RESEARCH ARTICLE

Negative effects of forest gaps on dung removal in a full-factorial experiment

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Abstract

1. Ecosystem functioning may directly or indirectly—via change in biodiversity—respond to land use. Dung removal is an important ecosystem function central for the decomposition of mammal faeces, including secondary seed dispersal and improved soil quality. Removal usually increases with dung beetle diversity and biomass. In forests, dung removal can vary with structural variables that are, however, often interrelated, making experiments necessary to understand the role of single variables on ecosystem functions. How gaps and deadwood, two main outcomes of forest management influence dung removal, is unknown.

2. We tested if dung removal responds to gap creation and deadwood provisioning or if treatment effects are mediated via responses of dung beetles. We expected lower removal rates in gaps due to lower dung beetle biomass and diversity.

3. We sampled dung beetles and measured dung removal in a highly-replicated full-factorial forest experiment established at 29 sites in three regions of Germany (treatments: *Gap*, *Gap + Deadwood*, *Deadwood*, *Control*). All gaps were experimentally created and had a diameter of around 30 m.

4. Dung beetle diversity, biomass and dung removal were each lower in gaps than in controls. Dung removal decreased from 61.9% in controls to 48.5% in gaps, irrespective of whether or not the gap had deadwood. This treatment effect was primarily driven by dung beetle biomass but not diversity. Furthermore, dung removal was reduced to 56.9% in the deadwood treatment.

5. Our findings are not consistent with complementarity effects of different dung beetle species linked to biodiversity-ecosystem functioning relationships that have been shown in several ecosystems. In contrast, identity effects can be pronounced: gaps reduced the abundance of a large-bodied key forest species (*Anoplotrupes stercorosus*), without compensatory recruitment of open land species. While gaps and deadwood are important for many forest organisms, dung beetles and dung removal respond negatively. Our results exemplify how

experiments can contribute to test hypotheses on the interrelation between land use, biodiversity and ecosystem functioning.

KEYWORDS
biodiversity, deadwood, dung beetles, ecosystem functions, trophic interactions

1 | INTRODUCTION

Biodiversity is a major determinant of ecosystem functioning (Tilman et al., 2014). Several familiar ecosystem functions such as pollination, seed dispersal or predation are a direct outcome of activities by animals (Yang & Gratton, 2014), and the relationship between land use and animal-mediated ecosystem processes has been frequently documented (e.g. Ambarlı et al., 2021; Felipe-Lucia et al., 2018; Schuldt et al., 2018). However, ecosystems are now globally altered by human activities (Ellis et al., 2010), with land use and management influencing biodiversity and the dependent ecosystem functions. Animal species diversity has declined in many terrestrial ecosystems (Dirzo et al., 2014; Seibold et al., 2019). Whether changes in animal diversity relate to changes in functions has often been postulated, but only experimentally measured for few functions such as pollination (Kaiser-Bunbury et al., 2017; Klein et al., 2003), seed dispersal (Griffiths et al., 2015; Griffiths et al., 2016) or dung removal (Dangles et al., 2012; Larsen et al., 2005; Slade et al., 2011). This is in contrast to plants, where the relationship between biodiversity and ecosystem functioning is now firmly established (Schuldt et al., 2018; Tilman et al., 2014). As biodiversity and ecosystem functions may independently respond to altered environmental conditions following land-use change, disentangling the drivers is challenging: change in function can be either driven by change in abiotic conditions, or by change in biodiversity following altered conditions. Hence, ecosystem functioning may directly or indirectly respond to land use. Large-scale experiments for identifying the drivers are needed (Blüthgen & Staab, 2021; Griffiths et al., 2018) but often lacking.

Dung beetles (Coleoptera: Geotrupidae, Scarabaeidae) perform important multidimensional ecosystem functions by removing mammalian faeces. Activity of dung beetles is central for dung decomposition, accelerating nutrient cycling and improving soil, and also has positive secondary effects, for example, by lowering disease risk and reducing parasite spread (Hanski & Cambefort, 1991; Nichols et al., 2008; Slade et al., 2016). Dung removal is related to the abundance and diversity of dung beetles (Larsen et al., 2005; Oliver et al., 2015), with usually positive relationships suggesting that complementarity effects in dung beetle communities for the provisioning of ecosystem functions are important (Buse & Entling, 2020; Dangles et al., 2012; Larsen et al., 2005; Slade et al., 2011). As dung beetles respond rapidly to habitat change (Frank et al., 2017; Gardner et al., 2008; Slade et al., 2011), land use can impair dung removal, for example when species with a high contribution to removal get lost (Dangles et al., 2012; Kaartinen et al., 2013; Larsen et al., 2005). Being mobile organisms with highly efficient olfaction (Larsen & Forsyth, 2005; Wurmitzer et al., 2017), for which the location of patchy and unpredictable dung resources is crucial for reproductive success, dung beetles can be easily sampled in a standardized way, which makes them established indicator organisms (Gardner et al., 2008; Hanski & Cambefort, 1991).

