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1 Title: Very low stocks and inputs of necromass in wind-affected tropical forests

2

3 Heading: Wind effects on deadwood dynamics

4

5 Kuo-Jung Chao^{1*}, Pin-Siou Liao^{1,2}, Yi-Sheng Chen^{1,2}, Guo-Zhang Michael Song³

6 Oliver L. Phillips⁴, and Hsing-Juh Lin²

7 ¹International Master Program of Agriculture, National Chung Hsing University,

8 Taichung 40227, Taiwan

9 ²Department of Life Sciences, National Chung Hsing University, Taichung 40227,

10 Taiwan

11 ³Department of Soil and Water Conservation, National Chung Hsing University,

12 Taichung 40227, Taiwan

13 ⁴School of Geography, University of Leeds, Leeds, LS2 9JT, U.K.

14

15 **Corresponding author**

16 Kuo-Jung Chao, Email: kjungchao@dragon.nchu.edu.tw

17 Tel: +886 4 22840850 ext. 626

18

19 **Authors' Contributions**

20 KJC and GZMS designed the study. KJC, PSL and YSC carried out analysis with

21 inputs from GZMS, OLP, and HJL. KJC, PSL and YSC wrote the manuscript with

22 inputs from GZMS, OLP, and HJL. PSL and YSC coordinated data collection with

23 the help of KJC, GZMS and HJL. All co-authors commented on the manuscript.

24

25

26 **ABSTRACT**

27 The relationships between climate and forest dynamics can help us to interpret
28 patterns of ecosystem carbon and to predict how forests react to climatic changes.
29 We report mass dynamics of deadwood (necromass) from tropical forest ecosystems
30 subject to some of the highest frequency of tropical cyclones in the world and to
31 regular, persistent seasonal monsoon winds. Plots that are influenced by typhoons
32 but exposed to different degrees of monsoon winds were monitored. We expected
33 that stocks and inputs of necromass would reflect the seasonal intensity of wind
34 events and be higher in the high wind exposure forest than in the low wind exposure
35 forest, especially for fallen woody debris. The results showed that necromass input
36 was indeed influenced by the magnitude of typhoons and aggravated by monsoon
37 winds. However, while there was no significant difference in stock of necromass
38 between plots, inputs of standing necromass were significantly higher in the high
39 wind exposure plot; these were mostly derived from dead resprouts. Both our forests
40 had very low values of total necromass stocks (3.47 - 4.32 Mg C ha⁻¹) and inputs
41 (2.1 - 2.5 Mg C ha⁻¹ yr⁻¹) compared with tropical forests worldwide. Our results
42 show that both monsoon and typhoon winds shape these tropical forests, favouring
43 low stature individuals and trees with ability to resprout, and that these strategies
44 provide these forests with remarkable resistance and resilience to wind disturbances.
45 Our findings from some of the most wind-affected forests in the world indicate how
46 woody carbon dynamics and forest structure in other regions may respond to future
47 changes in the frequency and intensity of winds.

48

49 **Key words:** carbon balance, decomposition, monsoon, necromass production,
50 tropical forests, typhoon, woody debris dynamics, climate change.

51

52 **HIGHLIGHTS:**

- 53 ● Locally, wind strength regulates the seasonal inputs of tropical forest
54 necromass
- 55 ● Globally, winds result in low carbon stocks in both biomass and
56 necromass in tropical forests
- 57 ● Key resistance and resilience mechanisms to winds are short stature and
58 resprouts

59

60 **INTRODUCTION**

61 Tropical forests are vital ecosystems for storing and sequestering carbon (Pan and
62 others, 2011; Quéré and others, 2018). The three major carbon pools in forest
63 ecosystems are biomass (above- and below-ground living plants), necromass (litter
64 and woody debris (deadwood)), and soil organic carbon. While all pools contribute
65 to carbon storage (stocks) and carbon sequestration (input and output fluxes), most
66 attention is usually given to aboveground biomass (IPCC, 2006; Köhl and others,
67 2015; Clark and others, 2017). The fluxes between each of these carbon pools are
68 critical for determining the overall carbon storage and budgets in the ecosystem.
69 Woody debris inputs into the necromass pool and losses of necromass are among
70 these key carbon fluxes (Trumbore, 2006; Palace and others, 2012), and given the
71 increased rates of tree mortality in some forests (e.g. McDowell and others, 2018)
72 necromass stocks may also increase (Brienen and others, 2015). Therefore, by
73 neglecting to account for the necromass pool and associated fluxes, we incompletely
74 assess the carbon balance in tropical forests and may not properly represent its true
75 climate sensitivity (*c.f.* Sullivan and others, 2020).

76

77 While forest necromass stocks are in practice highly correlated with biomass (Chao
78 and others, 2009a), they should also reflect the balance between necromass
79 fluxes—its input (necromass production) and its output (necromass decomposition).
80 Necromass input is contributed by the quantity of woody debris produced by both
81 tree death and branch-fall (van der Meer and Bongers, 1996; Palace and others,
82 2008), with the causes of necromass input being primarily senescence, competition,
83 stress, and disturbance (Franklin and others, 1987). The output of necromass is
84 mainly controlled by environmental factors, such as temperature (Chambers and
85 others, 2000; Berbeco and others, 2012), and less so by the local biodiversity of
86 decomposers and tree species traits (Pietsch and others, 2019). As annual
87 temperatures normally only change fractionally, the net balance between input and
88 output of necromass is likely to be most strongly determined by the frequency and
89 magnitude of the disturbances that can cause tree death and branch fall.

90

91 Examining different types of woody debris can indicate the causes of tree death
92 (Chao and others, 2009b). In general, the standing mode of death is related to
93 senescence, competition, or stress, whereas the fallen mode of death is strongly
94 associated with physical disturbance (Chao and others, 2009b; Esquivel-Muelbert
95 and others, 2020). For example, typhoons are likely to increase the number of fallen
96 branches and uprooted trees (Whigham and others, 1991), and trees may also die
97 snapped in wind events due to structural imbalances between root anchorage and
98 stem strength (Soethe and others, 2006). Therefore, understanding the types and
99 magnitudes of woody debris present in forests can help indicate the major
100 characteristics and mechanisms of woody debris dynamics.

