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1 **The contribution of insects to global forest deadwood**
2 **decomposition**

3

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21 **Summary**

22 **The amount of carbon held in deadwood globally is equivalent to almost one tenth of**
23 **the carbon stored in the atmosphere¹. Climate, together with diverse decomposer**
24 **communities – mostly microbes and insects – are key regulators of deadwood carbon²⁻**
25 **⁶. Yet, the global carbon emissions from deadwood and the functional role of different**
26 **decomposer groups remain unknown³. Using a global experiment, we show that**
27 **deadwood decomposition rates are driven by a complex interplay of temperature,**
28 **precipitation and the decomposer community. Rates generally increase with**
29 **temperature, suggesting that global warming could accelerate deadwood**
30 **decomposition where moisture is not limiting. The net effect of insects, including direct**
31 **consumption and indirect effects via interactions with microbes, accelerates**
32 **decomposition in tropical forests but has weak positive or negative effects in temperate**
33 **and boreal forests. Applying the experimentally derived decomposition function to a**
34 **global map of deadwood carbon synthesized from empirical and remote sensing data,**
35 **we estimate that 10.9 Pg of carbon is released from deadwood every year, with 93% of**
36 **this amount originating from tropical forests. Globally, insects account for 29% of the**
37 **carbon flux from deadwood which highlights the functional importance of insects for**
38 **deadwood decomposition and the global carbon cycle.**

39 **Main**

40 The world's forests are an important carbon sink¹, but global climate change is affecting carbon
41 sequestration and release by altering tree growth^{7,8}, mortality^{9,10} and decomposition^{11,12}.
42 Hence, a comprehensive understanding of the forest carbon cycle and its climate sensitivity
43 is critical for improving global climate change projections. While past research has focused
44 strongly on sequestration^{13,14}, carbon release, including the decomposition of deadwood,
45 remain poorly understood^{3,15}. Deadwood currently stores 73 ± 6 Pg (Petagram, 10^{15} g) of
46 carbon globally, which is about 8% of the global forest carbon stock¹ and 8.5% of atmospheric
47 carbon¹⁶. Deadwood decomposition is largely governed by climate^{2,6,17,18}, with the activity of
48 different decomposer groups contributing to the considerable variation in decomposition
49 rates². Recently, the role of fungi in forest carbon cycling has received much attention^{2,6} and
50 they are believed to be the principal decomposers of deadwood^{3,5,6}. While local and regional-
51 scale studies indicate that insects can also make a considerable contribution to wood
52 decomposition³, global assessments quantifying the role of microbes and insects are lacking.
53 Given the sensitivity of insects to climate change^{19,20} and the observed declines in insect
54 biodiversity^{21–23}, a better understanding of the interactions between insect decomposers and
55 climate is needed to more robustly project carbon flux from deadwood and the role of
56 deadwood in the global forest carbon sink^{10,15,24}.

57 Here, we quantified the role of deadwood-decomposing insects relative to climate by
58 conducting standardised field experiments of wood decomposition across 55 sites on six
59 continents (Fig. 1a). Our sites were selected to capture the gradient of temperature and
60 precipitation conditions under which forests occur globally. Insects and other animals
61 (hereafter collectively termed insects for brevity) had unrestricted access to wood placed on
62 the forest floor in the *uncaged* treatment in our experiment, while they were excluded from
63 wood in the *closed cage* treatment using mesh cages (Extended Data Fig. 1). Our estimate of
64 the effect of insects on wood decomposition was quantified as the difference between
65 decomposition rates in the *uncaged* and *closed cage* treatments. This measure can be

66 considered the “net effect of insects”, consisting of direct consumption of wood by insects and
67 indirect effects via interactions with microbes. The latter include, for example, competition for
68 resources, grazing on fungal mycelia, creation of entry ports or vectoring, and can thus either
69 increase²⁵ or decrease wood decomposition^{26,27}. Consequently, direct consumption by insects
70 could be higher than our net estimate where insect-microbe interactions decrease
71 decomposition rates. To explore effects of caging on microclimatic conditions and
72 decomposition rates, we implemented a third treatment (*open cage*) using cages with holes,
73 allowing insects access to wood samples under similar microclimatic conditions to those in the
74 *closed cage* treatment (Supplementary Information section 1). We assessed wood
75 decomposition as mass loss over a period of up to three years for wood samples with bark
76 (~3 cm in diameter, 50 cm in length) of locally dominant native tree species (142 tree species
77 in total) as well as for standardized wooden dowels without bark. In total, we recorded wood
78 mass loss for 4437 individual samples. We used a Gaussian generalized linear mixed log-link
79 model with site-specific random effects to quantify the influence of insects (*uncaged* vs. *closed*
80 *cage*), site-level temperature and precipitation as well as type of wood (angiosperm vs.
81 gymnosperm) on the annual rates of wood mass loss. Although some influence of caging on
82 microclimate cannot be ruled out, we focused on the comparison between *uncaged* and *closed*
83 *cage* treatments, because analyses across treatments indicated that this comparison provides
84 the most robust estimate for the net effect of insects on wood decomposition (Supplementary
85 Information section 1; Extended Data Table 1; Extended Data Fig. 2 and 3).

86 To provide a first estimate of the global carbon flux from deadwood decomposition (henceforth
87 referred to as deadwood carbon release) and to quantify the functional importance of insects
88 for global deadwood carbon, we applied the model derived from our decomposition experiment
89 to a novel global deadwood carbon map (Fig. 1a), which we synthesized from empirical and
90 remote-sensing data. As the global modelling of deadwood remains challenging, we
91 conducted in-depth analyses of uncertainty, evaluating the decomposition function derived
92 from our experiment against independent empirical data²⁸ and quantifying the relative

93 contribution of different sources of uncertainty in a sensitivity analysis (Supplementary
94 Information section 2 and Extended Data Table 2). The sensitivity analysis also highlights how
95 further research can improve the modelling of global carbon fluxes from deadwood.

