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Wood decomposition is increased by insect diversity, selection effects, and interactions between insects and microbes

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Abstract

Biodiversity drives ecosystem processes, but its influence on deadwood decomposition is poorly understood. To test the effects of insect diversity on wood decomposition, we conducted a mesocosm experiment manipulating the species richness and functional diversity of beetles. We applied a novel approach using computed tomography scanning to quantify decomposition by insects and recorded fungal and bacterial communities. Decomposition rates increased with both species richness and functional diversity of beetles, but the effects of functional diversity were linked to beetle biomass, and to the presence of one large-bodied species in particular. This suggests that mechanisms behind observed biodiversity effects are the selection effect, which is linked to the occurrence probability of large species, and the complementarity effect, which is driven by functional differentiation among species. Additionally, beetles had

Jörg Müller and Sebastian Seibold share senior authorship.

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significant indirect effects on wood decomposition via bacterial diversity, fungal community composition, and fungal biomass. Our experiment shows that wood decomposition is driven by beetle diversity and its interactions with bacteria and fungi. This highlights that both insect and microbial biodiversity are critical to maintaining ecosystem functioning.

KEYWORDS

biodiversity–ecosystem functioning, functional diversity, insect diversity, insect–microbe interactions, wood decomposition

INTRODUCTION

Biodiversity is fundamental for ecosystem processes (Cardinale et al., 2006; Tilman et al., 2014), especially primary production (Tilman et al., 1996), pollination (Brittain et al., 2013), decomposition (Heemsbergen et al., 2004), and nutrient cycling (Wagg et al., 2014). Considering the ongoing loss and changes in biodiversity across scales, a detailed understanding of how these changes result in alterations to ecosystem functioning through biodiversity–ecosystem functioning (BEF) relationships is required to make accurate predictions and to try to ameliorate these impacts (Cardinale et al., 2012). Positive BEF relationships, where increases in species richness underpin increases in ecosystem function, are frequently attributed to either niche-complementarity or selection effects (Fox, 2005; Loreau & Hector, 2001; Tilman et al., 1997). The niche-complementarity hypothesis assumes that dissimilar species exhibit niche partitioning with complementary resource use, which promotes stable coexistence and results in species making different contributions to ecosystem functioning. Therefore, under niche complementarity, increasing species richness should enhance ecosystem functioning for those functions linked to the efficacy of resource use because local resource pools are more efficiently utilized. In contrast, the selection-effect hypothesis suggests that some species contribute more strongly to ecosystem functioning than others. Thus, positive BEF relationships can be explained by the sampling effect, which predicts that the occurrence probabilities of functionally important species increase with increasing species richness (Loreau, 2010; Tilman et al., 1997). The complementarity effect is closely associated with functional differences between species in a multidimensional trait space, and thus, if stronger effects on ecosystem functioning are found when biodiversity is characterized by functional diversity than by species richness or dominant trait values, this is often considered support for the complementarity effect (Heemsbergen et al., 2004). In contrast, the selection effect could be associated with relatively few traits, especially those that confer a competitive advantage locally (Cadotte,

2017). If the selection effect is associated with traits such as biomass or body size or if the functional importance of a species arises from its occurrence in high density, this could be explained by the mass-ratio hypothesis (Grime, 1998). The mass-ratio effect predicts that ecosystem functioning increases with total abundance or biomass in a community or with the share of functionally important species (Grime, 1998; Mokany et al., 2008). Neither the selection effect nor the mass-ratio hypothesis is mutually exclusive with niche complementarity (Appendix S1: Figure S1).

Relationships between biodiversity and productivity have been studied intensively in BEF experiments manipulating species richness and functional composition of plants in grasslands (Fargione et al., 2007; Weisser et al., 2017) and forests (Huang et al., 2018; Schnabel et al., 2019). These studies frequently reported positive BEF relationships and found support for both niche-complementarity and selection effects (Cadotte, 2017; Fargione et al., 2007; Huang et al., 2018; Marquard et al., 2009; Weisser et al., 2017). In comparison, relationships between decomposer diversity and decomposition have received little attention, despite the importance of decomposer diversity for ecosystem processes (Gessner et al., 2010), and there are some indications that negative BEF relationships can occur in decomposer systems (Fukami et al., 2010; Hagge et al., 2019).

Decomposition of dead organic material (e.g., carrion, litter, and deadwood) is a key process for biogeochemical cycles (Benbow et al., 2019; Pan et al., 2011; Wall et al., 2008), and insects as well as microbes are among the primary decomposers (Bani et al., 2018; Lustenhouwer et al., 2020; Seibold et al., 2021; Ulyshen, 2016; Wall et al., 2008). For leaf litter decomposition, microcosm experiments have indicated that decomposition is positively associated with diversity of soil fauna, with stronger effects of functional dissimilarity than species richness (Heemsbergen et al., 2004). For deadwood decomposition, decomposition rates are usually higher when insects are present (Seibold et al., 2021), whereas for fungi, reduced decomposition rates were observed at higher species richness in laboratory experiments (Fukami et al., 2010). Deadwood represents a major

carbon pool in forest ecosystems worldwide (Pan et al., 2011), and deadwood carbon dynamics strongly depend on decomposition rates (Aryal et al., 2022). Yet, BEF experiments manipulating species richness and functional diversity of decomposers to identify underlying mechanisms are lacking.