101

102 Tropical cyclones are a major class of wind disturbance affecting many tropical
103 forests. While research on the effects of cyclones on tropical forests has been
104 focussed strongly on the North Atlantic Basin, the much less studied northwestern
105 Pacific basin is the most active region on Earth for tropical cyclones (Lin and others,
106 2020). As a tropical and subtropical island in the northwestern Pacific, Taiwan
107 experiences one of the highest typhoon disturbance rates of any landmass in the
108 world (Lugo, 2008; Lin and others, 2010; Lin and others, 2020) so forests here are
109 likely to be among the most affected by tropical cyclones. As well as typhoons,
110 though, the tropical northwestern Pacific is also influenced by northeast monsoons
111 in winter (Wang, 2004). The prevailing monsoon winds are known to influence
112 forest structure, such that monsoon-windward forests can be characterised by low
113 canopy height and high stem density (Lawton, 1982; Chao and others, 2010b)
114 (Appendix 1ab). Indeed, one patch of monsoon-windward forest that we monitor in
115 Taiwan (Lanjenchi Plot) has one of the highest stem densities among forests globally
116 (Lutz and others, 2018). However, the effects of typhoons and monsoon winds on
117 necromass dynamics here remain poorly understood, and by accounting for the
118 effects of these two distinctive climatic processes on necromass dynamics, it will be
119 possible to understand forest ecosystem carbon dynamics and their climate
120 sensitivities better. Furthermore, as the patterns of typhoons and monsoons are
121 changing (Xu and others, 2006; Tu and others, 2009; Jiang and Tian, 2013; Lin and
122 Chan, 2015), evaluating the potential ecological effects of these changes on a global
123 scale requires long-term monitoring of forest localities with pre-existing influences
124 of typhoons and monsoons.

125

126 This study aims to investigate the patterns of necromass dynamics and balance in
127 two forest ecosystems affected by both typhoons and monsoon winds - one located
128 in the high wind-exposed slopes of a coastal mountain (Appendix 1ab), the other
129 located in a relatively low wind-exposed valley (Appendix 1cd) (Figure 1a). At the
130 landscape scale, the two forests experience a different degree of influence from the
131 unidirectional, long-lasting, northeast winter monsoon (Figure 1). However, at the
132 regional scale, both forests have a similar probability to being disturbed by
133 short-period typhoons with unpredictable wind directions in summer (Figure 1). In
134 light of these differences and the fact that the study plots are close to each other (< 3
135 km apart, compared to the average 200 to 300 km radius of typhoons), we propose
136 the following general hypothesis and specific predictions.

137

138 Hypothesis: The combined effect of these winds results in unusually high
139 accumulation (stocks) and production (inputs) of woody debris. Our expectations are
140 listed below.

141 1. Necromass stock

142 Necromass stocks are greatest in localities exposed more to winds.

143 2. Necromass input

144 2.1. Necromass inputs are higher in localities exposed more to winds.

145 2.2. Fallen woody debris inputs are mainly determined by the magnitude of
146 winds, whereas standing woody debris inputs are unaffected by these.

147

148 **METHODS**

149 **Study area**

150 The first study plot, Lanjenchi Plot (5.88 ha; 220 m by 240 to 300 m; 120° 51' 38" E,

151 22° 03' 23" N), is located on coastal mountain upper slopes and hilltops which are
152 exposed to northeast monsoon wind (Chao and others, 2010b) (Figure 1a; hereafter
153 the high wind exposure plot). The second set of study plots, Nanjenshan Plots I (2.1
154 ha; 150 m by 140 m; 120° 50' 51" E, 22° 04' 54" N) and II (0.64 ha; 80 m by 80 m;
155 120° 50' 36" E, 22° 04' 52" N), is located on the valley of the same mountain range
156 which has low exposure to monsoon wind (Figure 1a) (Chao and others, 2010b). The
157 floristic composition of the Nanjenshan plots is very similar to one another (Chao
158 and others, 2010a), so results from Nanjenshan Plot I and Plot II are here treated
159 together as one sample, denoted the 'Nanjenshan' or 'low wind exposure plot'.

160

161 Although the two forests are close together and their elevations differ little, their
162 topographic characteristics, average wind speed (sustained and gust), and vegetation
163 types and structure are all significantly different (Figure 1; Table 1; Appendix 2).
164 The high wind exposure plot (Lanjenchi) is situated on the upper slope of a low
165 elevation coastal mountain range, directly facing the Pacific Ocean (Figure 1a). Due
166 to its lacking any protection from other mountain ranges, the median sustained wind
167 speed in the high wind exposure plot during the winter monsoon season is high
168 (Figure 1b; methods please see Appendix 2), which was proposed to be the major
169 causal factor of the high stem density and low aboveground biomass in the plot
170 (Table 1) (Chao and others, 2010b). The low wind exposure plot (Nanjenshan) is
171 further inland situated in a valley protected by two mountain ranges. The slopes of
172 the low wind exposure plot mostly face northeast and northwest, but are less
173 influenced by the winter monsoon due to mountain ranges to the northeast (Figure
174 1a).

175

176 The wind regimes of the plots are a complex of summer typhoons and winter
177 monsoon winds (Figure 1b). In monsoon season the ‘high’ wind exposure plot has
178 higher median sustained wind speed (Figure 1b). In typhoon season, because
179 typhoon wind directions are unpredictable, both plots can be affected by typhoons.
180 Therefore, in some years the maximum sustained wind speed can be high in typhoon
181 season at the ‘low’ wind exposure plot (Figure 1b). A preliminary analysis showed
182 that there are significant differences in sustained wind speed between plots (two-way
183 ANOVA using \log_{10} transformed wind speed, $F_{1,374256} = 47180$, $p < 0.001$) and
184 between seasons ($F_{3,374256} = 9567$, $p < 0.001$). Similar patterns can also be found
185 when examining gust wind speeds between months (Appendix 2).

186

187 **Necromass stock and input**

188 Woody debris was defined as those dead woody branches or trunks of plants with
189 diameter ≥ 1 cm. At the high wind exposure plot, three east to west transects (200 m,
190 200 m, and 198 m) were established in February 2012, and two north to south
191 transects (280 m and 190 m) were established in February 2013. At the low wind
192 exposure plot, eight transects were established in February 2013 (five in Plot I (111
193 m, 105 m, 105 m, 100 m, and 105 m) and three in Plot II (64 m, 60 m, and 60 m)).
194 Three of the transects are oriented east to west and five run north to south. A total of
195 1,778 m were sampled in the study plots (Liao, 2017). Since establishment,
196 investigation of newly formed/fallen woody debris (necromass input) on transects
197 was conducted seasonally every three months until February 2018. In the meantime,
198 necromass stocks were censused annually. The census times fall close to the
199 beginning of February, April, July, and October, but with adjustments of up to ± 30
200 days in some cases. Necromass stock and input were quantified and analysed for a

201 total of 6 years in the high wind exposure plot and 5 years in the low wind exposure
202 plot.