Forests cover a substantial proportion of the ice-free land and provide habitat for the majority of terrestrial species (FAO, 2010). Globally, undisturbed forests are decreasing (Hansen et al., 2013) and almost all forests in Europe have historically been used by humans and are nowadays managed or show, when set aside, legacies of management (Schall et al., 2021). While the proportion of unmanaged forests has been slightly increasing in the last decades (McGrath et al., 2015), a substantial proportion of forests will continue to be actively managed, not least to meet timber demands. Forest management determines the structural properties of forests (Schall, Schulze, et al., 2018) such as tree species composition, canopy openness and deadwood volume, which all relate to insect diversity (e.g. Knuff et al., 2020; Penone et al., 2019; Schall, Gossner, et al., 2018). However, many forest structure variables are inevitably interrelated, making experiments necessary to understand effects of individual structures. For example, gaps and deadwood usually occur at the same time, either when trees die naturally, which opens the canopy and simultaneously provides deadwood or when trees are harvested and a certain deadwood amount is retained. Deadwood is an important resource in forests, but many saproxylic (i.e. deadwood-dependent) species have become rare in managed forests because deadwood availability is low (Müller & Bütler, 2010). In gaps, among many other parameters such as accelerated nutrient cycling, light availability is increased and the microclimate is warmer and fundamentally different compared to closed stands, which can locally increase the abundance and diversity of many organisms (e.g. Eckerter et al., 2021; Griffiths et al., 2021; Knuff et al., 2020; Leidinger et al., 2019; Lettenmaier et al., 2022). Nevertheless, most studies used observational gradients in canopy openness and data from forest experiments are scarce, particularly concerning ecosystem functions. One of the few available studies showed that host-parasitoid networks were more connected in gaps compared to controls, but the associated function of parasitism did not differ (Eckerter et al., 2022). How two main consequences of forest management, gaps and deadwood, influence dung removal is unknown.

We combined dung beetle sampling with measurements of dung removal in a well-replicated, full-factorial forest experiment to test if dung removal is related to the abiotic conditions associated with different canopy conditions, or if any shift in removal is an effect of changes in dung beetle communities. As dung removal and dung

beetle abundance as well as diversity are lower in more open forests, and also lower in grasslands compared to forests (Ambarlı et al., 2021; Buse & Entling, 2020; Frank et al., 2017), we hypothesize lower dung removal in gaps. In contrast, deadwood will have no effect on dung removal, as dung beetles are not saproxylic and not directly utilizing this resource. Treatment effects will be due to lower abundance and diversity of function-providing dung beetles (Larsen et al., 2005; Slade et al., 2011) rather than an effect of altered abiotic conditions in gaps.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was conducted within the Biodiversity Exploratories (Fischer et al., 2010) in the German regions of Schwäbische Alb, Hainich-Dün and Schorfheide-Chorin (Figure 1) that differ in climate and topography, and are representative for the prevailing forest types in Central Europe. Forests in the Schwäbische Alb (elevation: 460–860 m a.s.l., mean annual temperature: 6–7°C, mean annual precipitation: 700–1000 mm) and Hainich-Dün (285–550 m a.s.l., 6.5–8°C, 500–800 mm) consist of European beech (*Fagus sylvatica*) and Norway spruce (*Pieca abies*). In Schorheide-Chorin (3–140 m a.s.l., 8–8.5°C, 500–600 mm) beech is also common together with Scots pine (*Pinus sylvestris*) and oak (*Quercus petraea*, *Q. robur*) forests. In each region, 50 research sites with a size of 100 m × 100 m were established in 2008 along gradients of land-use intensity, from intensively managed conifer forests to unmanaged beech forest. Full forest inventories, most recently in 2015–2018, were conducted to quantify forest variables such as deadwood quantities (Schall, Schulze, et al., 2018). Canopy structure was characterized

with terrestrial laser scanning (LiDAR) in summer 2019, with canopy openness calculated as the proportion of free sky pixels (Ehbrecht et al., 2019). The forest cover in the landscape around a site (1000 m radius), was quantified from vectorized ATKIs Basis DLM land cover data (Seibold et al., 2019). Each of the 150 sites is equipped with a weather station, which, among other variables, records air temperature (10 cm above the soil, accuracy 0.01°C) every 10 min (Ambarlı et al., 2021). Precipitation was derived from the radar-based RADOLAN precipitation estimates of the German Weather Service (accuracy 0.1 mm/h).