96 **Effects of climate and insects on wood decomposition**

97 In our global experiment, wood decomposition rate was highest in the tropics/subtropics
98 (henceforth called tropics; median = 28.2% mass loss per year), and was considerably lower
99 in the temperate (median = 6.3%) and boreal/hemiboreal (henceforth called boreal; median =
100 3.3%; Fig. 1b) biomes. Wood decomposition rates were highly climate-sensitive, driven by the
101 complex interplay between temperature and precipitation (Table 1). Decomposition rates
102 increased with increasing temperature across the full gradient of precipitation, but the effects
103 of temperature were strongest at high levels of precipitation (Fig. 2a; Extended Data Fig. 4a).
104 Precipitation affected decomposition rates negatively at low temperatures but positively at high
105 temperatures. The observed positive global relationship between wood decomposition and
106 temperature was similar to patterns observed at local to continental scales^{2,4}, as well as for
107 the decomposition of non-woody litter^{11,29}, and is consistent with general theory predicting an
108 increase in metabolic rates and enzymatic activity with temperature³⁰. Moreover, the length of
109 the vegetation period usually increases with temperature which may further increase annual
110 decomposition rates. Weaker positive effects of temperature on wood decomposition under
111 low levels of precipitation may be the result of low wood moisture levels, limiting microbial
112 activity^{31,32} and selecting for drought-tolerant fungal species which have a reduced ability to
113 decompose wood⁶. Given that temperature is predicted to increase globally³³, our results
114 indicate that wood decomposition rates are likely to increase in the future. The strength of this
115 increase will be modulated by current and future levels of precipitation and the emerging water
116 balance of a site³⁴. Decomposition rates were higher for angiosperms than for gymnosperms
117 (Table 1), which is consistent with results from a global meta-analysis and can be explained
118 by differences in wood traits³⁵. Results for standardized wooden dowels were similar to those
119 for wood of native tree species (Extended Data Table 1).

120 Insect access to deadwood affected decomposition, but this effect was contingent on climatic
121 conditions (Table 1). The net effect of insects on decomposition was particularly high in the
122 tropics (median = 3.9% mass loss per year, Fig. 1b). In contrast, effects were low in the
123 temperate biome and even negative in the boreal biome (median of 0.9% and -0.1%,
124 respectively; Fig. 1b). The net effect of insects generally increased with temperature, with
125 effect size strongly mediated by precipitation (Table 1). At low levels of precipitation,
126 temperature had only a minor influence on the net effect of insects. In contrast, at high levels
127 of precipitation, temperature was a strong driver of the net effect of insects on decomposition
128 (Fig. 2b; Extended Data Fig. 4b). At high temperatures, increasing precipitation increased the
129 net effect of insects, while at low temperatures, increasing precipitation resulted in a negative
130 net effect of insects. Thus, decomposition rates were higher when insects were excluded at
131 low temperatures and high precipitation. Complex relationships between insects and climate
132 are driving several mechanisms determining the net effect of insects on wood decomposition.
133 First, wood-feeding termites are a key group of decomposers^{3,36}, but are largely restricted to
134 regions with high temperatures (Fig. 2b). Nevertheless, considerable variation in the net effect
135 of insects also exists among sites where termites are present (Fig. 2b), underlining the
136 importance of factors beyond termite occurrence. Second, temperature affects the metabolic
137 rate of insects, increasing consumption and accelerating larval development directly¹⁹ as well
138 as indirectly via enhanced food quality³⁷. Third, insects can be negatively impacted by high
139 wood moisture when precipitation is high and evaporation low, as is the case e.g. in humid
140 boreal forests (Extended Data Fig. 4b), due to low aeration or high pathogen pressure³⁸.
141 Conversely, moisture is a limiting factor at high temperatures, restricting the period of high
142 insect activity to the rainy season³⁹. Fourth, interactions of insects and microbes can decrease
143 wood decomposition: Insects, for example, can introduce fungal species which do not
144 contribute significantly to wood decomposition themselves, while suppressing other principal
145 wood-decomposing fungi, thus lowering the overall decomposition rate²⁶. In cold and humid
146 regions, such biotic interactions might outweigh the effects of direct consumption, and lead to
147 an overall negative net effect of insects on wood decomposition.

148 Our findings indicate that wood decomposition is driven by the complex interplay of
149 temperature and precipitation with the decomposer community. Climate warming could
150 accelerate wood decomposition by increasing microbial activity and insect-mediated wood
151 decomposition, particularly where moisture is not limiting. However, increased drying as a
152 result of global change also could decrease deadwood decomposition. Our results support
153 that insect biodiversity loss has the potential to affect deadwood decomposition, but that
154 effects may vary regionally. To improve predictions of the functional effects of biodiversity loss,
155 more research is needed on how specific components of decomposer communities (i.e.,
156 biomass, species number, functional composition, species interactions) influence deadwood
157 decomposition³. Our work suggests that the strongest functional effects of changes in the
158 decomposer community will occur in regions with warm and humid climate, which should be
159 a particular focus of further research.

160 **Global carbon flux from deadwood decomposition**

161 To assess the role of deadwood decomposition in the global carbon cycle, we applied the
162 relationship between decomposition rates and local climate derived from our global
163 experiment (Table 1) to a map of the global carbon currently stored in deadwood (Fig. 1a).
164 Since our experiment focused on small-diameter deadwood over three years, we adjusted
165 decomposition rates to account for slower mass loss of large-diameter deadwood (for details
166 see Methods and Supplementary Information section 2). We evaluated our relationship
167 between decomposition rate and local climate against 157 independent empirical observations
168 from previous deadwood surveys²⁸, spanning the full range of deadwood diameters > 7 cm,
169 time since tree death and climatic conditions. We obtained a good match of the results from
170 our model to these independent data (Extended Data Fig. 5), suggesting our approach is
171 robust.

172 We estimate that 10.9 ± 3.2 Pg carbon is released from deadwood per year globally.
173 Therefore, deadwood decomposition represents an important flux in the global carbon cycle.