203

204 A line-intersect method (van Wagner, 1968) was used to investigate fallen woody
205 debris on the transect lines. A plot method (Harmon and Sexton, 1996) was used to
206 sample standing woody debris within 5 m on each side of the transect lines. For
207 fallen woody debris pieces on the intersect lines, their diameters (d) were measured
208 and void proportion was estimated. For those standing woody debris pieces
209 (including dead resprouts of multi-stemmed individuals) located within 5 m on each
210 side of the intersect lines, their diameters at the base (d_b) and top (d_t), and their
211 height (L_s (m)) were measured and void proportion was estimated. All measured
212 woody debris pieces were numbered and tagged with nylon strings to identify
213 samples of each census. Woody debris was classified into five decay classes, such
214 that decay class 1 indicates a piece of intact wood and decay class 5 indicates a piece
215 of rotten wood (Chao and others, 2017).

216

217 Volumes and carbon mass of fallen and standing woody debris were estimated,
218 respectively. (1) Volumes of fallen woody debris pieces were estimated by

$$v_f = (\pi^2 \sum d^2) / 8 L, \quad \text{eqn 1}$$

219 based on the line-intersect method (van Wagner, 1968), where v_f is the volume at the
220 unit area ($\text{m}^3 \text{ha}^{-1}$), d is the intercepted diameter (cm) of each fallen woody debris
221 piece and L is the total length (m) of each transect. The equation assumes that each
222 sample line will cross woody debris at various angles, making a set of vertical
223 elliptical cross-sections. Once integrated, the cross-sectional area per unit length
224 ($\text{cm}^2 \text{m}^{-1}$) can be used to estimate woody debris volume per unit area ($\text{m}^3 \text{ha}^{-1}$). If

225 there is any void proportion noted for a particular piece of woody debris, its actual
 226 volume is multiplied by (1 – void proportion). (2) Volumes of each standing woody
 227 debris piece were estimated by Smalian’s formula (Phillip, 1994):

$$v_s = (\pi / 8) \times L_S \times (d_b^2 + d_t^2), \quad \text{eqn 2}$$

228 where v_s is the volume (m^3) of the target standing woody debris, d_b and d_t (m) are
 229 the diameters at base and top, respectively, and L_S (m) is the length of the target
 230 standing woody debris. If there is any void proportion noted for a particular piece of
 231 woody debris, its actual volume is multiplied by (1 – void proportion). The standing
 232 woody debris volume per unit area ($\text{m}^3 \text{ha}^{-1}$) was computed as the sum of the total
 233 volume of standing woody debris sampled in a transect divided by the transect area,
 234 and standardised to a per hectare value. The averages of the plot-level volumes were
 235 weighted by transect length (Keller and others, 2004). Plot-level variance (σ^2) values
 236 were also weighted by transect length as suggested by Keller and others (2004).

$$\sigma_i^2 = \frac{[\sum L_j (v_{ij} - \bar{v}_i)^2]}{[(n-1) \sum L_j]}, \quad \text{eqn 3}$$

237 where L_j is the length of each transect; v_{ij} is the measured volume (either standing or
 238 fallen woody debris) of each transect j ($\text{m}^3 \text{ha}^{-1}$) at the decay class i ; \bar{v}_i is the
 239 weighted average of each plot at the decay class i ; n is the number of sampled
 240 transects. Standard error of the mean (SE) was calculated as σ/\sqrt{n} . Plot-level SE is
 241 the sum of each SE at each decay class (Chao and others, 2017).

242

243 Field measurement of woody debris volume (v_i) of woody debris (either standing or
 244 fallen) at decay class i can be converted to necromass carbon (NC , Mg C ha^{-1}) by
 245 multiplying with woody debris density (ρ , g cm^{-3}) and carbon concentration (c , g g^{-1}
 246 (*i.e.* carbon fraction)) at each decay class (i).

$$NC = \sum_{i=1}^5 v_i \times \rho_i \times c_i \quad \text{eqn 4}$$

247 In this study, we applied the woody debris density and carbon concentration at each
248 decay class reported in Chao and others (2017).

249

250 All newly encountered woody debris pieces were tagged and recorded as new input.

251 Necromass input was calculated for each census based on the necromass carbon of

252 newly recorded pieces of woody debris (either standing or fallen) at that census

253 divided by the number of days between censuses ($NC_I = NC / \text{number of days}$). As

254 the number of days varied from 49 to 128 days, necromass input rates were

255 standardised to annual equivalents ($NC_I, \text{Mg C ha}^{-1} \text{ yr}^{-1}$). Preliminary results showed

256 that fine woody debris (diameter $< 5 \text{ cm}$ and $\geq 1 \text{ cm}$ (FWD)) contributed

257 disproportionately to the number of pieces of necromass but represented relatively

258 small carbon stocks (Appendix 3). Thus, after July 2016, we only measured

259 intermediate ($\geq 5 \text{ cm}$; IWD) and coarse woody debris ($\geq 10 \text{ cm}$; CWD). To account

260 for the fine woody debris, estimates of total necromass after July 2016 were adjusted

261 by the plot-level and woody-debris type average ratios of fine to other woody debris

262 (intermediate and coarse), based on censuses between February 2012 and April

263 2016.