2.2 | Forest experiment

To disentangle two important factors related to forest management—gap creation and deadwood availability—and their influence on biodiversity and ecosystem functioning, the full-factorial multi-site FOrest gap eXperiment (FOX) was established in January–March 2020. Experiments were created at 29 sites within larger continuous mature forests stands; within each stand, tree species composition, diameter distribution, forest structure and abiotic site conditions were similar (Peter Schall and Christian Ammer, unpubl. data). FOX included the regionally most dominant forest types and differed in the number of sites among regions. In the Schwäbische Alb, eight experimental sites were established, three in spruce forests, three in beech forests and two in mixed spruce-beech forests. In Hainich-Dün, all nine experiments were in beech forests (five even-aged, four uneven-aged stands). Experiments in Schorfheide-Chorin covered twelve forests, three each in pine, beech, mixed pine-beech and oak forests. Four treatments (*Gap*; *Gap + Deadwood*; *Deadwood*; *Control*) were implemented (Figure 1). Newly created experimental plots
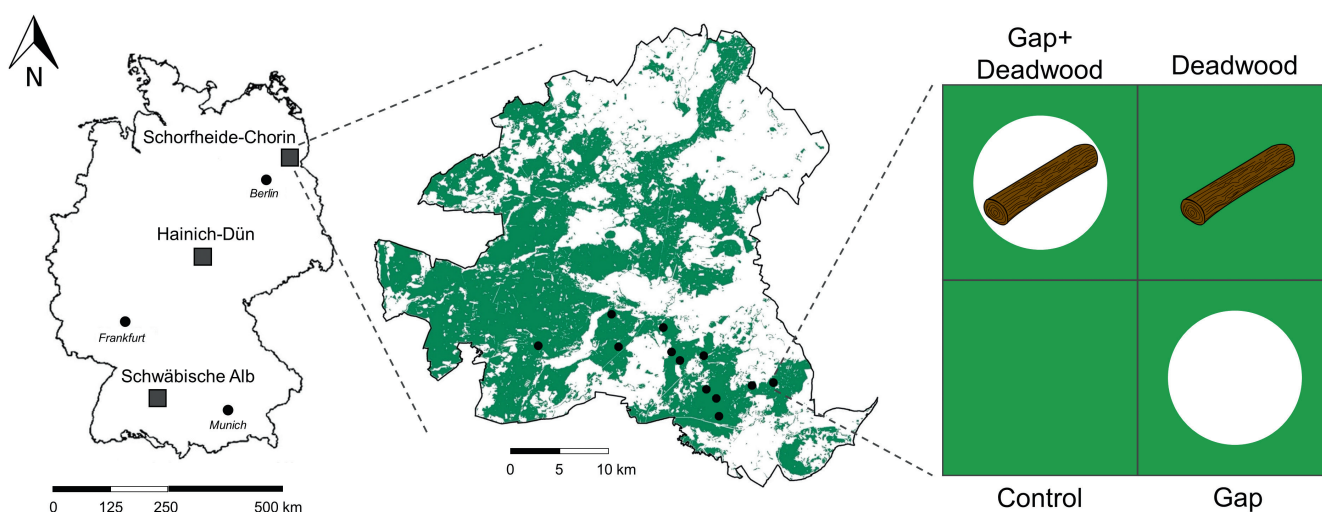

FIGURE 1 Overview on study design. In three regions of Germany, full-factorial experiments were established in 29 forest sites. Forested area is depicted in green and sites with experiments are indicated by black circles (here shown for the Schorfheide-Chorin region). At each site, four treatments were established: *Gap* (gap of ~30 m diameter, felled trees removed), *Gap + Deadwood* (gap of ~30 m diameter, deadwood left in place), *Deadwood* (deadwood addition in otherwise unmodified forest), and *Control* (no gap and no deadwood). Deadwood icon sourced from openclipart.org (creative commons zero 1.0 Licence).

measure 0.5 ha (71 m × 71 m) and the adjacent regular plot of the Biodiversity Exploratories (see above) serves as unmanipulated *Control*. All plots were spatially arranged to minimize variation in topography and exposition, keeping a minimum distance of 100 m among treatments. For *Gap*, a circular gap with a diameter of around 30 m (mean = 31.0 ± 3.2 m SD, range 25–37 m, equal to canopy height) was cut and all felled trees were removed. For *Gap + Deadwood*, an identically sized gap was cut with a specified amount of deadwood left in place. In turn, for *Deadwood*, a similar amount of deadwood was translocated into otherwise unmodified forest. Deadwood volume was predefined based on standing tree volume as *target volume*$_{(in\ m^3)}$ = *0.25*standing volume + 50*. Thus, the realized deadwood volume scaled with tree size and varied between 3.9–30.1 m^3 (mean = 13.9 ± 6.9 m^3 *SD*). To prevent tree-specific identity effects, each felled tree was cut into four equally-sized parts, of which two each were placed in *Gap + Deadwood* and *Deadwood* plots. About 1700 trees were cut to create the 2 × 29 = 58 gaps. Initial deadwood amount was much lower (mean = 13.0% ± 7.2% SD of target volume) than experimentally placed deadwood, not related to dung removal (Figure S2), and thus not further considered in analyses.

2.3 | Dung beetle sampling

Dung beetles can be easily sampled in a standardized way as they are attracted to dung volatiles from relatively large distances (Hanski & Cambefort, 1991). Sampling efficiency even of short trapping intervals is high, as most species in Central Europe are simultaneously active throughout the summer (Rössner, 2012). From early July to early August 2020, we exposed per plot one dung-baited pitfall trap for 48 h (Frank et al., 2017), summing to 116 traps (29 sites*4 treatments) and 5568 h (116 traps*48 h) trapping time. The mean temperature during the trapping times per site was 15.7°C (±2.1°C SD, range 12.2–21.4°C) with an average of 3.6 mm precipitation (±5.3 mm, 0–18.7 mm). Traps were placed 9 m in north-east direction from the plot centre. A plastic cup (9 cm diameter, 13 cm height) was dug flush into the ground and a teabag filled with ~35 g cow dung as bait was placed ~7 cm above the trap by fixing the teabag with a rubber band to a wooden skewer (Figure S1). Teabags were filled beforehand, frozen at −18°C and taken out of the freezer approximately 1 h before placement. Cow dung is very attractive to dung beetles and most species in the study regions are habitat specialists (Frank et al., 2017) but not specialized on dung types (Frank, Krell, et al., 2018). Traps were covered by an inward-facing lid with a 4 cm hole working as funnel (Figure S1), so attracted beetles were not able to escape again. As beetles were collected alive to avoid killing of non-target animals, a piece of tissue was added to provide shelter. One site in Schorfheide-Chorin was excluded, as traps were raided by Common Raven (*Corvus corax*). All dung beetle individuals (Geotrupidae, Scarabaeidae) were directly transferred into 70% ethanol and later identified to species (using Freude et al., 1969; Rössner, 2012). Dung beetle diversity was calculated

as Shannon entropy $e^{\wedge H}$ (corresponding to effective number of species, Jost, 2006). As the contribution of a dung beetle species to dung removal scales with body size (e.g. Buse & Entling, 2020; Nervo et al., 2014) we used biomass rather than individual number as abundance measure. Using the species-specific dry biomass values from Frank et al. (2017), who had collected dung beetles with the same method in the same regions on 150 grassland and 150 forest plots, and had measured individual mass on oven-dried specimens, individual numbers per species per plot were converted to total biomass (in g). Based on the comprehensive habitat preference analysis of Frank et al. (2017) all species were assigned a habitat preference category (open land, indifferent, forest; Table S1). Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen and Brandenburg. No ethical approval was required.