Accounting for 29% of decomposition of deadwood globally, insects play an important role in wood decomposition (Seibold et al., 2021). Ulyshen (2016) hypothesized that certain key taxa, such as termites and large cerambycid or passalid beetles, are the main drivers of wood decomposition, consistent with a selection or the mass-ratio effect, as they consume large amounts of deadwood due to their mutualistic relationships with microbes, their high abundance, or their large body size. Moreover, insects affect wood decomposition not only directly through consumption and fragmentation of deadwood but also indirectly via interactions with microbes, particularly fungi and bacteria (Birkemoe et al., 2018; Jacobsen et al., 2018; Ulyshen, 2016). Such indirect effects could be associated with both complementarity and selection effects since microbial communities are affected by the overall insect community (Seibold et al., 2019) as well as individual insect species closely associated with certain microbial species (Jacobsen et al., 2017, 2018). Ultimately, changes in microbial communities can be a strong driver of wood decomposition (Fukasawa & Matsukura, 2021). One challenge in studying BEF relationships for wood decomposition is that the contribution of insects cannot be quantified easily with the traditional approach measuring mass loss since it is usually based on subsamples taken from larger logs, leading to limited accuracy, and is an overall measure of decomposition reflecting both insect and microbial activity (Seibold et al., 2022). Fungi, however, can translocate nutrients and, thus, biomass from outside into the wood (Philpott et al., 2014) and competition between fungal species can reduce decomposition rates (Skelton et al., 2019). Therefore, an overall measure of decomposition may not adequately reflect decomposition by insects. Only recently has a new approach using computed tomography (CT) scanning to quantify insect tunnel volume in deadwood as a direct measure of decomposition by insects been developed (Seibold et al., 2022), opening new avenues for BEF research in deadwood.

To date, there has been a lack of experimental tests of the effects of insect richness and functional diversity on wood decomposition and the role of interactions of insects with fungi and bacteria. We aimed to close this gap using a mesocosm experiment manipulating beetle communities spanning gradients of species richness and functional diversity. We quantified the direct effect of beetles on wood decomposition using CT scanning. Furthermore, we

quantified overall mass loss, chemical characteristics and fungal biomass by measuring ergosterol content, and we identified fungal and bacterial communities. We used these experimental data to test hypotheses about the nature and strength of BEF relationships between insect diversity and wood decomposition.

Based on general BEF theory, we first predicted that decomposition rates would increase with increasing species richness of beetles. Second, based on the niche-complementarity hypothesis, we predicted that functional diversity would positively affect decomposition in addition affecting species richness. Third, based on the mass-ratio hypothesis, we predicted that decomposition rates would increase with increasing total beetle biomass. And fourth, based on the selection-effect hypothesis, we predicted that exceptionally large wood-decomposing beetles would have strong positive effects on decomposition. Because microbes are inherently involved in the decomposition process and closely interact with insects (Hagge et al., 2019; Jacobsen et al., 2017, 2018), we tested for direct effects of beetle diversity on wood decomposition, as well as for indirect effects via interactions with microbes. These a priori hypotheses dictated the experimental design and provided the backbone for our approach to data analysis. We used a stepwise modeling approach, starting with simple models that test the more general hypotheses, followed by more detailed models that account for potentially confounding variables and test more detailed hypotheses.

MATERIALS AND METHODS

Study area and experimental design

The study was conducted in the management zone of the Bavarian Forest National Park, southeastern Germany (Figure 1). The mesocosm experiment, manipulating beetle communities in deadwood, was established in spring 2015 and included 190 mesocosms arranged in five spatial blocks (Figure 1). The mesocosms consisted of mesh cages that measured $40 \times 40 \times 60$ cm and were made of white polyester mesh with 6450 holes/cm², which corresponds to a mesh width of ~0.5 mm (Seibold et al., 2021). Each mesocosm contained two fresh spruce logs (16–20 cm in diameter, 50 cm in length), which were placed on the mesh bottom but had otherwise full soil contact. Logs were obtained from 31 freshly cut trees originating from one forest stand and showed no signs of insect or fungal colonization. To obtain gradients of species richness (0–8 species) and the functional diversity of saproxylic beetles, we created 38 community types, including mixtures, monocultures, and controls without beetles (Figure 1,