264

265 **Necromass decomposition and net fluxes**

266 Decomposition constant of necromass (k) was investigated for one year in each

267 forest (April 2012 to April 2013 in the high wind exposure plot; April 2013 to April

268 2014 in the low wind exposure plot). In each plot we set up 16 quadrats (each 10 m

269 $\times 10 \text{ m}$) separate from the woody debris transects and measured the diameter of each

270 coarse woody debris piece (≥ 10 cm) at both ends. Additionally, decomposition class,
 271 length, and proportion of void space were recorded (Liao, 2017). Each coarse woody
 272 debris piece (≥ 10 cm) was numbered and tagged with a nylon string. Within each
 273 quadrat, a subquadrat (2 m \times 2 m in the high wind exposure plot; 1 m \times 1 m in the
 274 low wind exposure plot) was set up in the south-west corner to investigate the fine
 275 and intermediate woody debris (≥ 1 cm, < 10 cm). The diameters, decomposition
 276 class, and length of each fine and intermediate woody debris were also recorded. To
 277 distinguish the remaining woody debris from newly fallen pieces at the next census,
 278 we covered these measured fine and intermediate woody debris pieces with fishnets.
 279 The necromass carbon of each woody debris pieces at the beginning of the census
 280 (Y_0 , Mg of Carbon) in the selected quadrats was calculated using eqn 2 and eqn 4.
 281 Each woody debris piece was revisited a year later ($t = 1$ yr), and each parameter
 282 measured again to calculate the necromass at the end of the census (Y_t , Mg of
 283 Carbon). The negative single-exponential decay equation was applied to calculate
 284 the decomposition constant (k , yr⁻¹) (Olson, 1963):

$$k = \ln \left(\frac{Y_0}{Y_t} \right) / t \quad \text{eqn 5}$$

285 Thereafter, with the annual necromass census data and the decomposition constant,
 286 the annual decomposition quantity of necromass carbon (NC_D) of a specific year (t)
 287 can be estimated as

$$NC_D = NC_{S,t} - NC_{S,t+1} = NC_{S,t} - (NC_{S,t} \times e^{-k \times 1}) \quad \text{eqn 6}$$

288 where $NC_{S,t}$ and $NC_{S,t+1}$ (Mg ha⁻¹) is the stock of necromass at time t and remaining
 289 stock at $t+1$. Note that the $NC_{S,t+1}$ here was calculated based on the decomposition
 290 constant k , rather than from our direct field measurement at time $t+1$, because the
 291 direct field measurement at time $t+1$ would also include inputs of new woody debris.

292

293 The net flux of necromass is the difference between the annual input quantity (April,
294 July, October of year t and February of year $t+1$) of necromass carbon and annual
295 decomposition quantity of necromass carbon at time t (calculated based on
296 measurement of year t).

297

298 **Estimating wind disturbance**

299 Climatic data, including the number of typhoons, sustained wind speed, and
300 precipitation, were extracted from the records recorded in the Hengchun Station (No.
301 467590; about 20 km away from the study plots) in the Central Weather Bureau
302 climate database (Central Weather Bureau, 2019). We used the power dissipation
303 index (PDI) (Emanuel, 2005; Yu and Chiu, 2012), including annual wind (PDI_{annual}),
304 seasonal wind (PDI_{seasonal}) and typhoon (PDI_{typhoon}), to evaluate the effect of winds.
305 Only one weather station dataset was used for the PDI indices because the
306 Hengchun station records the required maximum sustained wind speed data at 10 m
307 above ground as proposed by Emanuel (2005). This provides a background regional
308 magnitude of winds, rather than the local sustained wind speed data at 2 m height
309 (*c.f.* those in Figure 1a and Appendix 2).

310

311 PDI was first proposed by Emanuel (2005) to estimate the power and magnitude of
312 typhoon winds. The original equation is as follows:

$$\text{PDI} \equiv \int_0^{\tau} V_{max}^3 \quad \text{eqn 7}$$

313 V_{max} is the maximum sustained wind speed at 10 m and integrated over lifetime τ (in
314 units of second) of the typhoon. The V_{max} (m s^{-1}) in our study was the 6-hourly
315 maximum sustained value of each typhoon (V_{max} in PDI_{typhoon}) or daily-maximum
316 sustained wind speed of each day (V_{max} in PDI_{annual}, PDI_{seasonal}). PDI ($10^9 \text{ m}^3 \text{ s}^{-2}$) was

317 the integral of V_{max} . For $PDI_{typhoon}$, we included each typhoon that the Central
 318 Weather Bureau had issued warning reports for Taiwan Island (Central Weather
 319 Bureau, 2019). Although warning reports for Taiwan may not always relate to a visit
 320 of typhoons to the study forests, it provides a consistent basis for extracting
 321 wind-speed data that reflect the approximate magnitude of each typhoon on the
 322 study region.

323

324 In the literature, PDI is used only for evaluating the magnitude of typhoons. Here we
 325 applied the same index to evaluate the effects of prevailing winds throughout the
 326 year. In annual and seasonal PDI of this study, the V_{max} was the daily-maximum
 327 sustained wind speed of each day (*c.f.* the 6-hourly maximum sustained wind data
 328 used in the typhoon PDI index) and integrated over each woody debris census study
 329 period. A trapezoidal rule was applied to approximate the results of annual and
 330 seasonal PDI ($10^9 \text{ m}^3 \text{ s}^{-2}$).

$$\begin{aligned}
 PDI &\equiv \int_0^{\tau} V_{max}^3 \\
 &\approx \sum_{t=0}^{n-1} \frac{\Delta t}{2} (V_{max\ t=0}^3 + 2V_{max\ t=1}^3 + 2V_{max\ t=2}^3 + \dots + 2V_{max\ t=n-1}^3 + V_{max\ t=n}^3),
 \end{aligned}$$

eqn 8

331 where Δt represents the total time (in seconds) of the study period. Our calculations
 332 of PDI_{annual} and $PDI_{seasonal}$ overestimate the magnitude of wind of each day due to
 333 only daily V_{max} being used (*c.f.* $PDI_{typhoon}$). However, as 6-hourly data are not readily
 334 available in the study forests, the estimation can provide a consistent index of
 335 relative wind magnitude throughout our study period.

336

337 **Data analysis**

338 Linear mixed-effect models were used to examine the relationships between
339 necromass and variables. The package lme4 (Douglas and others, 2015) in the
340 program R (R Core Team, 2019) was applied. We use each transect as the random
341 intercept effect (denoted as 1|transect) to account for repeat measurements of each
342 transect. Other factors, including Plot, PDI, number of typhoons, and precipitation
343 were used as fixed effects. If dependent or independent variables were not normally
344 distributed when constructing the models, we transformed the variables to have an
345 approximately normal distribution pattern. Where variables include the value 0,
346 which cannot be log-transformed, we added a small fixed value of 0.1 or 0.01,
347 depending on which leads to a better approximation to a normally distributed pattern.
348 Sample-size corrected Akaike information criterion (AIC_c) values were used for
349 model comparison (Burnham and Anderson, 2002), such that the model with the
350 lowest AIC_c value was considered to be the best model (*i.e.* AIC_c differences Δ
351 $AIC_c = 0$).