2.4 | Dung removal

Adopting the method described in Frank et al. (2017), dung removal was measured simultaneously with dung beetle sampling. Fresh cattle dung was sourced from an organic farm (Hofgut Oberfeld, Darmstadt) where cattle is only feed grass and hay and no vermicides are used (same dung used as trap bait). Prior to exposure, approximately 170 g dung each (mean 166.6 ± 9.8 g *SD*, individual weight noted) were weighted, sealed individually in plastic bags and frozen at −18°C. In the field, frozen dung was placed on cellulose paper on the ground. Per plot, five replicates were conducted, one in the plot centre and one each in 9 m distance towards each cardinal direction (Figure S1), summing to 580 dung samples (29 sites*4 treatments*5 replicates). Dung was retrieved after 48 h, eventually attached debris was carefully removed, and samples were oven-dried at 60°C to constant weight. To convert fresh weight into dry weight, the water content (mean 88.0% ± 1.2 *SD*) was determined by drying 40 randomly selected additional dung samples. Dung removal (r_{dung}), that is, the proportion mass loss, with 1 indicating complete removal and 0 no removal, was calculated as r_{dung} = (*dry weight$_{before}$* − *dry weight$_{after}$*)/*dry weight$_{before}$*, where *before* refers to the weight before exposition and *after* to the weight following retrieval. Removal was calculated for samples with holes in the underlying cellulose paper indicating dung beetle activity (no rolling dung beetles occur in the study sites). When no holes were present and eventually missing dung could not with certainty be associated to dung beetles, r_{dung} was set to 0 (11.9% of cases) and these samples were included in analyses. In turn, when no dung could be retrieved due to complete removal (Figure S1), r_{dung} was correspondingly set to 1 (28.8% of cases, also included in analyses).

2.5 | Data analysis

All analyses were conducted in R 4.1.2 (www.r-project.org) applying the packages APE (Paradis & Schliep, 2019), CAR (Fox &

Weisberg, 2019), EMMEANS (Lenth, 2022), LME4 (Bates et al., 2015), PIECEWISESEM (Lefcheck, 2016) and VEGAN (Oksanen et al., 2020). Sampling efficiency for all samples and for subsets per treatment was assessed with jackknife1 estimators (*vegan*).

First, to test for differences in dung beetle diversity, dung beetle biomass (square-root-transformed) and dung removal among *Gap*, *Gap + Deadwood*, *Deadwood* and *Control* plots, we calculated linear (i.e. Gaussian errors) mixed-effects models (*lme4*) and tested for differences in categorical treatments with ANOVA (*car*). To account for the hierarchical data structure with plots nested in sites and sites nested in regions, we specified appropriate random intercepts: *site-in-region* in models for beetle diversity and biomass (one trap per plot); *plot-in-site-in-region* in the dung removal model (five measurements per plot). Significance tests were based on Kenward-Roger-approximated degrees of freedom. Pairwise contrasts among treatments were calculated in *emmeans*, using Tukey tests accounting for multiple comparisons.

Next, to test whether effects of experimental treatments on dung removal are direct (i.e. solely via the exogenous treatment variables), or mediated via treatment-specific variation in dung beetle diversity and biomass (the endogenous variables), a path model was calculated (*piecewiseSEM*). This approach also accounted for temperature and precipitation, as dung beetle diversity and activity (Finn et al., 1998) and thus dung removal (Ambarlı et al., 2021) are related to weather. Because weather data are only available for the *Control* plots, they reflect variation among plots rather than treatment-induced differences. The path model included landscape-scale forest cover and canopy openness, as both might moderate the experimental treatments. For example, in open forests with many small natural gaps or tree species with less foliage, the experimental creation of more gaps could have a weaker effect than in closed forests with few natural canopy openings. To analytically link these considerations, we specified an a priori path model (Figure 3) with paths from gap, deadwood, canopy openness and forest cover on dung removal as well as paths of these four variables via dung beetle diversity and dung beetle biomass. Precipitation and temperature (with their interrelation modelled as correlated error) were linked to dung removal through diversity and biomass, accounting for their potential influence on beetle activity. As dung beetle biomass is expected to increase with diversity (sensu Hallmann et al., 2021), a path from dung beetle diversity to dung beetle biomass was specified (reversing this path results in a very similar model, ΔAIC = 0.1). For the path model, the categorical treatment variables were recoded into 0 and 1 (e.g. *Gap* had 1 for gap and 0 for deadwood; *Gap + Deadwood* had 1 for gap and 1 for deadwood). Component models for the endogenous variables dung beetle diversity, dung beetle biomass and dung removal were linear mixed-effects models with the same random effects structure each as the ANOVA models described above. Dung beetle biomass, precipitation and temperature were square-root-transformed to increase normality. All variables were scaled (mean = 0, $SD = \pm 1$). Residuals of all component models were inspected for normality and variance homogeneity, which were always met. We rejected potential spatial autocorrelation with Moran's I coefficients on residuals in *ape* (all $I_{observed} < -0.011$, $p > 0.778$).