174 It corresponds to 15–25% of the annual release of carbon from soils globally (estimated to 50–
175 75 Pg carbon a⁻¹ ²⁹), and is 115% of the current anthropogenic carbon emissions from fossil
176 fuels (9.5 Pg carbon a⁻¹ ¹⁶). We note, however, that not all carbon released from deadwood
177 through decomposition is emitted to the atmosphere, as parts are immobilized in the biosphere
178 or in soils^{40,41}. Carbon release from deadwood is highest in tropical biomes (10.2 Pg carbon a⁻¹
179 ¹, Fig. 3a, Extended Data Table 3), where large deadwood carbon pools and high
180 decomposition rates coincide (Extended Data Fig. 6). Although deadwood carbon stocks are
181 also considerable in temperate and boreal biomes (amounting to 35% of all carbon stored in
182 deadwood globally), the climatic limitations for wood decomposition as well as differences in
183 decomposer communities (e.g., the absence of termites) render annual carbon fluxes from
184 deadwood much smaller (i.e., 0.44 Pg carbon a⁻¹ and 0.28 Pg carbon a⁻¹ in boreal and
185 temperate forests, respectively), accounting for less than 7% of the global carbon release from
186 deadwood. Globally, the net effect of insects on wood decomposition results in a carbon flux
187 of 3.2 ± 0.9 Pg a⁻¹, which represents 29% of the total carbon released from deadwood (Fig.
188 3a; Extended Data Fig. 6).

189 Our global estimates are only a first step in a better quantification of the role of deadwood
190 decomposition in the global carbon cycle. Uncertainties related to the underlying data, the
191 statistical models, and other assumptions necessary for upscaling our experimental results
192 were assessed in a global sensitivity analysis. This analysis bounded the uncertainty of global
193 annual carbon release from deadwood and the net effect of insects at approximately ±25%
194 around the mean. Of the various sources of uncertainty that were considered, the underlying
195 data on deadwood carbon stocks contributed most strongly to overall uncertainty (Fig. 3;
196 Extended Data Table 2; Supplementary Information section 2). Our results suggest that global
197 deadwood carbon cycle assessments could be improved by more accurately quantifying
198 deadwood stocks in tropical forests. While the effects of wildfire were included in our
199 deadwood carbon map via the underlying inventory data, we did not explicitly consider
200 deadwood carbon release from fire. We note, however, that a large portion of the carbon

201 stored in deadwood is not combusted in wildfires^{42,43}. Further uncertainty results from our
202 experimental design: It cannot be ruled out that altered microclimatic conditions in cages
203 affected estimates of the net effect of insects derived from the comparison between *closed*
204 *cage* and *uncaged* treatments. Such a bias would lead to an underestimation of the net insect
205 effect in the tropics and an overestimation in the temperate zone (Supplementary Information
206 section 1). When the global annual net effect of insects on deadwood decomposition was
207 derived from the comparison of *closed cage* and *open cage* treatments, it still amounted to
208 1.76 Pg carbon. However, this value underestimates the true effect of insects due to reduced
209 insect colonization in the *open cage* treatment (Supplementary Information section 1;
210 Extended Data Fig. 2).

211 Our experiment highlights that deadwood and wood-decomposing insects play an important
212 role in the global carbon cycle. In contrast to the prevailing paradigm that insects generally
213 accelerate wood decomposition³, our results indicate that their functional role is more variable,
214 and is contingent on the prevailing climatic conditions. We conclude that ongoing climate
215 warming³³ will likely accelerate decomposition by enhancing the activity of microbes and
216 insects, an effect that will be particularly strong in regions where moisture is not limiting. To
217 robustly project the future of the forest carbon sink^{24,44}, dynamic global vegetation models
218 need to account for the intricacies of both deadwood creation (e.g., via natural disturbances)
219 and deadwood decomposition.

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331 **Figure legends**

332 Figure 1 | **Decomposition rates and insect effects per biome.** a) Estimated carbon pools in
333 deadwood with diameter >2 cm (Mg C ha^{-1}) with 5 arc minutes spatial resolution and the
334 location of the 55 experimental sites (grey dots). b) Annual mass loss of deadwood of native
335 tree species when all decomposer groups have access (treatment *uncaged*) and c) difference
336 in annual mass loss between *uncaged* and *closed cage* treatments attributed to the net effect
337 of insects. Data show predicted values for both angiosperm and gymnosperm species at 55
338 and 21 sites, respectively, based on a Gaussian generalized linear mixed log-link model for
339 2533 logs with site-specific random effects and temperature, precipitation, treatment and host
340 type, as well as their interactions, as fixed effects (Table 1). Boxes represent data within the
341 25th and 75th percentile, black lines show medians, and whiskers extend to 1.5× the
342 interquartile range. Note that the classification into biomes is shown for illustrative purposes,
343 while the statistical model is based on continuous climate variables.

344 Figure 2 | **Decomposition rates and net insect effects in climate space.** a) Annual mass
345 loss of deadwood of native tree species, considering all possible groups of decomposers
346 (treatment *uncaged*) and b) annual mass loss attributed to insects (difference in mass loss
347 between treatments *uncaged* and *closed cage*), relative to mean annual temperature and
348 mean annual precipitation. Symbols indicate whether termites occur in the study areas. Points
349 represent predicted values for angiosperm species at 55 sites and gymnosperm species at 21
350 sites based on a Gaussian generalized linear mixed log-link model for 2533 logs with site-
351 specific random effects and temperature, precipitation, treatment, host division, as well as their
352 interactions, as fixed effects. Note that the lower sample size for gymnosperm species
353 represents their global distribution.

354 Figure 3 | **Global annual carbon release from deadwood and sensitivity analysis.** a)
355 Annual carbon released (Pg C a^{-1}) from deadwood per biome. Error bars indicate the
356 uncertainty of the biome-specific estimate as determined by the sensitivity analysis. b) Relative

357 contributions to the overall uncertainty of the global estimate of total carbon release from
358 deadwood decomposition. The color of the bars indicates uncertainty category. See Extended
359 Data Table 2 for a detailed description of each factor and an uncertainty assessment of the
360 net insect effect.