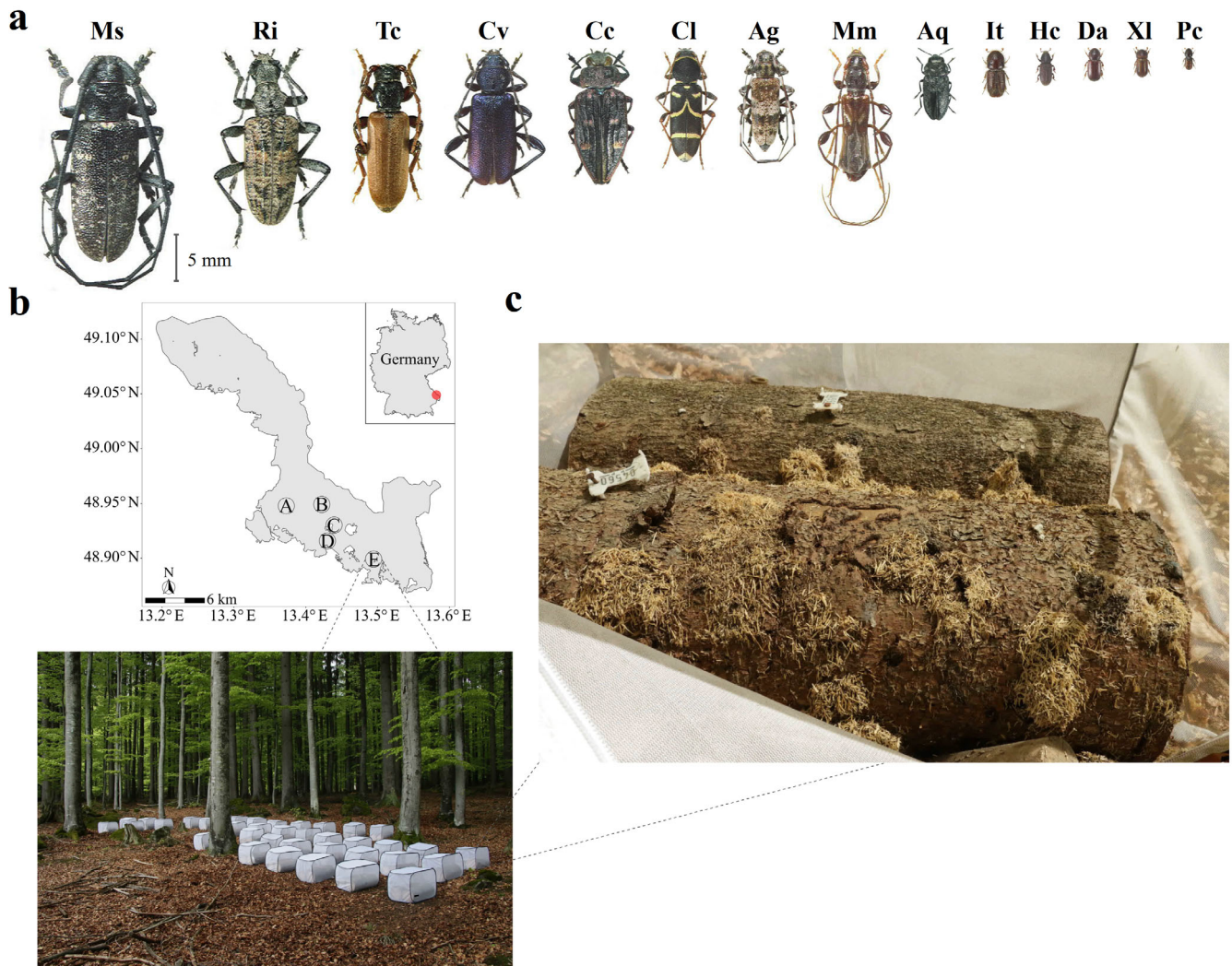


FIGURE 1 Mesocosm experiment setup and arrangement of installations per block. (a) Photographs of the 14 saproxylic beetle species used for the experiment (photos by Bruno Dries, with permission) with displayed body size ratio representing approximate natural ratio. Abbreviations represent species names: Ag, *Acanthocinus griseus*; Aq, *Anthaxia quadripunctata*; Cc, *Chrysobothris chrysostigma*; Cl, *Clytus lama*; Cv, *Callidium violaceum*; Da, *Dryocoetes autographus*; Hc, *Hylastes cunicularius*; It, *Ips typographus*; Mm, *Molorchus minor*; Ms, *Monochamus sutor*; Pc, *Pityogenes chalcographus*; Ri, *Rhagium inquisitor*; Tc, *Tetropium castaneum*; XI, *Xyloterus lineatus*. (b) One of five replicates containing all 38 community types, with each enclosed in a mesh bag mesocosm in the Bavarian Forest National Park, Southeast Germany (photo by Sebastian Seibold). (c) Beetles emerged after the first year and frass indicates successful colonization and reproduction (photo by Sebastian Seibold).

Appendix S1: Tables S1 and S2). Our goal was to create species-richness levels 0, 1, 2, 4, 6, and 8, each occurring in equal numbers in each of the five blocks, but since not all species could be sampled at a sufficient number, this was not always possible (see Appendix S1: Table S1). Blocks were ~150 m² in size, and mesocosms were arranged randomly in a 1 × 1-m matrix. All five blocks were located at forest edges in semishady conditions.

Community types were created from a selected set of 14 saproxylic beetle species that are early colonizers of spruce (*Picea abies* [L.] H. Karst.) deadwood, spanning a body size gradient of 1.6–19.5 mm and belonging to three different taxonomic families (Appendix S1: Table S2).

In total, ~6000 individuals were collected from wild populations in the national park using pheromone traps for Scolytinae and hand collection for Cerambycidae and Buprestidae between April and early July, depending on the flight season of the species. Each mesocosm received the same number of individuals per species ranging from four to five for larger Cerambycidae and Buprestidae to 10–20 for small Scolytinae; thus, the number of individuals and beetle biomass varied between treatments (Appendix S1: Table S2). It was not feasible to create gradients in species richness with constant total abundance and biomass, since the abundance of large species per mesocosm could not be reduced (one pair per log must

be considered the minimum), and the number of small species could not be increased since the selected number of individuals already represented the maximum density per log considering the minimum area required per gallery system (Ehnström & Axelsson, 2002). Total biomass was thus correlated with species richness and functional diversity ($r = 0.65$ and 0.22 , respectively; Appendix S1: Figure S2). Nevertheless, correlation coefficients were below 0.7, which is considered a threshold for including variables in the same model (Dormann et al., 2013). Likewise, the collinearity was also within the limits in the models established in subsequent analysis (variance inflation factor < 2).

Wood decomposition

We quantified wood decomposition after two growing seasons, which approximates the first stage of succession, and considerable turnover of beetle species occurs after this period (Stokland et al., 2012). We used different measures of wood decomposition representing different decomposer groups.

Mass loss

To quantify overall decomposition by beetles and microbes, we quantified the dry mass loss. The initial dry mass of each log was recorded by taking a wooden disc (3 cm wide) from each log. The fresh weight of discs and logs was measured, and the discs were dried in a well-ventilated oven at 65°C until a constant weight was obtained (the average initial wood density of the discs was 0.38 g/cm^3). The dry weight of each log was estimated as $\text{dry mass log} = (\text{fresh mass log} / \text{fresh mass disc}) \times \text{dry mass disc}$. In November 2016, we collected one log from each mesocosm (the second log, which is not included in this study, was left in the field to study the long-term trajectories of decomposer assembly), and each entire log was dried at 65°C until mass constancy was reached. We then measured the final dry mass and calculated the dry mass loss.

CT-based relative tunnel volume

To quantify wood decomposition by insects, we employed a novel approach combining CT scanning with semiautomatic image analysis to quantify the relative volume of wood consumed by the beetles (hereafter relative tunnel volume) (Seibold et al., 2022). All logs were scanned by MITOS GmbH (Garching, Germany) immediately

following collection from the field and before drying using a Philips iCT SP 181 scanner in helix scan mode, 120 kVp, at a slice thickness of 0.67 mm and pixel spacing of 0.29 mm. Data were processed to obtain the volume of each log, and a segmentation approach based on gray-scale values of the images was applied to detect and quantify the volume of beetle galleries in bark and wood (for details, see Seibold et al. [2022]). Briefly, thresholding in combination with binary morphological operations was utilized to detect cavities and beetle tunnels in wood and bark. The drillings and shrinkage cracks could be separated from beetle tunnels by their geometric characteristics, and the remaining cavities were tagged as beetle tunnels. Finally, the tunnel volume was determined by counting pixels representing beetle tunnels for the complete log.