To test if open plots with gaps (*Gap*, *Gap + Deadwood*) had a different dung beetle community than plots covered by a canopy (*Deadwood*, *Control*), we used a PERMANOVA (10,000 permutations) based on Bray–Curtis dissimilarity in *vegan* on a matrix of normalized dung beetle biomass per plot. Composition was visualized with two-dimensional non-metric multidimensional scaling (NMDS, same input data). Finally, we inferred whether open plots are being colonized by open land species. For this, we used linear mixed-effects models (*lme4*, site-in-region as random intercept) with the share of species and biomass from species with a preference for forests (preferences from Frank et al., 2017) as response variables and open vs. covered as explanatory variable.

3 | RESULTS

In total 17 dung beetle species (2 Geotrupidae, 15 Scarabaeidae) with 1336 individuals and a biomass of 150.6 g were found. *Anoplotrupes stercorosus* was the most common species in each treatment, contributing 72.8% of individuals and 83.5% of biomass, which was strongly correlated with the biomass of all dung beetles (Spearman's ρ = 0.933, Figure S3). Sampling efficiency was high, with the recorded species accounting for 77.3%–94.4% of the expected 20 ± 2 species (based on jackknife1; Table S1). Recorded (range 11–14) and expected species numbers (range 14–18 ± 2) were similar among treatments while biomass was highest (56.1 g, mean 2.0 ± 3.3 g *SD*) in *Control* and approximately half in *Gap* (29.1 g, 1.0 ± 1.3 g) and *Gap + Deadwood* (28.4 g, 1.0 ± 1.1 g) plots. Nine species were known for preferring forests and the six species preferring open land were rare (27 individuals). On average, 54.4% ± 38.4% of dung were removed by dung beetles. Removal per treatment aligned with dung beetle biomass, with highest average removal in *Control* (61.9% ± 36.4%), reduced removal in *Deadwood* (56.9% ± 39.7%), and lowest removal in *Gap* (48.5% ± 37.8%) and *Gap + Deadwood* (48.5% ± 39.6%; Table S1).

Experimental treatments had a significant effect on dung beetle diversity (ANOVA, F = 3.202, p = 0.027), dung beetle biomass (F = 3.928, p = 0.011), and dung removal (F = 13.703, $p < 0.001$; Figure 2), with the consistently largest differences between *Gap* and *Control*. All variables were lower in *Gap* and *Gap + Deadwood* than in *Deadwood* and *Control*, with always significant pairwise contrasts between both treatments with gaps and *Control* ($p < 0.05$; except for *Gap + Deadwood* vs. *Control* for dung beetle diversity, p = 0.129). In contrast, the *Deadwood* treatment (Table S2) differed significantly from the open treatments (*Gap*, *Gap + Deadwood*) only for dung removal, which was intermediate between treatments with gaps and *Control*, but not for dung beetle diversity and biomass. Open treatments were always similar to each other. Likewise, covered treatments (*Deadwood*, *Control*) never differed.

The a priori path model was statistically supported (Fisher's C = 8.702, p = 0.069; p-values >0.05 indicate support) and revealed how experimental gaps and deadwood influence dung removal (Figure 3, Table S3). Dung removal was lower in gaps and in more
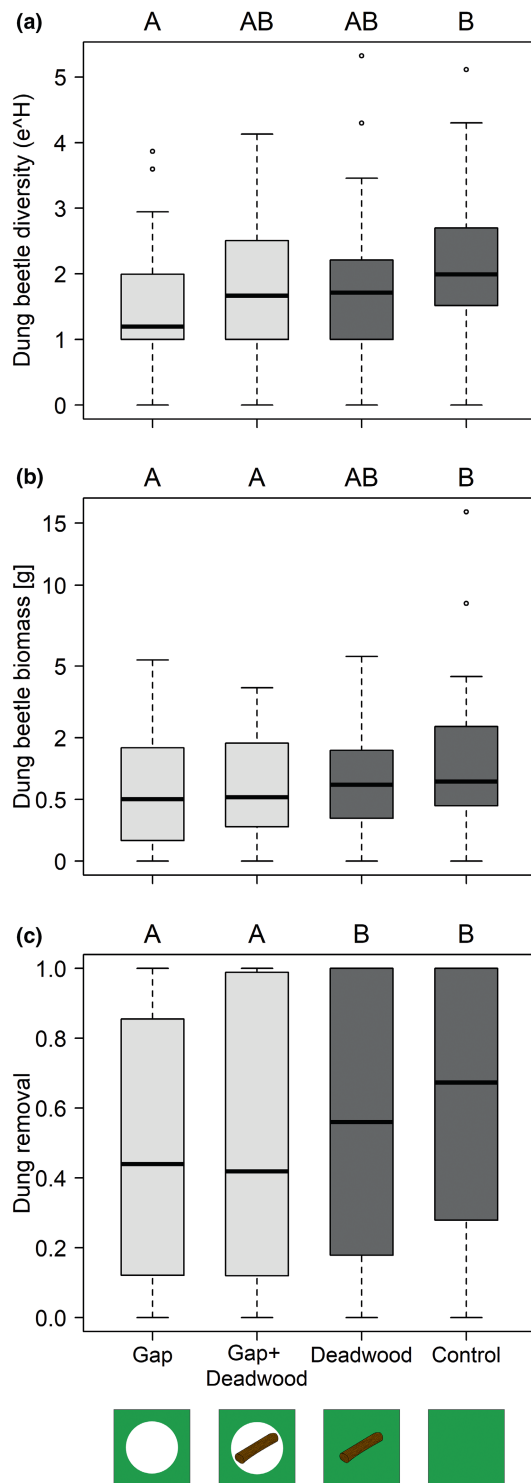
FIGURE 2 Differences in (a) dung beetle diversity, (b) dung beetle biomass and (c) dung removal among experimental treatments. For every variable there was a significant treatment effect (ANOVA, $p < 0.05$), with values in *gap* being lower than in *control*. Pairwise contrasts are reported in Table S2. Note that the *y*-axis of (b) is on a square-root scale.