352

353 **RESULTS**

354 **Quantity of necromass carbon stock**

355 The total necromass stock was 3.47 ± 0.32 Mg C ha⁻¹ (average \pm SE) from 2012 to
356 2018 at the high wind exposure plot and 4.32 ± 0.43 Mg C ha⁻¹ from 2013 to 2018
357 at the low wind exposure plot (Appendix 4). The annual variation of total stock
358 reflects the patterns of the fallen stock rather than the standing stock (Figure 2).
359 Standing stock was significantly higher in the low wind exposure plot than the high
360 wind exposure plot (Mann-Whitney U test, $p = 0.014$; Appendix 5c), but plots were
361 indistinguishable in terms of total and fallen stocks ($p = 0.101$, $p = 0.836$,
362 respectively; Appendix 5ab). When controlling for the differences of transects, none

363 of the investigated variables helped explain the patterns of the total, fallen, and
364 standing stocks, as their AIC_c values were all higher than the Null model ($\Delta AIC_c >$
365 0; Appendix 6).

366

367 **Quantity of necromass input**

368 The quantity and variations of woody debris input showed that total necromass input
369 (Figure 3a) was mainly contributed by fallen woody debris (Figure 3b). The quantity
370 of standing necromass input is low (Figure 3c), and contributes less to the ‘total’
371 necromass input (Figure 3a), as with stocks.

372

373 The number of typhoons varied between years (Figure 3), with high PDI
374 corresponding with high rates of inputs of total, fallen, and standing woody debris
375 (Appendix 7Figure 4). As necromass input was not normally distributed
376 (Shapiro-Wilk normality test, $p < 0.001$), we \log_{10} transformed the data to have an
377 approximately normal distribution before applying the following tests. Total, fallen
378 and standing necromass input differ significantly between seasons (Appendix 7).
379 The results of the linear mixed-effect model indicated that PDI_{seasonal} was the best
380 climatic variables for explaining the seasonal variation in the total, fallen, and
381 standing necromass input (Table 2). The best models ($\Delta AIC_c = 0$) were those
382 included both Plot and PDI_{seasonal} (Table 2). Including the interaction variables (Plot
383 and the best climatic variable) improved the fallen input and the standing input
384 models (Table 2). Notably, the coefficients of the Plot variable of the best models
385 were opposite for the fallen and the standing necromass input models (Table 3).

386

387 **Necromass decomposition and net fluxes**

388 The decay rate constant of the study area ranged from 0.57 to 1.09 yr⁻¹ (Appendix 8).
389 The fast decomposition of IWD and FWD in the low wind exposure plot, resulted in
390 the half-life of woody debris < 10 cm being less than one year. We found that the
391 annual necromass input and decomposition fluxes fluctuated annually (Figure 5a).
392 Also, the net flux fluctuated around 0 (Figure 5b). On average, net flux was 0.40 ±
393 0.43 (Mg C ha⁻¹ yr⁻¹) at the high wind exposure plot and 0.08 ± 0.69 (Mg C ha⁻¹ yr⁻¹)
394 at the low wind exposure plot during the study period (Figure 5b; Appendix 4).

395

396 **DISCUSSION**

397 **Necromass stock and input at the global scale**

398 Our study forests are located on a tropical island that experiences strong
399 disturbances from both typhoon and monsoon winds (Wang, 2004; Tu and others,
400 2009). Remarkably, the total quantity of necromass carbon stock in both plots was
401 very low compared to other tropical forests (Figure 6a). Lutz and others (2018)
402 compared many temperate and tropical forests and found that our high wind
403 exposure plot (Lanjenchi) was ranked as one of the smallest biomass forests globally.
404 Chao and others (2009a) proposed that there is a relationship between aboveground
405 biomass and necromass stock in Amazonian forests. Our study supports this
406 relationship but, by mobilising considerably more data (Figure 6a), it is now clear
407 that necromass tracks tropical forest biomass stocks over a very broad geographical
408 range (Figure 6a).

409

410 The necromass input measured in our study plots is also low relative to other studies
411 in mature tropical forests (Figure 6b). Notably, the differences in necromass *inputs*
412 between our study forests and other studies (up to half) (Figure 6b) are less marked

413 than the differences in necromass *stocks* (up to one-tenth less) (Figure 6a). Lin and
414 others (2020) noted that the major consequences of typhoons on forest ecosystems in
415 Taiwan are typically defoliation, rather than tree death. Our study further shows that
416 at the global scale, the input of branch-fall and tree-fall in highly wind-disturbed
417 forests are low compared to other tropical forests (Figure 6). The low necromass
418 inputs and stocks are likely to be mediated by their low biomass.

419

420 The causal reasons for low biomass in the study forests can be attributed to the
421 dwarfing effect of typhoons, as hypothesised by Lin and others (2020), or of
422 monsoon winds, as hypothesised by Chao and others (2010b), or both. Our study
423 provides evidence that both wind regimes shape the structure of these forests (see
424 Discussion in ‘Short-term effects of climatic variables on necromass input’). Across
425 the tropics, we expect that due to the long-term interaction of forests with wind
426 disturbances, other localities with frequent typhoon and monsoon winds will also
427 have low necromass stocks and unusual forest structure. These forests are expected
428 to develop a wind-resistant physiognomy that includes many slim and short stems
429 which generate relatively small quantities of woody necromass (Figure 7a).

430

431 **Necromass stock and input at the landscape scale**

432 At the landscape scale, despite the significant structural differences in stem density
433 and biomass (Table 1), we detected no significant difference in total necromass stock
434 between the study plots. Moreover, total necromass carbon stock quantities were not
435 readily explained by any of the variables (Appendix 6). These results do not support
436 our prediction 1 and suggest that at the landscape scale, total necromass stocks are
437 unrelated to the effects of the regional prevailing wind, when accounting for transect

438 variations (Appendix 6). This indicates that the differences are due to specific
439 conditions of some transects being more likely to accumulate higher necromass than
440 others. Thus, at the landscape scale, there is no evidence of direct effects of wind
441 magnitude on necromass stocks.