Chemical measures of wood decomposition

To characterize wood decomposition related mainly to the activity of fungi and bacteria, we measured several chemical characteristics. For this, two wood samples were taken from each log after collection from the field and before logs were dried. The extraction was performed using an electric drill equipped with a 0.8-cm wood auger, operated at 15 and 25 cm from one end of each log. The drilling was carried out perpendicular to the stem axis and perpendicular to the forest floor covering the full log diameter to capture the heterogeneity within logs. The wood auger was cleaned and sterilized between logs, and the two samples per log were pooled for further analysis. All wood samples were freeze-dried and milled using Mixer Mill Retsch MM 400 (Retsch, Haan, Germany) with steel balls and steel cups at a frequency of 28 Hz. Depending on the initial size, decay, and moisture content, different grinding times between 6 and 12 min (with intermediate freezing in dry ice) were employed to ensure a uniform grain size across all samples. The resulting fine sawdust was divided for microbial molecular analyses (see below) and chemical analyses characterizing wood decomposition. We measured the pH value (aqueous extract), water-soluble lignin fragments (WSLFs), total organic carbon (TOC) and total nitrogen, and the concentrations of the bioavailable metals Ca, K, Mg, Cu, Zn, Fe, and Mn. For detailed protocols, see Appendix S1: Section S1.

Microbial diversity and ergosterol content

DNA extraction, sequencing and bioinformatics

To obtain microbial diversity and community composition, we performed DNA isolation, polymerase chain

reaction (PCR) amplification, sequencing, and bioinformatic analysis on all wood samples (details are provided in Appendix S1: Section S2).

Ergosterol content

Ergosterol content is a proxy for fungal biomass (Baldrian, Větrovský, et al., 2013), which was measured for two wood samples of each log. Both samples of a log were pooled, and total ergosterol was extracted with 10% KOH in methanol and analyzed using high-performance liquid chromatography (HPLC) (Šnajdr et al., 2008).

Statistical analysis

We quantified the functional diversity of beetles using nine selected traits that were considered to specify how the different beetle species affect wood decomposition. We calculated the Chao1 index for bacterial and fungal diversity indices and quantified the community composition of fungi and bacteria using nonmetric multidimensional scaling (NMDS) based on Bray-Curtis distances. Additionally, we summarized the associations of the nine measured nutrients (C, N, Mn, Cu, Zn, Fe, Mg, K, Ca) and C/N ratio using principal component analysis (PCA). More detailed information on the calculations of beetle functional diversity, microbial diversity indices and community composition, and PCA of nutrients can be found in Appendix S1: Section S3.

To test the effects of insect presence on wood decomposition, we fitted generalized linear mixed models to compare dry mass loss, relative tunnel volume, pH, WSLF content and nutrient PCA components between treatments with beetles and controls without beetles. Block was included as a random effect in these models, with a Beta error structure for relative tunnel volume to account for proportion data, and with a Gaussian error structure for other response variables.

To address our first two hypotheses, we used generalized linear mixed models, testing the effects of species richness and functional diversity of beetles on wood decomposition (i.e., relative tunnel volume). To address our third hypothesis, we then examined the effects on decomposition rates of including beetle biomass and, for our fourth hypothesis, the presence of a potential keystone species. Among the taxa, Ulyshen (2016) suggested as potential keystone species (i.e., termites, large cerambycid or passalid beetles) only cerambycids occur in Central Europe. We considered *Monochamus sutor* to have the highest potential to serve as keystone species since it is by far the largest species in our study system

(Klausnitzer et al., 2016) and tunnels deeper into wood than most other species (Ehnström & Axelsson, 2002). Nevertheless, we also repeated the model for the second (*Rhagium inquisitor*) and third (*Tetropium castaneum*) largest species. In these mixed models, we standardized predictor variables and included block as a random effect. We then estimated the standardized coefficient and coefficient of determination (marginal R_m^2). All mixed models were fitted using the `glmmTMB` package (Brooks et al., 2017), which allows beta regression with mixed effects, and model diagnostics were conducted using the `DHARMA` package (Hartig, 2020). To assess the robustness of our results above, we performed sensitivity analyses using the model structure for alternative measures of decomposition (see details in Appendix S1: Section S3).

To examine the direct effects of insects (i.e., species richness, functional diversity, and biomass) and indirect effects via microbial community variables on decomposition measures, we developed piecewise structural equation models (pSEMs). The full number of microbial variables was too large to include them all in the models. Since our main question was how beetles affect wood decomposition and not how microbes affect decomposition independently of beetles, we limited our pSEMs to those microbial variables that were significantly correlated with beetle richness or functional diversity (i.e., Bacteria Chao1, Bacteria NMDS1, Fungi NMDS2, and ergosterol; Appendix S1: Figure S2). Bacteria NMDS1 and Fungi NMDS2 were correlated with a high correlation coefficient ($|r| > 0.70$, Appendix S1: Figure S2). To prevent the model from overfitting, we excluded Bacteria NMDS1 and retained Fungi NMDS2 because fungi are known to be more important for decomposition than bacteria (Tláskal et al., 2021) and because bacteria were already represented in the model. The same model structure was applied to all decomposition measures (i.e., relative tunnel volume, mass loss, pH, WSLF content, nutrients PC1, nutrients PC2, and nutrients PC3). Predictor variables were standardized using the “`scale`” function in R (beetle biomass was natural logarithm transformed prior to standardization), and relative tunnel volume was transformed using the arcsine transformation. Single models were built using the “`lme`” function of the `nlme` package and included the block as random effect. The pSEMs were run using the `piecewiseSEM` package (Lefcheck, 2016). All data analyses were conducted in R version 4.1.2 (R Core Team, 2021).