361

362 Table 1 | **Drivers of wood decomposition.** Results from a Gaussian generalized linear mixed
363 log-link model for relative annual mass loss of wood of native tree species derived from a
364 global deadwood decomposition experiment. The model is based on data from *closed cage*
365 and *uncaged* treatments, comprising 2533 logs of native tree species from 55 sites. Fixed
366 effects were mean annual temperature and mean annual precipitation sum which were both
367 centered and scaled, host tree type (angiosperm vs. gymnosperm) and treatment, as well as
368 their two- and three-way interactions, with site as random effect. Estimates and standard
369 errors are for temperature and precipitation transformed back to °C and dm a⁻¹. The main
370 effects for each variable are interpretable when the remaining variables are fixed at their
371 reference value (15 °C and 13 dm a⁻¹). A relative effect (i.e., exp(estimate)) of, for instance,
372 0.989 means that for a temperature increase of 1 °C with all other variables fixed (precipitation
373 at 13 dm a⁻¹, host and treatment), the deadwood dry mass after one year would be 98.9% of
374 the mass without this change in temperature. This represents an additional mass loss of 1.1%
375 induced by a 1 °C increase in temperature. The marginal R² of the model was 0.84.

Predictor	Estimate * 10 ³	Std.Error * 10 ³	z-value	p-value	Relative effect and 95% confidence interval
Temperature (in °C - 15)	-11.009	3.021	-3.644	<0.001	0.989 (0.983 - 0.995)
Precipitation (in dm a ⁻¹ -13)	-3.135	3.322	-0.944	0.345	0.997 (0.990 - 1.003)
Host: angiosperm	-150.477	22.506	-6.686	<0.001	0.860 (0.823 - 0.899)
Host: gymnosperm	-82.825	24.862	-3.331	0.001	0.921 (0.877 - 0.966)
Treatment: uncaged vs. closed	-29.228	5.694	-5.133	<0.001	0.971 (0.960 - 0.982)
Temperature*precipitation	-0.565	0.401	-1.408	0.159	0.999 (0.999 - 1.000)
Temperature*host	5.016	1.250	4.014	<0.001	1.005 (1.003 - 1.007)
Precipitation*host	-0.434	3.587	-0.121	0.904	1.000 (0.993 - 1.007)
Temperature*treatment	-4.161	0.742	-5.608	<0.001	0.996 (0.994 - 0.997)
Precipitation*treatment	-5.236	0.923	-5.675	<0.001	0.995 (0.993 - 0.997)
Temperature*precipitation*host	0.104	0.327	0.317	0.751	1.000 (0.999 - 1.001)
Temperature*precipitation*treatment	-0.728	0.113	-6.451	<0.001	0.999 (0.999 - 0.999)

376

377 **Methods**

378 **Experimental set-up**

379 We established 55 experimental sites in currently forested areas on six continents and three
380 major biomes, spanning gradients in mean annual temperature from -1.4°C to 27.0°C and
381 mean annual precipitation from 2.90 dm a^{-1} to 33.86 dm a^{-1} (Fig. 1a). Sites were located in
382 mature, closed-canopy stands of the dominant zonal forest type, and were selected so that
383 structural and compositional characteristics were similar to those of natural forests. To quantify
384 the net effect of insects on wood decomposition, we compared decomposition between
385 uncaged wood accessible to all decomposers (treatment *uncaged*) and wood in closed cages
386 excluding insects and other invertebrates (treatment *closed cage*; Extended Data Fig. 1).
387 Cages excluded vertebrate and invertebrate decomposers, but for simplicity, and since insects
388 comprise the functionally most important taxa, we refer to insects throughout the manuscript.
389 To explore microclimatic effects of caging⁴⁵, we added a third treatment of wood in cages with
390 large openings (treatment: *open cage*), that allowed colonization by insects, but also provided
391 similar microclimatic conditions as in the *closed cage* treatment (Supplementary Information
392 section 1). Analyses across treatments showed that the most robust assessment of the net
393 effect of insects on wood decomposition originated from the *uncaged* versus *closed cage*
394 treatment, since cages had a significant effect on insect colonization, but not on microclimatic
395 conditions, and thus decomposition rates were reduced in the *open cage* compared to the
396 *uncaged* treatment (Supplementary Information section 1; Extended Data Fig. 2 and 3).

397 Cages measured 40 x 40 x 60 cm and were made of white polyester mesh with 1000 mesh
398 per square inch. The honeycomb-shaped mesh holes had a width of approx. 0.5 mm. Open
399 cages had four rectangular openings measuring 3 x 12 cm at both front sides and four
400 rectangular openings measuring 10 x 15 cm at the bottom, representing in total 6% of the
401 surface area of the cage. Furthermore, open cages had a total of ten 12 cm slits at the top and
402 long sides. Cages were placed on stainless steel mesh (0.5 mm mesh width), which had the

403 same openings as the bottom side of the cages in the open cage treatment. The top layer of
404 fresh leaf litter was removed before the installation of treatments. The cages and layers of
405 steel mesh were both tightly fixed to the ground using tent pegs, to ensure that all deployed
406 logs had close contact with the soil and to allow water uptake and fungal colonization from the
407 soil. At each site, the three treatments were applied three times, i.e. three installations per
408 treatment per site, resulting in a total of nine installations per site (Extended Data Fig. 1). The
409 nine installations were arranged in a matrix of 3 x 3 with a spacing of 2 m between installations,
410 resulting in a total size of approx. 15 m x 15 m. Treatments were assigned randomly to each
411 of the nine locations within a site. The mean spore size and hyphae width of saprotrophic
412 fungal species (mean spore length and width: 8.9 μm and 5.5 μm ⁴⁶; hyphae width: 5-20
413 μm ^{47,48}) is by an order of magnitude smaller than the mesh width of our cages. Rhizomorphs,
414 i.e. linear aggregations of several hyphae, can be wider, but during mycelial growth each
415 hypha extends apically rather than the whole rhizomorph⁴⁹⁻⁵¹. Therefore, it is unlikely that the
416 cages hampered fungal colonization. Data loggers recorded air temperature and humidity for
417 the three treatments at nine sites (see Supplementary Information section 1 for details).

