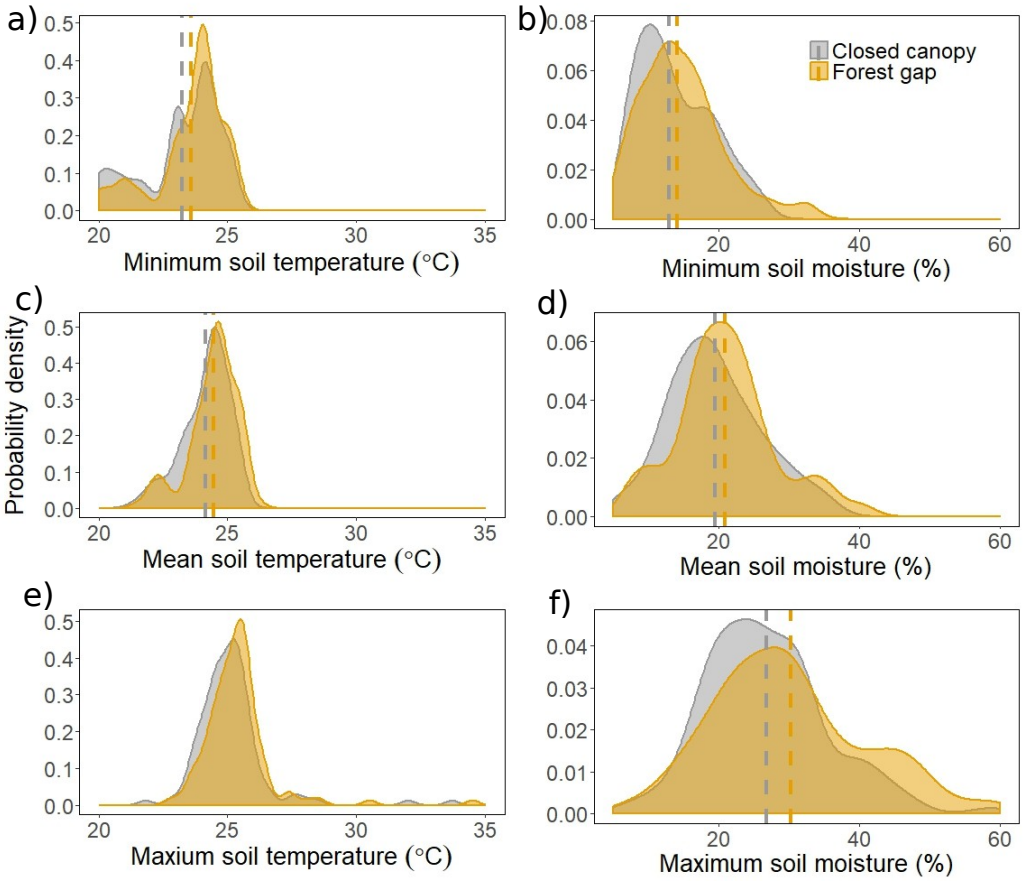
1087 **Figure 1.**



1088

1089 **Figure 2.**

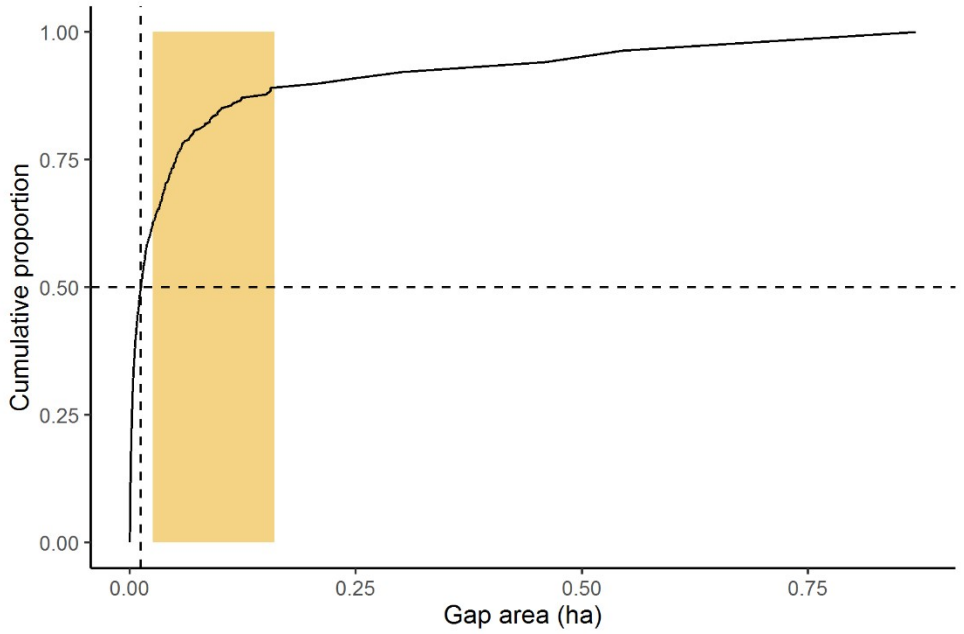
1090



1091

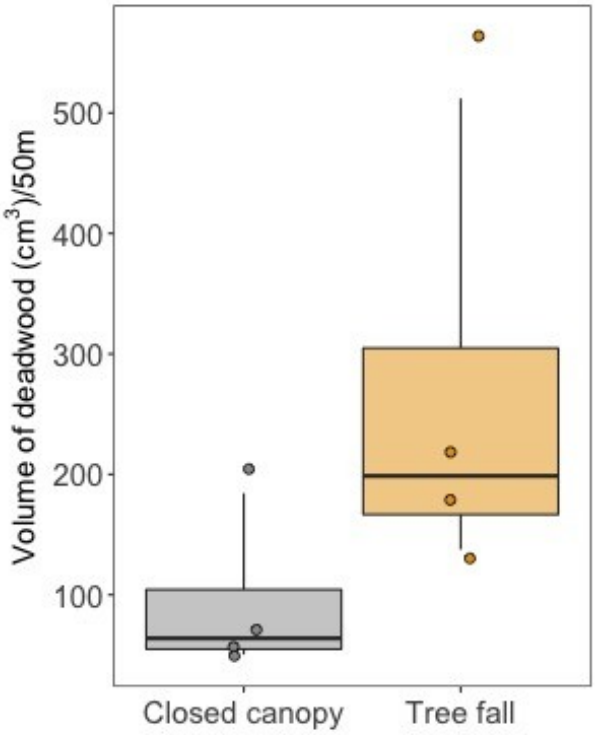
1092 **Figure. 3**

1093



1094

1095 **Figure 4.**



1096

1097 **Figure 5.**