442

443 Necromass input, however, is greater for the high wind exposure plot than the low
444 wind exposure plot, after accounting for the differences at each transect (Table 3).
445 The coefficient of the Plot variable for the total necromass input model was positive
446 (Table 3), suggesting that the high wind exposure plot had greater total necromass
447 input during our study period, which supports our prediction 2.1. Apart from
448 disturbance exposure degree, differences in necromass input between sites could
449 also be affected by (1) forest structure, (2) species composition, and (3) frequency
450 and modal size of woody debris. We discuss these factors in turn. (1) Forest
451 structure: forest biomass and height are lower in the high wind exposure plot than
452 the low wind exposure plot (Table 1), but necromass input was no lower, so the
453 difference in necromass input cannot be explained by forest structure at the
454 landscape scale. (2) Species composition: the two forests have distinct floristic
455 composition from one another (Chao and others, 2010b), so this might be causally
456 related to the dissimilarity of necromass input at the landscape scale, potentially via
457 differences in monsoon wind regimes favouring different species. (3) Frequency and
458 modal size of woody debris: examining the patterns in woody debris size, we found
459 that the quantities of fine and intermediate standing woody debris were quite high in
460 the high wind exposure plot (Appendix 3b). Thus, a likely explanation is that the
461 accumulation of fine and intermediate standing woody debris in the high wind
462 exposure forest results in a total necromass input comparable to the quantity

463 produced in the high biomass, low wind exposure forest. In other words, the patterns
464 of necromass input are ‘small but many’ in the high wind exposure plot, and ‘large
465 but few’ in the low wind exposure plot.

466

467 The fallen necromass input was lower and the standing necromass input was greater
468 in the high wind exposure than the low wind exposure plot (Table 3). This is not
469 what we expected (prediction 2.2). According to the literature, the major causal
470 reasons for trees dying standing are senescence, competition, drought, fire, or
471 large-scale pathogen attacks (e.g. Carey and others, 1994; Nakagawa and others,
472 2000; Chao and others, 2009b). Here there were no records of drought or fire, nor
473 were there large-scale pathogen attacks during the study period. Based on our field
474 observations, we found that the majority of the standing dead woody debris have
475 signs of wind breakages and many had re-sprouting stems. This natural coppicing
476 process is consistent with elsewhere in the tropics (Zimmerman and others, 1994)
477 and indicates that the major survival strategy of trees growing in wind-influenced
478 forests is re-sprouting. Thus, we conclude that standing necromass does not
479 necessarily indicate trees or stems dying due to competition or senescence, but can
480 also arise indirectly from the strategy adopted by many trees to survive wind stress
481 by growing multiple stems. In short, at the landscape scale, the relatively high
482 necromass input in the high wind exposure forest, despite its low stature, was likely
483 caused by direct wind effects, indirect wind effects through species composition, and
484 the multiple small dead stems of coppicing trees (Figure 7b).

485

486 **Short-term effects of climatic variables on necromass input**

487 There were significant seasonal variations in wind magnitude (Figure 1b) and fallen

488 necromass input (Appendix 7b) during the study period, with greater quantities and
489 greater variation typically in typhoon and monsoon seasons. Although we refer to
490 the main typhoon season as mid-July to mid-October, typhoons can occur at any
491 month of the year. For example, the typhoon Noul (201506) was recorded in May
492 but with very low PDI ($0.01 \cdot 10^9 \text{ m}^3 \text{ s}^{-2}$) (data not shown). Strong wind mostly
493 occurred before the October and February census during our study period (Figure 3).
494 There was also among-site variation: at times the low wind exposure plot had
495 greater fallen necromass input (February 2014), while at others the high wind
496 exposure plot experienced more (January 2017) (Figure 3b). This demonstrates that
497 there are annual variations in the study forests, especially in the monsoon season.

498

499 Among the seasonal climatic variables, PDI was the best for predicting necromass
500 input when controlling for differences between transects (Table 2). Compared to
501 $\text{PDI}_{\text{seasonal}}$, neither precipitation, nor $\text{PDI}_{\text{typhoon}}$, nor the number of typhoons was a
502 good predictor (Table 2). Typhoon metrics alone ($\text{PDI}_{\text{typhoon}}$ or number of typhoons)
503 cannot reflect the major climatic patterns on necromass input. However, $\text{PDI}_{\text{seasonal}}$
504 includes not only the magnitude of typhoons but also monsoon winds, thus
505 reflecting the strength of winds from both processes. Moreover, the best model
506 includes both Plot and $\text{PDI}_{\text{seasonal}}$, suggesting that despite any other possible inherent
507 differences between plots (e.g. Table 1), $\text{PDI}_{\text{seasonal}}$ was a crucial driving force of
508 necromass input (Table 2). Moreover, including the interaction terms improved the
509 linear-mixed effect models of both the fallen and standing models, demonstrating
510 that there were different responses of plots to $\text{PDI}_{\text{seasonal}}$. Table 3 showed that large
511 $\text{PDI}_{\text{seasonal}}$ may increase the quantities of fallen but not standing woody debris in the
512 high wind exposure plot (negative coefficient of the interaction term; see also Figure

513 4). This suggests that even for a forest ecosystem frequently influenced by winds,
514 increased wind strength can still increase the likelihood of fallen woody debris, but
515 not standing woody debris.

516

517 The effects of typhoons on forest ecosystems have drawn considerable research
518 attention (Lugo, 2008; Lin and others, 2010), but those of monsoon winds much less
519 so (Yu and others, 2014). In our study, the month with the highest quantity of
520 necromass input was not October (right after the peak season of typhoons) but was
521 usually January or February, especially for fallen woody debris (Figure 3b). This
522 shows that monsoon winds can have at least as strong influence on forest carbon
523 dynamics as typhoons. This could be due to two reasons. First, the effects of each
524 typhoon at one location normally last fewer than three days, while the period of the
525 northeast monsoon can last for more than three months (from mid-October to
526 mid-February). In other words, typhoons bring winds for a short period, whereas
527 monsoons winds are relatively long-lasting. Thus, even though a single typhoon may
528 have a strong daily PDI, the cumulative seasonal PDI was stronger during monsoon
529 seasons than during typhoon seasons (Figure 3).