open forests. However, most relationships on dung removal were mediated via the endogenous variable dung beetle biomass and its positive relationship with dung beetle diversity. Dung beetle biomass

decreased in treatments with gaps and deadwood. Furthermore, biomass decreased with canopy openness, while it was higher when temperatures were warmer. Likewise, dung beetle diversity decreased in both experimental manipulations and was also negatively related to precipitation. The effect sizes of deadwood were always approximately one third of the effect sizes of gap. Only dung beetle biomass but not dung beetle diversity was related to dung removal, with more dung removed when beetle biomass was high. Opposed to canopy openness, forest cover was not significantly related to any variable. Precipitation and temperature correlated negatively.

Dung beetle community composition did not differ between open (*Gap, Gap + Deadwood*) and covered treatments (*Deadwood, Control*) (Figure S4). Species preferring open land were not occurring in sizeable quantities in gaps. Species and biomass were dominated by forest species, with no significant difference between open and covered treatments (Figure S4).

4 | DISCUSSION

The creation of gaps in forests reduces the ecosystem function dung removal, with likely subsequent effects on decomposition, soil fertility, secondary seed dispersal, and disease prevalence. Agreeing with expectations, removal was mediated by treatment effects on dung beetle biomass but, against expectations, not via effects on dung beetle diversity. Nevertheless, gaps had also a negative effect on dung removal, while there was also an unexpected negative effect of deadwood on dung beetles. Our results illustrate with the example of gaps and deadwood in forests, how large-scale field experiments successfully allow to separate inherently related ecosystem properties, and thus to increase our understanding of functional consequences of land use.

4.1 | Dung beetle biomass, not diversity, mediates the effect of gaps on dung removal

Gaps have during the day a warmer microclimate and, compared to closed forests, temperature is more variable (Ehbrecht et al., 2019; Geiger, 1965). As light penetrates to the ground, energy availability is high, which influences microhabitat selection and activity of ectothermic organisms, including insects. Unsurprisingly, species communities across taxa thus differ in gaps and open forests, and may also be more diverse (e.g. Ambrožová et al., 2022; Eckerter et al., 2022; Lettenmaier et al., 2022). However, for dung beetles we found lower diversity and biomass in gaps than in controls. These differences translated into the ecosystem function dung removal, which was reduced in gaps. While the direction of the gap effect was expected based on consistent findings of lower dung removal in open land compared to forests in Central Europe (Ambarlı et al., 2021; Buse & Entling, 2020; Frank et al., 2017), we go beyond previous studies by disentangling how experimental gap effects on dung beetle diversity and biomass explain dung removal. We found that dung beetle biomass, not diversity, mediated
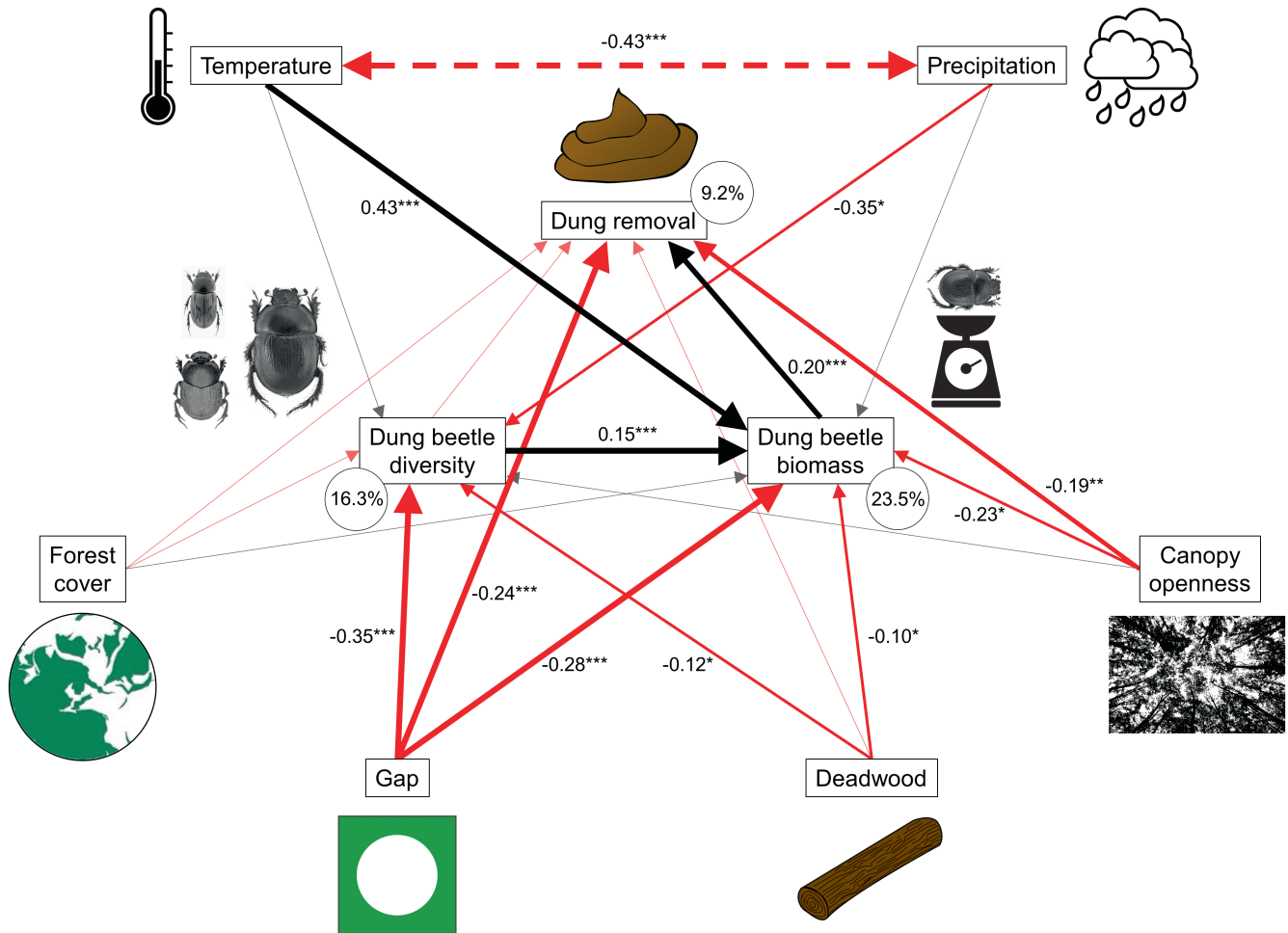
FIGURE 3 Path model (Fisher's $C = 8.702$, $p = 0.069$) illustrating how experimental manipulations (gap, deadwood) affect dung removal. The influence of weather and forest conditions is also considered. Numbers next to arrows are standardized path coefficients (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). Black and red arrows indicate positive and negative relationships, respectively, with thickness of arrows scaling with the level of significance. The correlated error term between temperature and precipitation is indicated by a dashed arrow. Percentage values give explained marginal variances of endogenous variables. Thin transparent arrows indicate non-significant relationships, with coefficients omitted for clarity. Full details are provided in Table S3. Icons are either curtesy of the authors or (thermometer, cloud, scale, dung, deadwood) sourced from openclipart.org (creative commons zero 1.0 Licence).