RESULTS

Decomposition rates were significantly higher when insects were present for relative tunnel volume ($Z = 2.21$, $p = 0.027$)

and marginally nonsignificant for mass loss ($Z = 1.71$, $p = 0.088$) and WSLF content ($Z = 1.71$, $p = 0.087$; Appendix S1: Figure S4a,b,d). No significant effects of insect presence were observed for other chemical measures of wood decomposition (i.e., pH and nutrients PCA components; Appendix S1: Figure S4c,e-g). Wood decomposition rates increased with increasing species richness ($Z = 6.65$, $p < 0.001$) and functional diversity ($Z = 2.23$, $p = 0.03$) of beetles for relative tunnel volume (Appendix S1: Table S4; Figure 2a,b). For mass loss, the effects of beetle species richness ($Z = 1.01$, $p = 0.315$) and functional diversity ($Z = 0.11$, $p = 0.914$) had the same sign as for relative tunnel volume but were not significant (Appendix S1: Table S4; Figure S5a,b). When insect biomass was included in the mixed models, only species richness and insect biomass had significant effects on relative tunnel volume (Appendix S1: Table S4). Moreover, in the models that also included biomass and the presence of *M. sutor*—the largest species in this study and a potential key species—only species richness and *M. sutor* had significant positive effects on relative tunnel volume, and only *M. sutor* had significant positive effects on mass loss (Appendix S1: Table S4). In addition, no significant positive effects were found for the models that included both biomass and the presence of the second or third largest species, *Rhagium inquisitor* and *Tetropium castaneum* (Appendix S1: Table S4). Among the 14 species included in this study, *M. sutor* was associated with the highest decomposition rates, particularly for relative tunnel volume (Figure 3). Sensitivity analyses focusing on the net biodiversity effect (ΔY) provided

qualitatively similar results despite somewhat weaker effects (Appendix S1: Table S5).

Structural equation models revealed that 47% of the variation in relative tunnel volume and 7%–29% of the variation in other decomposition measures (i.e., mass loss, pH, WSLF content, nutrients PC1 [related to Mg, Mn, Ca, Zn and Cu], nutrients PC2 [related to C/N ratio and N] and nutrients PC3 [related to C]) were explained by measures of beetle communities, bacterial diversity, fungal community composition, and ergosterol content. Beetle species richness had a direct positive effect on relative tunnel volume, while functional diversity had no direct effects on any of the decomposition measures (Figure 4). Furthermore, beetle species richness affected wood decomposition (relative tunnel volume, WSLF content, nutrients PC2, and nutrients PC3) indirectly via beetle biomass (Figure 4a,d,f,g). Beetle species richness also affected wood decomposition (relative tunnel volume and WSLF content) indirectly by influencing fungal community composition (NMDS2). Both beetle species richness and functional diversity of beetles indirectly affected wood decomposition (relative tunnel volume, mass loss, pH, WSLF content, nutrients PC1, and nutrients PC3) via ergosterol content (Figure 4a–e,g).

DISCUSSION

Manipulating beetle communities in deadwood showed that, as predicted, wood decomposition is higher when

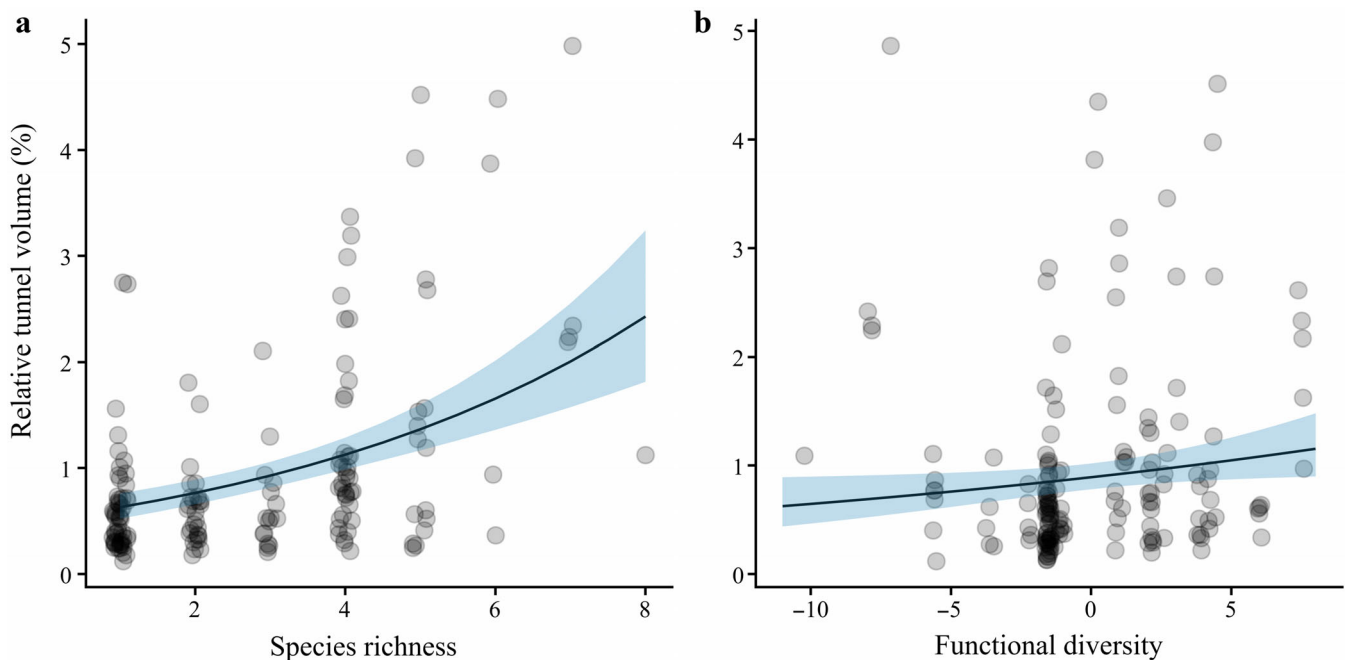


FIGURE 2 Partial effect plot of beetle diversity on relative tunnel volume. (a) Species richness and (b) functional diversity. Solid line represents partial fit, dots represent residuals, and shaded area indicates 95% CI of partial effect curve.