530

531 Second, the effects of typhoons on necromass input may be delayed. Based on our
532 observations, some trees did not die immediately after being uprooted or broken by
533 typhoons. It was common to find some fallen trunks with new sprouts after the
534 typhoon season and these may last for some time. A similar phenomenon was also
535 observed in another tropical cyclone disturbed forest (Uriarte and others, 2019).
536 However, the long-lasting monsoon wind could then have further weakened the
537 vitality of the fallen but still living trees, resulting in peak necromass input in the

538 February census (Figure 3). Also, Figure 3 reveals that in some years with weak
539 typhoon effects on the study region (e.g. September 2014 (Feng-Wong) and August
540 2015 (Soudelor and Goni)), even though the winter still has strong monsoon winds,
541 the quantity of necromass input is low. Thus, in years where the strength of typhoon
542 winds was insufficient to affect trees based on our measured variables, the
543 long-lasting monsoon winds did not result in substantial necromass inputs. However,
544 in years with strong magnitude typhoons (e.g. September 2013 (Usagi) and
545 September 2016 (Meranti and Megi)), the input of necromass was high (Figure 3).
546 An exception was recorded in February 2018 for which the previous typhoon season
547 (October 2017) have a low PDI_{seasonal} , but still had high necromass inputs (Figure 3).

548

549 In sum, our results suggest that the main driving factor of necromass carbon balance
550 is typhoons, but that monsoons are a contributing and aggravating factor. Large
551 numbers of fallen, dead trees result from the combination of the two climatic events,
552 such that typhoons cause initial stem breakage and monsoon winds subsequently
553 weaken tree vigour (Figure 7c). Therefore both typhoons and monsoons need to be
554 accounting for when modelling forest dynamics.

555

556 **Net fluxes and implication of the future trend**

557 The decay rate constants of other tropical trees reported in the literature range from
558 0.015 to 0.67 (yr^{-1}) for fresh woody debris ≥ 10 cm (Chambers and others, 2000;
559 Baker and others, 2007). Thus, the decay rate constants of our high wind exposure
560 and low wind exposure plots are relatively high (Appendix 8). A global-scale study
561 of woody debris decomposition has suggested that subtropical forests may be
562 particularly influenced by the activities of soil macrofauna and with special

563 decomposition pathways (Martin and others, 2021).

564

565 Although the necromass net fluxes (differences between necromass input and
566 decomposition output) were weakly positive in most years (Figure 5), the standard
567 errors were large relative to the estimate values (Appendix 4), reflecting large year
568 to year variation. Besides, the stocks of necromass were relatively low compared to
569 other forests (Figure 6a), so any accumulation of necromass over the past few years
570 was small. This suggests that the ecosystem both before and during our study period
571 has been close to a dynamic equilibrium status.

572

573 Changes in climatic patterns could affect necromass dynamics in our forests. There
574 is evidence of a long-term decline in monsoon wind intensity (Xu and others, 2006),
575 and there are suggestions that such a trend may continue in the future associated
576 with warming winters (Xu and others, 2006). For typhoons, the northwest tropical
577 Pacific has experienced a historical strengthening in intensity but a decrease in
578 frequency and duration (Tu and others, 2009; Lin and Chan, 2015). Some climate
579 modelling suggests that both these trends will continue as the planet warms (Jiang
580 and Tian, 2013; Mei and Xie, 2016) and while such changes are likely to affect these
581 forests it remains challenging to predict precisely how. As the forest structure and
582 composition of our study forests are strongly influenced by monsoon winds (Chao
583 and others, 2010b), any decline in the intensity of monsoon wind could result in
584 greater biomass growth after release from its stress (monsoon). In the meantime,
585 since we see that PDI significantly influences the seasonal pattern of fallen and
586 standing inputs (Table 2) we can expect a shift in the seasonality of necromass
587 production, with more intense typhoons generating more woody debris during

588 typhoon seasons but weakening monsoons contributing less woody debris.
589 Consequently, the net balances of biomass and necromass stocks are likely to shift
590 over short time scales at least.

591

592 **Conclusion**

593 At the global scale, necromass stocks and inputs were exceptionally low in forests
594 influenced by both typhoon and monsoon winds. While the magnitude of winds
595 helps to explain the seasonal patterns of necromass input at the landscape scale, our
596 analysis points to typhoons as being the primary cause and monsoon winds as
597 aggravating factors in the production of necromass inputs. Therefore, both
598 monsoons and typhoons need to be accounted for when modelling the dynamics of
599 forest carbon balance in tropical and sub-tropical forests away from the equatorial
600 belt. Our study also demonstrates how tropical trees adapt to windy environments,
601 with reduced stature and the ability to resprout contributing to ecosystem resistance
602 and resilience. Changes in wind intensity and duration need greater attention from
603 climatologists and ecologists as they are likely to drive changes in forest structure,
604 carbon balances and dynamics this century.

605

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869

870 **Tables**

871 Table 1. Characteristics of the high wind exposure plot (Lanjenchi) and the low wind exposure plot (Nanjenshan Plots) (average \pm SE).

Plots	Vegetation type[*]	Elevation^{**} (m)	Stem density^{**} (stem ha⁻¹)	Basal area^{**} (m² ha⁻¹)	Aboveground biomass^{***} (Mg ha⁻¹)	Aboveground biomass of carbon^{***} (Mg C ha⁻¹)
High wind exposure (Lanjenchi)	<i>Illicium-Cyclobalanopsis</i> tropical winter monsoon forest	284 to 341	9,836 \pm 203 ^a	44.7 \pm 0.3 ^a	129.4 \pm 1.3 ^a	58.1 \pm 0.6 ^a
Low wind exposure (Najenshan)	<i>Dysoxylum-Machilus</i> tropical mountain zonal foothill evergreen broad-leaved forest	196 to 275	3,886 \pm 157 ^b	46.9 \pm 2.1 ^a	183.2 \pm 4.5 ^b	81.2 \pm 1.6 ^b

872
 873 *Li and others (2013); ** updated after Chao and others (2010b); *** updated after Liao (2017)
 874 Lower case letters indicate a significant difference between Plots using the Kruskal-Wallis test.