treatment effects on dung removal, suggesting that in the studied forests this process is not scaling with the diversity of the function-providing organisms (e.g. Larsen et al., 2005; Manning et al., 2016), as would be predicted from biodiversity-ecosystem functioning theory (Tilman et al., 2014). Thus, there were no complementarity effects of different dung beetle species that have been shown across ecosystems (e.g. Cheng et al., 2022; Dangles et al., 2012; Larsen et al., 2005; Slade et al., 2011). For example, Slade et al. (2011) found lower dung removal in logged rainforest. Even though dung beetle abundance, biomass and diversity were similar among differently used forests, dung removal correlated positively with dung beetle diversity but not abundance or biomass, indicating complementarity. Nevertheless, we acknowledge that fully causal inference would require the experimental manipulation of dung beetle diversity and biomass, which is challenging under field conditions.

In contrast, our findings suggest a species identity effect, driven by a single forest species with a high contribution to dung removal

(Buse & Entling, 2020; Kaartinen et al., 2013; Slade et al., 2011). The large-bodied Geotrupidae *A. stercorosus*, a forest specialist (Frank et al., 2017; Rössner, 2012) reaching highest densities in closed forests (Buse & Entling, 2020; Hülsmann et al., 2020), was the most common species in all experimental treatments contributing over 80% to total biomass. While *A. stercorosus* also occurred in open treatments, its abundance and hence its contribution to dung removal was lower, explaining the relationship between dung beetle biomass and dung removal (Buse & Entling, 2020) among treatments. However, community composition between open and covered treatments was similar. Thus, gaps reduced the abundance of a large-bodied key forest species (see also Nervo et al., 2014; Nichols et al., 2007) without compensating for these losses by recruiting open land species like in Heteroptera at the same sites (Rafael Achury, unpubl. data). As the amount of dung used for measuring removal was larger than the amount used in dung beetle traps, we cannot exclude that relatively more individuals were attracted to the larger dung patches and thus

not collected. Possibly, sampling with more bait would reveal a more comprehensive account of the dung beetle community, including more individuals of open land species.

Even though habitat selection of dung beetles can occur at small spatial scales (Perrin et al., 2021), the experimental gaps are potentially too small and open patches in forests too sparse to provide habitat for open land species. Being organisms depending on a scarce and patchy resource (Hanski & Cambefort, 1991) equipped with highly efficient olfaction to locate dung (Wurmitzer et al., 2017), these open land species could be promoted by opening forest canopies (Ambrožová et al., 2022; Nichols et al., 2007) and should at least theoretically be able to disperse into gaps. An alternative explanation for the limited functional substitution is that in particular large-bodied open land species have declined in Central Europe during the last decades due to intensified land use (Buse et al., 2018; Buse & Entling, 2020), while communities in forests have maintained their large species that have a high contribution to dung removal (Nervo et al., 2014).