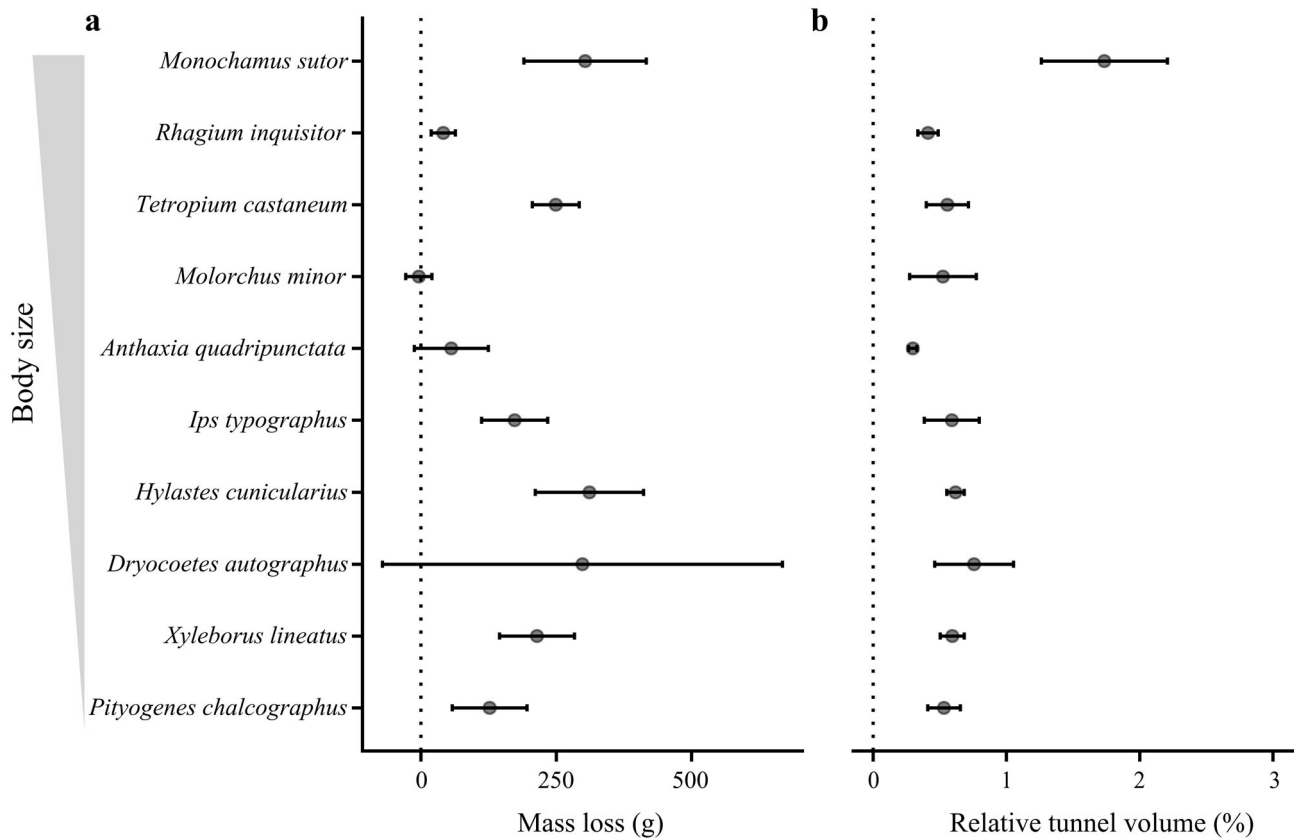


FIGURE 3 Effect of single beetle species on wood decomposition. Points indicate mean value of (a) mass loss and (b) relative tunnel volume, and bars indicate 95% CIs. Here these two measures of wood decomposition are based on the data from monoculture treatments only. Beetle species are arranged in order of body size from largest (i.e., *Monochamus sutor*) to smallest (i.e., *Pityogenes chalcographus*).

beetles were present and that both species richness and functional diversity had independent positive effects. The effects of functional diversity were associated with higher beetle biomass and the presence of one large-bodied species. Moreover, in line with our prediction, beetle species richness and functional diversity affected wood decomposition directly and indirectly through interactions with wood-decomposing bacterial and fungal communities.

The effects of beetles on decomposition were qualitatively similar for both decomposition measures that represent decomposition by insects, that is, relative tunnel volume and mass loss. Effects were, however, weaker for mass loss and not significant in several cases, such as for effects of beetle species richness. Mass loss generally suffers from limited accuracy since it is based on subsampling for estimating initial dry mass, which can lead to higher levels of noise in the data compared to CT-based estimates of the tunnel volume due to the heterogeneity in wood density and water content (Seibold et al., 2022). This could explain the high standard errors around the effects of beetles on mass loss compared to relative tunnel volume. Moreover, mass loss represents decomposition by both insects and microbes, while

CT-based tunnel volume represents only decomposition by insects (Seibold et al., 2022; Ulyshen & Wagner, 2013). Fungi are the primary decomposers of deadwood (Lustenhouwer et al., 2020; Zanne et al., 2022), yet fungi can translocate nutrients from outside into deadwood (Philpott et al., 2014), and competition between fungal species can decelerate decomposition (Skelton et al., 2019), which may explain why even increases in wood mass are sometimes found during early decomposition stages (Seibold et al., 2021). It is therefore possible that the effects of beetles were weaker for mass loss than for relative tunnel volume due to fungal activity decelerating dry mass loss and, thus, reducing overall decomposition. However, since ergosterol content had positive effects on mass loss in our pSEMs, weaker effects for mass loss than relative tunnel volume are more likely due to higher noise levels in the mass loss data.