875
 876

877 Table 2. Linear mixed-effect model comparison of necromass carbon inputs
 878

Necromass input type	Random effect	Fixed effect			ΔAIC_c
		Plot	Climate	Interaction	
log₁₀(Total)	transect	Plot	log PDI_{seasonal}	–	0.0
	transect	Plot	log PDI _{seasonal}	log PDI _{seasonal} × Plot	1.5
	transect	–	log PDI _{seasonal}	–	1.7
	transect	Plot	–	–	21.4
	transect	–	log PDI _{typhoon}	–	21.6
	transect*	–	–	–	23.2
	transect	–	Precipitation	–	25.2
	transect	–	No. of typhoon	–	25.1
log₁₀(Fallen)	transect	Plot	log PDI_{seasonal}	log PDI_{seasonal} × Plot	0.0
	transect	–	log PDI _{seasonal}	–	0.8
	transect	Plot	log PDI _{seasonal}	–	1.8
	transect	–	log PDI _{typhoon}	–	9.6
	transect*	–	–	–	16.0
	transect	Plot	–	–	16.9
	transect	–	Precipitation	–	17.0
	transect	–	No. of typhoon	–	17.5
log₁₀(Standing)	transect	Plot	log PDI_{seasonal}	log PDI_{seasonal} × Plot	0.0
	transect	Plot	log PDI _{seasonal}	–	0.9
	transect	Plot	–	–	12.8
	transect	–	log PDI _{seasonal}	–	17.8
	transect	–	No. of typhoon	–	23.5
	transect	–	Precipitation	–	26.4
	transect	–	log PDI _{typhoon}	–	26.6
	transect*	–	–	–	29.8

879
 880 PDI_{seasonal} denotes the seasonal power dissipation index; PDI_{typhoon} denotes the power
 881 dissipation index of typhoons. The best models for each necromass category are
 882 marked in bold. To avoid zero values before log-transformation, 0.1 was added to
 883 total necromass, fallen necromass, and PDI_{typhoon}, and 0.01 was added to standing
 884 necromass.

885 *Null Model: with only transect, treated as a random effect (log₁₀ (necromass input)
 886 = 1 + (1|transect)).

887

888 Table 3. Parameters from the best linear mixed-effect models of necromass carbon input
 889

Necromass input type	log PDI _{seasonal}	Plot*	log PDI _{seasonal} × Plot*	Intercept
log ₁₀ (Total) (df = 5; conditional r ² = 0.12)	0.52 ± 0.10	0.15 ± 0.07	–	-0.2 ± 0.06
log ₁₀ (Fallen) (df = 6; conditional r ² = 0.09)	0.29 ± 0.14	-0.13 ± 0.12	0.45 ± 0.22	-0.18 ± 0.08
log ₁₀ (Standing) (df = 6; conditional r ² = 0.30)	0.74 ± 0.18	0.93 ± 0.16	-0.50 ± 0.29	-1.59 ± 0.11

890
 891 PDI_{seasonal} denotes seasonal power dissipation index. Transect is included in these models as a random effect (dependent n=274).
 892 To avoid zero values before log-transformation, a value of 0.1 was added to total necromass, fallen necromass, and PDI_{typhoon}, and a value of
 893 0.01 was added to standing necromass.
 894 *using the low wind exposure plot as the reference categorical variable

895 **Figure legends**

896 Figure 1 Map (a) and wind patterns (b) of the study plots.

897 (a) The study plots include high wind exposure (Lanjenchi Plot) and low wind
898 exposure plot (Nanjenshan Plot I and II). The high wind exposure plot is on the first
899 mountain range facing the northeast monsoon, whereas the low wind exposure plot
900 is located on the valley between the first and second mountain ranges. Inset map on
901 the right shows Taiwan, with a black rectangle indicating the location of the study
902 landscape. (b) Sustained wind speed at 2 m of the high wind exposure plot and the
903 low wind exposure plot. The typhoon season (mid-July to mid-October) is indicated
904 in light grey and the monsoon season (mid-October to mid-February) in light blue.
905 Lower and upper case letters indicate, respectively, significant differences between
906 seasons and plots using Tukey's HSD *post hoc* test.

907

908 Figure 2. Stocks of necromass carbon and annual power dissipation index (PDI_{annual})
909 at the high wind exposure (Lanjenchi) and low wind exposure (Nanjenshan) plots.
910 (a) Total stock; (b) fallen stock; (c) standing stock (transect-length-weighted plot
911 necromass average \pm SE).

912

913 Figure 3. Inputs of necromass carbon and seasonal power dissipation index
914 (PDI_{seasonal}) at the high wind exposure (Lanjenchi) and low wind exposure
915 (Nanjenshan) plots.

916 (a) Total input; (b) fallen input; (c) standing input (transect-length-weighted plot
917 average \pm SE). Typhoon seasons are indicated in light grey, monsoon seasons in
918 light blue. Red arrows indicate tracks of typhoons with $PDI \geq 0.1$ ($10^9 \text{ m}^3 \text{ s}^{-2}$) based
919 on the 20 km distant Hengchun weather station, and include Typhoons Tembin (No.
920 201214), Usagi (201319), Fung-Wong (201416), Soudelor (201513), Goni (201515),
921 Meranti (201614), and Megi (201617).

922

923 Figure 4. Necromass input and seasonal power dissipation index (PDI_{seasonal}) at the
924 high wind exposure (Lanjenchi) and the low wind exposure (Nanjenshan) plots.
925 Each point represents transect length weighted average of each plot.

926

927 Figure 5. Fluxes and net values of necromass carbon at the high wind exposure
928 (Lanjenchi) and low wind exposure (Nanjenshan) plots during the study period.
929 Input fluxes include both fallen and standing necromass of carbon (NC_I); output
930 fluxes are the decomposition quantity (NC_D); the net flux is the difference between
931 input and output fluxes.

932 Figure 6. Necromass carbon stock in tropical primary forests and its relationships
933 with (a) aboveground biomass carbon stock and (b) necromass carbon input.

934 (Data compiled from Baker and others, 2007; Chao and others, 2008; Palace and
935 others, 2008; Chao and others, 2009a; Gurdak and others, 2014; Sato and others,
936 2016; Gora and others, 2019. Literature values are recalculated assuming 50% of
937 necromass is carbon because the original reports did not measure sample carbon
938 concentrations (*c.f.* Chao and others, 2017; Martin and others, 2021)).

939

940 Figure 7. Schematic synthesis of the effects of typhoon and monsoon winds on
941 tropical forest ecosystems: (a) at the global scale; (b) at the landscape scale over the

942 long-term; and (c) at the landscape scale over the short-term.

943

944 **Supplemental files**

945 Appendix 1

946 Appendix 2

947 Appendix 3

948 Appendix 4

949 Appendix 5

950 Appendix 6

951 Appendix 7

952 Appendix 8