418 **Decomposition measurements**

419 Decomposition was measured as mass loss for unprocessed wood of three of the locally most
420 abundant autochthonous tree species at each study site (Supplementary Table S3-1), as well
421 as for standardized machined wooden dowels. Unprocessed wood of local tree species with
422 the bark retained is more likely to be colonized by local insects and fungi than machined wood
423 without bark⁴⁵. The latter was used to compare decomposition based on a standardized
424 substrate replicated across all sites. We cut wood of local tree species (~3 cm in diameter and
425 ~60 cm in length) from either branches or stems of young healthy trees without visible signs
426 of insect or fungal activity. One 5 cm long section was cut from each end of all fresh logs, and
427 the fresh mass of both the cut sections and the resulting 50 cm logs were weighed. The dry
428 mass of all 5 cm sections was measured after drying them at 40°C until no further mass loss
429 was observed. We calculated the dry mass of the respective 50 cm logs as dry mass 50 cm =

430 (fresh mass 50 cm / fresh mass 5 cm) x dry mass 5 cm. Each installation received three 50
431 cm long logs of each of the three local tree species and one (*closed cage*) or two (*open cage*
432 and *uncaged*) standardized wooden dowels, giving a total of 96 logs at each site. Standardized
433 dowels (3 cm in diameter, 50 cm in length) were dried machined dowels of *Fagus sylvatica* L.
434 without bark. They were obtained from a single producer in Germany and were then distributed
435 to all sites. Initial dry mass of the dowels was measured directly after drying. All logs and
436 dowels were labeled using numbered plastic tags and assigned randomly to one of the nine
437 installations.

438 The experiment was established between March 2015 and August 2016 depending on the
439 seasonality of each site. After approximately one, two and three years, one of the three
440 installations of each treatment per site were randomly selected and collected to measure wood
441 decomposition. That is, all logs from one *uncaged*, one *closed cage* and one *open cage*
442 treatment were collected per site at the same time. We chose this approach because the
443 maximum distance between installations was 6 m and thus within-site variation was expected
444 to be rather low. Moreover, we wanted to ensure that the same number of logs could be
445 sampled per treatment and year and failure of cages over time would have resulted in an
446 unbalanced number of logs per treatment. Due to loss of some cages, high decomposition
447 rates at some sites and logistical restrictions, we were not able to maintain the experiment for
448 three years at all sites (Supplementary Table S3-1). Litter and soil attached to the wood was
449 removed carefully upon collection, while fungal fruit bodies were retained. We assessed insect
450 colonization (presence/ absence) for each log based on visible feeding marks, larval tunnels,
451 or exit holes for 3430 (91%) of the analyzed logs. The collected logs were dried at 40°C until
452 mass remained constant and dry mass was measured. At sites where termites were present,
453 logs were burned to account for soil that might have been carried into the wood by these
454 insects⁴⁵. This involved placing one sample at a time onto a steel pan atop a propane burner,
455 and an electrical fan was used to provide aeration and to blow away ash. The residual soil
456 was weighed and its mass subtracted from the dry mass of the wood.

457 **Statistical analyses of the decomposition experiment**

458 All statistical analyses were performed in R version 4.0.4⁵². For each site, we derived
459 information on average climate conditions from WorldClim (v2)⁵³, specifically BIOMOD
460 variables 1 (mean annual temperature) and 12 (mean annual precipitation sum). We modelled
461 relative wood mass loss of local tree species over time using a Gaussian generalized linear
462 mixed model (function *glmer* in package *lme4*⁵⁴, version 1.1.26) with log link. Dry mass of each
463 individual log at time t served as the response variable and log-transformed initial dry mass (t
464 = 0) was used as an offset term. For each increase of one time unit (one year), the relative
465 reduction is given by $\exp(\beta)$. Note that the model contained no intercept due to the constraint
466 $\exp(\beta)^0 = 1$. The rate $\exp(\beta)$ was modelled depending on treatment (i.e. *closed cage* versus
467 *uncaged*), and host type (angiosperm versus gymnosperm), as well as mean annual
468 temperature [$^{\circ}\text{C}$] and mean annual precipitation sum [dm a^{-1}]. Temperature and precipitation
469 were centered and scaled before modelling, but model coefficients were then back-
470 transformed for ease of interpretation. Reference values for temperature and precipitation
471 were 15°C and 13 dm a^{-1} , respectively. The model included site-specific random time slopes
472 to deal with clustered observations. Based on this model, we computed the fitted annual
473 relative mass loss (in %) for each site considering temperature and precipitation. This was
474 done separately for angiosperm and gymnosperm wood for all sites where respective tree
475 species were present. Note that differences in decomposition between tree species could not
476 be tested but were subsumed in the random slope of the site, since most tree species occurred
477 at only a few sites (Supplementary Table S3-1).

478 To evaluate potential differences in decomposition rates between the wood of native tree
479 species and standardized wood samples, we estimated the same model for standardized
480 wooden dowels. Further models were fitted to evaluate potential microclimatic effects of the
481 cages on decomposition rates and insect colonization. This included one model for wood
482 decomposition of native tree species for the treatments *closed cage* versus *open cage*, and
483 one model comparing wood decomposition between all three treatment levels (*uncaged*,

484 *closed cage* and *open cage*) using a post-hoc test. A binomial generalized linear mixed model
485 was fitted for insect colonization and linear mixed models were fitted for mean daily
486 temperature and mean daily relative humidity. Post-hoc tests were applied to these models
487 for comparisons among the three treatments.

488 **Estimation of global carbon fluxes from deadwood decomposition**

489 To estimate the global carbon flux from deadwood decomposition, we fitted an additive beta
490 regression model (function *gam* with family *betar* in package *mgcv*⁵⁵, version 1.8) to site
491 specific predicted relative annual mass loss using temperature and precipitation as predictors,
492 separately for angiosperm and gymnosperm. Based on predicted relative annual mass loss
493 for the *uncaged* treatment, this model was used to predict total deadwood carbon release
494 globally (i.e. attributable to all kinds of decomposers). To quantify the amount of carbon
495 released from deadwood due to the net effect of insects, we applied the beta regression model
496 to predicted relative annual mass loss for the *closed cage* treatment and calculated it as
497 $\text{carbon release}_{\text{uncaged}} - \text{carbon release}_{\text{closed cage}}$.