Effects of beetle diversity on decomposition

Higher decomposition rates when insects were present compared to insect exclusion treatments have been

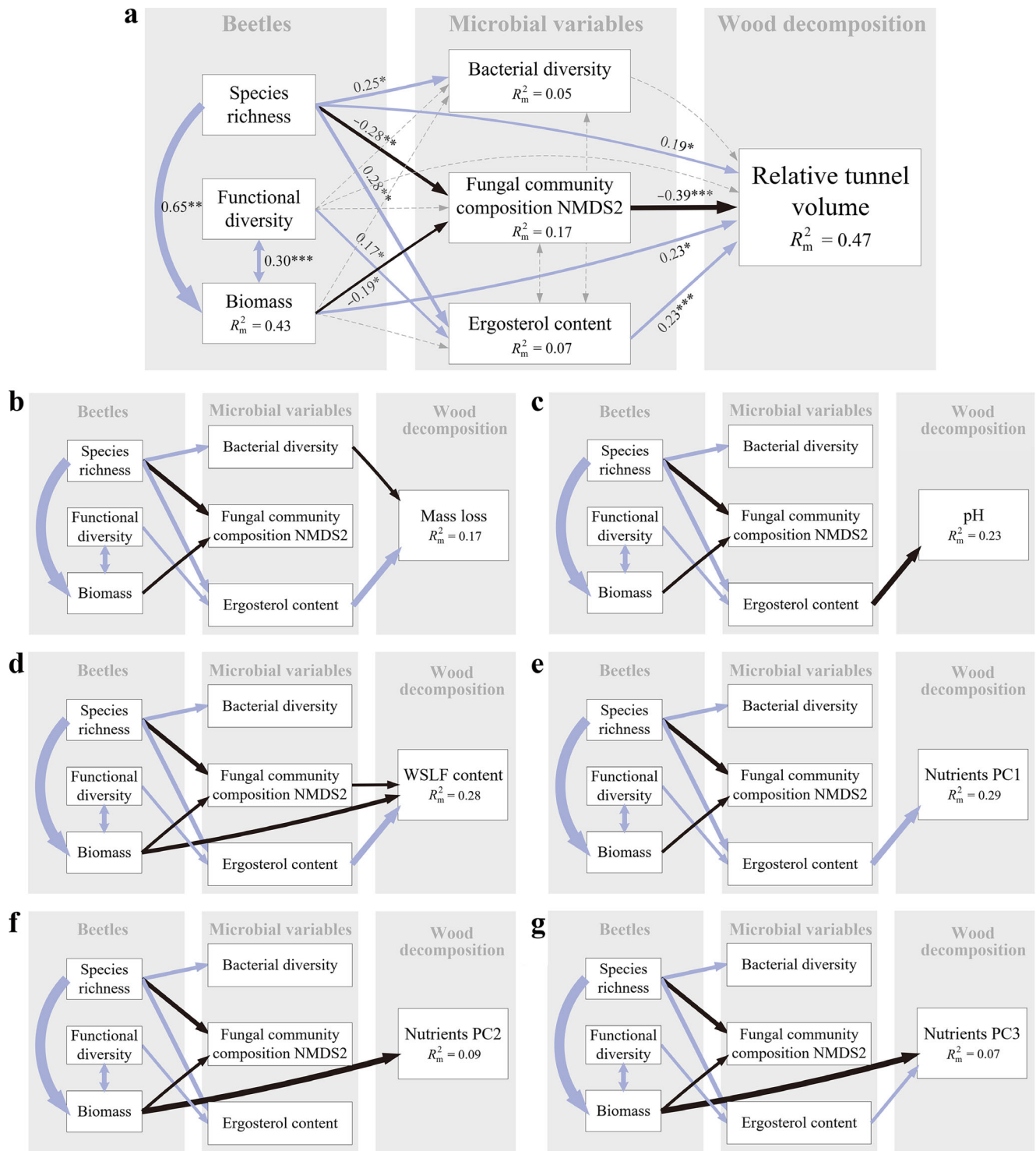


FIGURE 4 Direct and indirect effects of insects on wood decomposition. The structural equation models for the direct and indirect effects of species richness, functional diversity, and total biomass (Biomass) of added beetle species on (a) relative tunnel volume, (b) mass loss, (c) pH, (d) water-soluble lignin fragment (WSLF) content, (e) Nutrients PC1, (f) Nutrients PC2, and (g) Nutrients PC3 via bacterial diversity, fungal biomass (ergosterol content), and community composition. Arrows represent hypothesized causal relationships between variables. Solid lines indicate positive (light blue) and negative (black) relationships; the thickness of the solid lines indicates the strength of the causal effects. Dashed lines indicate nonsignificant relationships. Bidirectional arrows indicate correlated errors. R_m^2 values are marginal R^2 . Note that panels (b) to (g) showed only significant paths. Model fit was good (Fisher's $C = 5.27$; $p = 0.07$).

observed in local, regional, and global studies (Seibold et al., 2021; Ulyshen, 2016). In line with these earlier findings, we observed higher decomposition rates (significant for relative tunnel volume and marginally significant for mass loss) in treatments with beetles compared to treatments without beetles. Considering declines in insect biodiversity and changes in community composition (Dornelas & Daskalova, 2020; Outhwaite et al., 2022; van Klink et al., 2020), a more detailed understanding is needed about the importance of different facets of biodiversity on wood decomposition. In contrast to earlier studies that assessed insect effects on decomposition using only insect presence or absence (see Ulyshen, 2016 for a review) or correlated unmanipulated species richness of natural beetle communities to decomposition rates (Kahl et al., 2017; Pietsch et al., 2019), our experimental approach allowed us to identify and separate the effects of species richness and functional diversity. Consistent with our first hypothesis, we found independent positive effects of species richness of beetles on wood decomposition, suggesting that BEF relationships for beetles and wood decomposition are in line with general BEF theory. The functional diversity of beetle communities had positive effects on wood decomposition independently of species richness, but this effect vanished when beetle biomass was included in the models. Furthermore, the effect of biomass became nonsignificant when the presence of a potential key species (i.e., *M. sutor*) was included in our models. Thus, we found overall support for our first and fourth hypotheses, that wood decomposition would increase with beetle species richness and with the presence of the *M. sutor*, but not with functional diversity and overall biomass.