4.2 | Possible mechanisms behind lower dung removal in gaps

Mechanistically, large forests dung beetles might avoid gaps for several reasons, including predator avoidance and physiological constraints. In particular, predation pressure might be higher in forest gaps compared to closed forest (Perrin et al., 2021). Many diurnal birds prey on the day-active and rather slow-moving dung beetles (Young, 2015), which are more conspicuous and thus more prone to predation in the open gaps. While deadwood could principally provide some shelter from predators, this is not suggested by the data. Similar avoidance of open habitats to escape predators is documented for other taxa, such as rodents that under predation pressure often prefer cover (Bedoya-Perez et al., 2019; Dickman, 1992). Furthermore, predation pressure in insects can increase with body size (Remmel & Tammaru, 2009), which could contribute to explain why biomass was lower in gaps. Exploring whether predation on dung beetles is a function of body size and higher in gaps, for example, by video recording tethered individuals, would be a promising theme for future research.

Alternatively, forest dung beetles could avoid gaps as they cannot cope with increased water loss when being exposed to sunlight (Nico Blüthgen, unpubl. data). Physiological stress in dry and sunny conditions can lower the reproduction rate of forest-adapted dung beetles (Vessby, 2001). Most adult dung beetles cannot process dried-out dung (Holter, 2016), making it likely that dung in gaps is only attractive for a short period of time until it desiccates (Davis & Scholtz, 2001). This time-constrained lower attractiveness of the key resource likely explains the found direct gap effect on dung removal. Physiological mechanisms are further suggested from the relationships between dung beetles and temperature and precipitation. Dung beetle diversity was lower when it rained, possibly because not all species are active during rain. Dung beetle biomass, in turn, increased with temperature due to higher activity of ectothermic organisms in warm weather (Prather et al., 2018). Also, volatile

emission from dung is temperature-depended, providing more olfactory cues and easing resource finding at higher temperatures (Wurmitzer et al., 2017).

4.3 | Deadwood may accentuate gap effects on dung removal

In contrast to expectations, deadwood was negatively related to dung removal by reducing dung beetle diversity and biomass, even though dung beetles have no a priori relation to deadwood. Nevertheless, deadwood played a minor role compared to gaps, with path coefficients being approximately one third as large. At present, we can only speculate on the mechanisms behind the deadwood effect. Downed logs could impose a physical barrier, as they hinder the low flights (Hanski & Cambefort, 1991) of beetles in search for dung (Michael Staab, pers. obs.). Deadwood logs could also impair the spread of volatiles (Frank, Brückner, et al., 2018) by sheltering dung from wind, reducing the probability that dung is found by beetles (Wurmitzer et al., 2017). Furthermore, there could be an ecological effect of deadwood: in a 'landscape-of-fear' herbivorous mammals avoid areas with logs, as the logs impede flight when being ambushed by carnivores (Ripple & Beschta, 2007). Thus, in the vicinity of deadwood there might be less dung and thus fewer resident dung beetles that could immediately remove dung without the need of dispersal, partly explaining deadwood effects on dung beetles. As herbivores preferentially forage in gaps (Kuijper et al., 2009), the same reasoning could have implied a positive effect of gaps on dung beetles, which was not found. Vegetation in gaps was in the first year after experimental tree removal still relatively sparse, making effects on habitat selection by herbivores unlikely, which may, however, change over time.

While the deadwood effect on dung beetles was negative, there are many saproxylic species for which deadwood is a crucial and that can be promoted by providing deadwood (Gossner et al., 2016). Several non-saproxylic organisms can also benefit from deadwood (Eckerter et al., 2021). At the time of sampling, deadwood was fresh and started to being colonized by saproxylic organisms. It will be interesting to see how the influence of gaps and deadwood on other organisms develops over time when the decomposition stage enters succession. Likely differences between deadwood in gaps and covered plots will appear, as decomposition rates and decomposer abundance can be shaped by canopy openness (e.g. Griffiths et al., 2021; Wu et al., 2021) and as rapid growth of vegetation in gaps is expect. Thus, with ongoing time of the experiment, the initially negative effect on dung beetles might vanish if deadwood in advanced decomposition and regrown trees provide shelter or buffer microclimate.

5 | CONCLUSIONS

Without question, gaps and open forests as well as dead wood availability can increase the diversity of organisms in forests and can be important for the conservation of endangered species

requiring open conditions and deadwood (Seibold et al., 2015). Nevertheless, our data indicate that these relationships are not universal for all forest organisms. Dung beetles and their multidimensional ecosystem process 'dung removal' respond negatively to experimental gaps. These relationships—and whether functional changes are responses to altered environmental conditions—could only be unravelled by using a controlled and replicated experiment, exemplifying how experimental approaches can contribute to test hypotheses on the interrelation between land use, organismic diversity and ecosystem functioning. The lower dung removal in gaps may impair soil functions (Slade et al., 2016) and increase the prevalence of disease and parasites for mammals (Nichols et al., 2008), especially because herbivorous mammals are expected to preferentially forage on the upgrowing vegetation in the gaps.

AUTHOR CONTRIBUTIONS

Michael Staab and Nico Blüthgen conceived the ideas; Michael Staab, Hendrik Mohr, Veronika Irmscher and Martin Ehbrecht collected the data; Christian Ammer and Peter Schall designed the FOX experiment; Michael Staab analysed the data and led the writing. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All raw data are permanently archived and are available in the BExIS repository (https://www.bexis.uni-jena.de/). Accession numbers 31246 (dung beetles), 30938 (dung removal), 27828 (canopy openness), 26007 (forest cover). Climate data are also available from BExIS (https://www.bexis.uni-jena.de/tcd/PublicClimateData/Index).

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SUPPORTING INFORMATION

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