498 We applied this model to a spatially-explicit global map of carbon stored in deadwood of
499 angiosperms and gymnosperms, which we synthesized from empirical and remote sensing
500 data sets. We used mean annual temperature and mean annual precipitation sum from
501 WorldClim (v2)⁵³ as predictor data. The GlobBiom (<http://globbiomass.org>) data set provides
502 high-resolution estimates of forest biomass based on Earth Observation data within the
503 framework of ESA's GlobBiomass project. We used the GlobBiom aboveground biomass layer
504 (i.e., stem, bark, and branch compartments) for the reference year 2010, and aggregated
505 information to the base resolution of WorldClim, i.e., 5 arc minutes (Extended Data Fig. 7a).
506 We extended the aboveground biomass information provided by GlobBiom to total live carbon
507 (including roots) by applying biome-specific root expansion factors⁵⁶ and biome-specific
508 biomass to carbon conversion factors between 0.47 and 0.49¹⁵ (Extended Data Fig. 7b). The
509 delineation of forest biomes was taken from FAO⁵⁷.

510 We calculated deadwood carbon stocks at a spatial grain of 5' by relating deadwood carbon
511 stocks to total live carbon stocks (i.e., deadwood carbon fraction). To quantify regional
512 deadwood carbon fractions, we used data compiled by Pan et al.¹, which are based on forest
513 inventory data and represent the most comprehensive analysis of global forest carbon stocks
514 available to date. We reanalyzed their data set and amended it with data from the FAO Forest
515 Assessment Report⁵⁸ where values were missing (Extended Data Table 3). Our estimate of
516 global deadwood carbon stocks therefore reflects local differences in forest productivity,
517 mortality, and land management. The values reported in Pan et al.¹ defined deadwood as “all
518 non-living woody biomass not contained in the litter, either standing, lying on the ground, or in
519 the soil” with a diameter >10 cm. We extended our deadwood carbon pool estimate to include
520 all deadwood >2 cm diameter by applying an expansion factor based on empirical allometric
521 relationships⁵⁹. Our global map of deadwood (Fig. 1a) thus represents the total amount of
522 carbon stored in standing and downed deadwood with a diameter of >2 cm for the reference
523 year 2010.

524 To differentiate between deadwood of angiosperms and gymnosperms, we used the
525 proportion of broad- and needle-leaved biomass derived from the global land cover product
526 GLCNMO2013⁶⁰. The resolution of GLCNMO2013 is 1/240 degree (i.e., each of our 5' cells
527 contains 400 land cover pixels), and it provides information on 20 land cover classes. We
528 reclassified these to "Broadleaved", "Needle-leaved", and "Mixed forest", and aggregated to
529 5' cells for each of the three forest types. The final proportion of each group was calculated
530 assuming that carbon in mixed forests was equally distributed between angiosperms and
531 gymnosperms (Extended Data Fig. 7c).

532 The experimental sites were chosen to span the global bioclimatic space inhabited by forests.
533 Nonetheless, gaps remained in very cold and dry climatic conditions for both angiosperm and
534 gymnosperm species as well as in very warm and wet climatic conditions for gymnosperm tree
535 species. We constrained the application of our decomposition models to the climate space
536 covered by the experiment to avoid extrapolation beyond our data. Specifically, we defined

537 the bioclimatic space for robust predictions via a convex hull around experimental sites in
538 temperature - precipitation space (using a buffer of 3° and 3 dm, respectively). Subsequently,
539 climatic conditions outside that convex hull were mapped to the nearest point within the hull
540 in our modelling (Extended Data Fig. 8).

541 Our statistical model was derived from deadwood samples with a diameter of ~3 cm, and thus
542 overestimates annual decomposition rates when applied over the full diameter range of
543 deadwood (Supplementary Information section 2). To address this potential bias, we used a
544 conversion factor relating wood mass loss of fine woody debris (FWD, < 10 cm in diameter)
545 to coarse woody debris (CWD, > 10 cm). We based our conversion factor on data from eleven
546 peer-reviewed studies reporting data on both CWD and FWD decomposition, covering all
547 major global biomes (Supplementary Table S2-1). As the relationship of CWD mass loss rate
548 over FWD mass loss rate was robust across different climates, we used its median value
549 (0.53) in our upscaling. An evaluation of the final deadwood decomposition rates used for
550 deriving a first global estimate of the carbon flux from deadwood was performed against
551 independent data from 157 observations compiled by Harmon et al.²⁸. This evaluation against
552 independent data indicated good agreement across all major biomes and diameter classes
553 (Extended Data Fig. 5).

554 Finally, we accounted for the slower carbon release from standing deadwood relative to
555 downed woody debris, particularly in dry regions of the boreal and temperate biome. Based
556 on a wood decomposition data set for standing and downed deadwood across several decay
557 classes for the temperate and boreal biome⁶¹, we estimated decomposition of standing
558 deadwood to be 33-80% slower compared to lying logs. This is consistent with a detailed
559 analysis for temperate forests in Switzerland⁶² that found a slowdown of 42%. In the tropics,
560 however, decomposition rates of standing trees have the same or sometimes even higher
561 decomposition rates as downed trees^{18,63,64}. We assumed a reduction of decomposition rates
562 by 50% for standing deadwood in temperate and boreal forests, and no reduction in the tropical

563 biome in our upscaling. Based on large-scale inventories^{65–69} we estimated the proportion of
564 standing deadwood on total deadwood as 25% and 30% for the boreal and temperate biome,
565 respectively.

566 Our global estimate of the carbon fluxes of deadwood decomposition required a number of
567 analytical steps and assumptions, each of which is associated with uncertainties. These can
568 be classified into uncertainties related to deadwood carbon stocks (“Data uncertainties”),
569 uncertainties related to the statistical modelling of deadwood decomposition (“Model
570 uncertainties”), and uncertainties in the upscaling of model results to the global scale (“Scaling
571 uncertainties”). To assess the robustness of our estimate, we performed a global sensitivity
572 analysis⁴⁸ where we selected three to four indicators for each of these three categories of
573 uncertainty, and estimated their influence on the overall result. For each of the ten indicators
574 analyzed in total, we selected either a single alternative (e.g., use of the standardized dowels
575 instead of native species) or an upper and lower bound around the default value based on
576 available data or indicator-specific assumptions (Extended Data Table 2). With regard to data
577 uncertainty, we investigated uncertainties associated with the GlobBiom data set used as
578 important data basis here, the deadwood carbon pool estimates¹, and the expansion factors
579 used to derive total biomass from aboveground biomass⁵⁶. Model uncertainties were
580 considered by employing alternative models using the 97.5th and 2.5th percentile of parameter
581 values for fixed effects of the original model, an additional model accounting for potential
582 microclimatic effects of cages (i.e., using the *open cage* instead of the *uncaged* treatment),
583 and a model based on results for the standardized dowels (instead of the native tree species).
584 Lastly, scaling uncertainties were addressed by analyzing alternative expansion factors to
585 include deadwood <10 cm, varying relationships between FWD and CWD decay rate,
586 alternative assumptions regarding the proportion and decay rate of standing deadwood, and
587 the treatment of regions outside of the climate envelope covered by our experiment (see
588 Extended Data Table 2 for details). All factor levels of all indicators were allowed to vary
589 simultaneously, resulting in a total of 4860 estimates for annual deadwood carbon release and