Our results suggest that the effects of beetle biodiversity on wood decomposition can be partly explained by the selection-effect hypothesis associated with the presence of large-bodied key species. Since the presence of this large-bodied species resulted in greater total beetle biomass, inclusion of this key species is compatible with the mass-ratio hypothesis. This finding is also of relevance for nature conservation, considering that larger species of saproxylic beetles are more prone to extinction than smaller ones (Seibold et al., 2015). However, since wood decomposition rates in treatments with other large-bodied species were considerably lower than in treatments with *M. sutor* (Figure 3), the observed patterns cannot simply be explained by larger body size but instead appear to be related to the functional characteristics or the behavior of *M. sutor*. Moreover, species richness had a significant effect on wood decomposition in the model that included beetle biomass and the presence of *M. sutor*, which suggests that species richness positively affects wood decomposition beyond a simple biomass and selection effect.

A potential explanation for this is complementarity between dissimilar species, which was not quantified by those traits that we considered in our measure of functional diversity. Such unmeasured traits, like consumption or metabolic rates, may increase decomposition rates in multispecies communities (niche-complementarity hypothesis). Our results for wood decomposition partly contrast with a mesocosm study conducted for leaf-litter decomposition (Heemsbergen et al., 2004) that found decomposition rates were driven by functional dissimilarity rather than species richness of soil fauna. This difference may be partly due to the higher resistance of deadwood to decomposition than most leaf litter (Benbow et al., 2019) and the dissimilar physical sizes between them, which should require different decomposers. This implies that the importance of functional dissimilarity of decomposer communities might change with ongoing decomposition. Future studies should involve more potential key species, explore the effects of further functional traits, and study different types of necromass in similar approaches to better understand the generality of the importance of large-bodied species, the role of niche complementarity, and the generality of mechanisms across necromass types.

Effects of insect–microbe interactions on decomposition

In addition to the direct effects of beetles on wood decomposition via consumption and fragmentation of deadwood, our results indicated that beetles affected wood decomposition indirectly via insect–microbe interactions (Birkemoe et al., 2018; Jacobsen et al., 2018; Ulyshen, 2016). By producing specific enzymes and their ability to degrade lignin, fungi and, to a lesser degree, bacteria play an important role in wood decomposition (Baldrian, Šnajdr, et al., 2013; Bani et al., 2018; Kahl et al., 2017; Leonhardt et al., 2019; Tláskal et al., 2021). Insects affect wood-inhabiting bacteria and fungi by fragmenting wood, creating entry ports, especially for spores or hyphae, and vectoring microbes (Birkemoe et al., 2018; Jacobsen et al., 2017, 2018; Seibold et al., 2019; Ulyshen, 2016), which can ultimately affect wood decomposition processes. Indirect effects of beetles via microbes were found for mass loss as well as chemical measures of decomposition (i.e., pH, WSLF content, and nutrients), which is not surprising since these measures either integrate direct consumption by insects and microbial activity (e.g., mass loss) or represent mainly chemical decomposition by bacteria and fungi (Baldrian, Šnajdr, et al., 2013; Leonhardt et al., 2019).

Beetle richness and biomass affected fungal community composition, which can further affect wood

decomposition. Beetles facilitate specific fungal species, potentially leading to increasing wood decomposition rates if these fungal species are efficient decomposers (Jacobsen et al., 2018) or decreasing wood decomposition rates if these vectored fungal species compete with other wood-decomposing species (Skelton et al., 2019). Moreover, beetle species richness and functional diversity positively affected fungal biomass (i.e., ergosterol). This suggests that facilitating the effects of beetles on fungi not only alters fungal community composition but promotes overall fungal colonization and performance. Furthermore, we found that beetle richness indirectly affected wood decomposition by increasing bacterial diversity. This effect led to lower mass loss. A potential explanation for this is that wood decomposition is carried out primarily by fungi and, to a lesser extent, by bacteria (Tláškal et al., 2021) and that fungal and bacterial communities interact closely (Odriozola et al., 2021). Although bacteria play a lesser role in the decomposition of wood, they may nevertheless exert an influence on the decomposition process by inhibiting principal decomposer fungi.

CONCLUSIONS

Following classic BEF experiments, our study highlights the importance of insect richness for wood decomposition. Stepwise analyses indicate that the effects of beetle diversity were associated with the presence of large-bodied key species (selection effect) as well as with additional effects of species richness, indicating unmeasured complementarity. Moreover, we show that insect–microbe interactions play a key role in decomposition processes. Our results highlight the importance of the conservation of insect diversity and particularly of large-bodied species for maintaining decomposition processes; they also show that conservation should not focus on single taxa or taxonomic groups but consider biotic interactions as well.

AUTHOR CONTRIBUTIONS

Sebastian Seibold conceived the idea of this study. Sebastian Seibold, Jörg Müller, and Roland Brandl designed the experiment, with contributions from Claus Bässler and Marc W. Cadotte. Sebastian Seibold conducted field work and measured wood decomposition rates. Petr Baldrian, Werner Borcken, and Elisa Stengel conducted laboratory analyses. Jia-Yun Zou performed statistical analyses with inputs from Ya-Huang Luo, Sebastian Seibold, and Jörg Müller. Jia-Yun Zou and Sebastian Seibold wrote the first draft. All co-authors revised the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Zou et al., 2023) are available in Figshare at <https://doi.org/10.6084/m9.figshare.22109165>.

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SUPPORTING INFORMATION

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