590 the net effects of insects. The relative influence of each indicator on total uncertainty was
591 derived by means of ANOVA, determining the percent of variance explained by each factor.
592 The contribution at the level of uncertainty categories was derived as the sum of the factors
593 per category. The uncertainty range for the global annual deadwood carbon release estimated
594 from this global sensitivity analysis was ± 3.14 Pg, and the net effect of insects varied by ± 0.88
595 Pg carbon. Data uncertainty was identified as the most important factor (~40%), but both
596 model and scaling uncertainty were also highly influential, each contributing 25-30% to the
597 overall variation in the results (Extended Data Table 2).

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660 **Data availability**

661 Raw data from the global deadwood experiment, our global map of deadwood carbon and our
662 map of predicted decomposition rates are publicly available from figshare
663 <https://figshare.com/s/ffc39ee0724b11bf450c> (doi: 10.6084/m9.figshare.14545992).

664 **Code availability**

665 An annotated R code including the data needed to reproduce the statistical analyses, global
666 estimates, and sensitivity analysis is publicly available from figshare
667 <https://figshare.com/s/ffc39ee0724b11bf450c> (doi: 10.6084/m9.figshare.14545992).

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680 **Author contributions**

681 S.S., J.M., R.S. perceived the idea of this manuscript. S.S., J.M. and M.U. designed the
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686 J.M collected data. S.S., T.H., and W.R. analyzed the data. S.S., J.M., R.S. and W.R. wrote
687 the first manuscript draft with significant inputs from M.U., M.C. and D.L., and finalized the
688 manuscript. All authors commented on the manuscript.

689 **Additional Information**

690 **Supplementary Information** This file contains supplementary information about methods,
691 descriptions of supplementary analyses and a detailed discussion addressing methodological
692 challenges.

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695 Extended Data Table 1 | **Supporting analyses of drivers of wood decomposition.** Results
696 from Gaussian generalized linear mixed log-link models for relative annual mass loss of a)
697 standardized wooden dowels comparing the treatments *uncaged* versus *closed cage* (415
698 logs from 55 sites) and b) wood of native tree species comparing the treatments *open cage*
699 and *closed cage* 2522 logs from 55 sites). Models include mean annual temperature and mean
700 annual precipitation sum which were both centered and scaled, host tree type (angiosperm
701 vs. gymnosperm; in model b only) and treatment, as well as their two- and three-way
702 interactions, as fixed effects and site as the random effect. Estimates and standard error are
703 for temperature and precipitation transformed back to °C and dm a^{-1} . The main effects of each
704 variable is interpretable when the remaining variables are fixed at their reference value (15°C
705 and 13 dm a^{-1}).

706 Extended Data Table 2 | **Uncertainty in global carbon fluxes from deadwood**
707 **decomposition, determined in a global sensitivity analysis.** Important factors per
708 uncertainty category were selected and allowed to vary simultaneously, resulting in a total of
709 4860 analyzed combinations. The uncertainty of total annual deadwood carbon released and
710 of the net effect of insects was calculated as the standard deviation over all combinations for
711 each factor, with all other factors fixed to their default value. Similarly, the uncertainty per
712 category was calculated over all combinations within a category, with all factors from other
713 categories fixed to the default value. The relative contribution of each factor to overall
714 uncertainty was derived by means of an ANOVA, estimating the percent of variance explained
715 for each factor. The contribution at the level of uncertainty categories is the sum of the
716 respective factors in each category. CI = confidence interval; FWD= fine woody debris; CWD=
717 coarse woody debris; SWD= standing woody debris; DWD= downed woody debris.

718 Extended Data Table 3 | **Comparison of global carbon stock estimates and results for**
719 **biomes. a)** Global estimates of total live carbon and carbon in deadwood (>10 cm) from Pan
720 et al.¹ compared with estimates obtained in this study (>2 cm) in Pg. Numbers in brackets
721 indicate the difference in percent. Note that Pan et al.¹ defined biomes at country level while

722 we here define biomes using the FAO Global Ecological Zones. Differences between these
723 biome definitions are especially significant for the temperate biome, as temperate parts of
724 Russia and Canada are included in the boreal biome in Pan et al.¹, while we here divide Russia
725 and Canada into boreal and temperate regions. Furthermore, missing and unrealistic
726 deadwood carbon stocks for a number of areas (specifically Japan, South Korea, China,
727 Australia, and Alaska) in Pan et al.¹ were complemented with data from the FAO Forest
728 Assessment Report⁵⁸ in this study, which contributes to higher deadwood carbon estimates
729 relative to Pan et al.¹. **b)** annual deadwood carbon release and net insect effect per biome (in
730 Pg), and calculated residence time of deadwood carbon (years).

731

732 Extended Data Figure 1 | **Arrangement of installations per site and treatments.** a) Each
733 site received three installations of three treatments randomly assigned to a 3 x 3 grid.
734 Treatments included b) closed cages to exclude insects, c) open cages providing similar
735 microclimatic conditions as closed cages but giving access to insects and d) uncaged bundles
736 of logs. Cages measured 40 x 40 x 60 cm and were made of white polyester with honeycomb-
737 shaped meshes with a side length of approx. 0.5 mm. Open cages had four rectangular
738 openings measuring 3 x 12 cm at both front sides and four rectangular openings measuring
739 10 x 15 cm at the bottom representing in total 6% of the surface area of the cage as well as a
740 total of ten 12 cm slits at the top and long sides. All cages were placed on stainless steel mesh
741 (0.5 mm mesh width), which had the same openings as the bottom side of the cages in the
742 open cage treatment. Photographs show the site in the Bavarian Forest National Park,
743 Germany.

744 Extended Data Figure 2: **Effects of treatments on wood decomposition and insect**
745 **colonization.** Coefficients and confidence intervals from post-hoc tests assessing all three
746 pairwise comparisons between the *uncaged*, *closed cage* and *open cage* treatments for a)
747 annual mass loss (same structure as the model shown in Table 1 based on 3578 logs) and b)
748 insect colonization (binomial model for insect presence and absence based on 3430 logs) of
749 wood of native tree species. 95% confidence intervals not intersecting the zero line (dashed)
750 indicate significant differences. Largest differences in both response variables were observed
751 between *uncaged* and *closed cage* treatments. Annual mass loss was higher in *uncaged* than
752 *open cages* and higher in *open cages* than in *closed cages*, although the latter was not
753 significant. This indicates that the *open cage*, despite its openings for insects, has a clearly
754 reduced decomposition rate compared to the *uncaged* treatment. Insect colonization for the
755 *open cage* differed significantly from both *uncaged* and *closed cage*, but was more similar to
756 *uncaged* than *closed cage*. This indicates that *open cages* were colonized by insects, but not
757 as frequently as the *uncaged* treatment. *Open cages* thus excluded parts of the wood-
758 decomposing insect community, which may explain the rather small difference in annual mass

759 loss between *closed cage* and *open cages*. These results suggest that the comparison of
760 *uncaged* versus *closed caged* provides a more reliable estimate of the net effect of insects on
761 wood decomposition than the comparison of *closed cage* versus *open cage* treatments, which
762 is likely underestimating the net effect of insects.

763 Extended Data Figure 3 | **Comparison of wood decomposition between all three**
764 **treatments.** Pairwise comparison of fitted annual mass loss (in %) between each of the three
765 treatments in the global deadwood decomposition experiment. Points represent predicted
766 values for angiosperm species at 55 sites and gymnosperm species at 21 sites based on three
767 Gaussian generalized linear mixed log-link models for 3758 logs with site-specific random
768 effects and temperature, precipitation, treatment (*closed cage* versus *uncaged*, *open cage*
769 versus *uncaged* and *closed cage* versus *open cage*, respectively), host division, as well as
770 their interactions, as fixed effects. The difference between annual mass loss in *closed cage*
771 and both treatments with insect access (*uncaged* and *open cage*) increased from boreal to
772 tropical, whereas the difference between *uncaged* and *open cage* hardly deviated from the
773 1:1 line. This indicates that the reported mass loss differences between *closed cage* and
774 *uncaged* treatments, as well as the accelerating effect of temperature and precipitation (Table
775 1), can be attributed to insects and are not an artefact of potential microclimatic effects of the
776 cages (Supplementary Information section 1).

777 Extended Data Figure 4: **Interaction effects of temperature and precipitation on wood**
778 **decomposition.** Predictions based on the model presented in Table 1 for a) annual mass loss
779 of deadwood of native tree species (2533 logs at 55 sites), considering all possible groups of
780 decomposers (treatment *uncaged*) and b) annual mass loss attributed to insects (difference in
781 mass loss between treatments *uncaged* and *closed cage*), relative to temperature and
782 precipitation. The length of the lines is limited to the gradients in precipitation covered by the
783 sites.

784

785 Extended Data Figure 5 | **Model evaluation against independent data.** Comparison of 157
786 independent observations of annual deadwood decomposition rates measured for larger
787 diameter wood in previous deadwood surveys (red dots, Harmon et al.²⁸) with the predictions
788 from our model for the same locations (blue triangles). Lines indicate the relationship between
789 decomposition rate and mean annual temperature from Harmon et al.²⁸ (red dashed line,
790 $k=0.0184e^{0.0787*temperature}$) and for our model (blue line, $k=0.0171e^{0.0812*temperature}$). Good
791 correspondence of both curves indicates that our models of global carbon release from
792 deadwood provide robust estimates despite being based on experimental deadwood with ~3
793 cm diameter (for detailed discussion, see Supplementary Information section 1).

794 Extended Data Figure 6: **Global deadwood carbon fluxes.** a) Total annual release of
795 deadwood carbon from decomposition including all decomposers and b) annual release of
796 deadwood carbon due to the net effect of insects. Light grey areas indicate values of ± 0.1 Mg
797 carbon $ha^{-1} a^{-1}$ and white areas are non-forest systems. c) Latitudinal distribution of global
798 deadwood carbon fluxes per hectare.

799 Extended Data Figure 7 | **Processing steps for the global deadwood carbon map** a)
800 Aboveground forest biomass ($Mg ha^{-1}$) aggregated to 5' from the GlobBiom data set. b) Total
801 live carbon ($Mg ha^{-1}$) by extending a) with root biomass⁵⁶ and conversion to carbon. c)
802 Proportion of gymnosperm forests derived from the GLCNMO2013⁶⁰ data set. The proportion
803 of angiosperm cover is $1 - \text{gymnosperm cover}$. White = non-forested area.

804 Extended Data Figure 8 | **Bioclimatic space for robust predictions.** Climate conditions
805 outside of the range of prediction models for a) angiosperm and b) gymnosperm species in
806 climate space (left) and mapped (right). Left: dark-blue points are outside of the range defined
807 by a convex hull around the experimental sites (black triangles). Right: The colors on the maps
808 indicate the absolute difference between the local climate and the climate used for prediction
809 for temperature (red color channel) and precipitation (blue color channel) with black meaning
810 no difference. White areas indicate that no gymnosperm or angiosperm forest, respectively,

811 occurs here. Experimental sites are indicated by yellow dots. Temperatures outside of the
812 range are mainly located in north-eastern Siberia and northern Canada, whereas offsets in
813 precipitation are stronger for gymnosperms in south-eastern Asia, Indonesia, and in the
814 Amazon region. The land surface area not covered by our experimental data is 23.5% for
815 gymnosperms and 17.7% for angiosperms, representing together 13.2% of the C stored in
816 deadwood. These areas were included in our upscaling by mapping them to the nearest point
817 at the convex hull in climate space.

818