

# Coppicing and topsoil removal promote diversity of dung-inhabiting beetles (Coleoptera: Scarabaeidae, Geotrupidae, Staphylinidae) in forests

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- Abstract**
- 1 Central European forests experience a substantial loss of open-forest organisms due to forest management and increasing nitrogen deposition. However, management strategies, removing different levels of nitrogen, have been rarely evaluated simultaneously.
  - 2 We tested the additive effects of coppicing and topsoil removal on communities of dung-inhabiting beetles compared to closed forests. We sampled 57 021 beetles, using baited pitfall traps exposed on 27 plots.
  - 3 Experimental treatments resulted in significantly different communities by promoting open-habitat species. While alpha diversity did not differ among treatments, gamma diversity of Geotrupidae and Scarabaeidae and beta diversity of Staphylinidae were higher in coppice than in forest. Functional diversity of rove beetles was higher in both, coppice and topsoil-removed plots, compared to control plots. This was likely driven by higher habitat heterogeneity in established forest openings. Five dung beetle species and four rove beetle species benefitted from coppicing, one red-listed dung beetle and two rove beetle species benefitted from topsoil removal.
  - 4 Our results demonstrate that dung-inhabiting beetles related to open forest patches can be promoted by both, coppicing and additional topsoil removal. A mosaic of coppice and bare-soil-rich patches can hence promote landscape-level gamma diversity of dung and rove beetles within forests.

**Keywords** Dung beetle, forest management, functional diversity, insect decline, nitrogen uptake, rove beetle.

## Introduction

The conversion and degradation of natural habitats is causing global biodiversity declines (Newbold *et al.*, 2015). Terrestrial insect abundance has declined by ~9% in past decades (van Klink *et al.*, 2020), with adverse effects on ecosystem functioning, including the provision of food sources for higher trophic levels (Bowler *et al.*, 2019), and nutrient cycling (Yang & Gratton, 2014). While insect decline is particularly strong in landscapes dominated by agriculture, forests experienced a

decline of *e.g.*, 41% arthropod biomass in Germany between 2008 and 2017 (Seibold *et al.*, 2019). This loss has been attributed to the combined effects of *e.g.*, removal of large old trees (Lindenmayer *et al.*, 2014), homogenization of forest structures and increasing canopy closure (Miklín *et al.*, 2018; Thorn *et al.*, 2020), cumulative uptake of nitrogen (Midolo *et al.*, 2019) and the abandonment of traditional forest management (Benes *et al.*, 2006; Weiss *et al.*, 2021).

Traditional forest management, such as pollarding, wood pastures and coppicing, has promoted forest heterogeneity and hence enabled the co-existence of species with various habitat requirements (Sebek *et al.*, 2013; Helbing *et al.*, 2014; Horak

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*et al.*, 2014). The abandonment of coppicing has caused an unprecedented decline of light-demanding species across European landscapes (Benes *et al.*, 2006; Streitberger *et al.*, 2012; Müllerová *et al.*, 2014). Hence, coppicing is currently used to support specialized plants (Vild *et al.*, 2013; Douda *et al.*, 2017; Lanta *et al.*, 2020), saproxylic beetles (Vandekerkhove *et al.*, 2016) or butterflies (Fartmann *et al.*, 2013; Sebek *et al.*, 2015; Dolek *et al.*, 2018).

Nitrogen deposition changes plant species composition towards communities composed of more nutrient-demanding species with greater biomass and lower diversity (Hautier *et al.*, 2009). Therefore, a simplified plant community hosts simplified communities of insects with lower richness but higher abundances (Haddad *et al.*, 2000). Hence, nitrogen removal has been suggested to restore ecosystems and to manage nitrogen-limited habitats such as heathlands (Niemeyer *et al.*, 2007). Nitrogen accumulation can be reduced by prescribed burning (Hubbard *et al.*, 2004), grazing, mowing (Jones *et al.*, 2017), litter harvesting (Sayer, 2006), removal of tree-biomass and logging residues (Lundborg, 1997) or humus and topsoil removal (Prietzel & Kaiser, 2005; Tarvainen *et al.*, 2011). However, such measures might only have a short-term effect, given the continuous atmospheric nitrogen deposition, yet topsoil removal is one of the most efficient and long-lasting measures (Jones *et al.*, 2017; Neff *et al.*, 2020). Topsoil removal was implemented to restore plant communities (Hölzel & Otte, 2003; Kiehl *et al.*, 2010), support the re-establishment of light-demanding herb species (Emsens *et al.*, 2015), restore communities of herbivorous insects (Neff *et al.*, 2020) and support thermophilic and epigeic arthropods, such as many carabids and spiders (Borchard *et al.*, 2014). So far, topsoil removal has been barely applied in forest ecosystems (but see Ewald & Pyttel, 2016; Soto & Puettmann, 2018).

While both, topsoil removal and coppicing, remove nitrogen to a certain degree, studies investigating the effects of topsoil removal and coppicing have mainly focused on either the one or the other (Šipoš *et al.*, 2017; Neff *et al.*, 2020). Yet, changes in forest management are accompanied by a continuous aerial nitrogen input (Bobbink *et al.*, 2010). Hence, potential forest biodiversity conservation measures need to account for both, while it remains unclear whether nitrogen removal, *e.g.*, topsoil removal, on top of tree-biomass removal by coppicing has additional benefits for biodiversity.

Primeval European forests were likely more open than managed forests today, due to natural disturbances, *e.g.*, windthrows, insect outbreaks, fires and grazing of large herbivores, creating temporal gaps and increasing forest heterogeneity (*e.g.* Bradshaw *et al.*, 2003). The anthropogenic suppression of the effects of natural disturbances (Wohlgemuth *et al.*, 2002; Thorn *et al.*, 2017), the lack of large herbivore grazing (Vera, 2000) and the transition from traditional forest management to modern forestry (Douda *et al.*, 2017) additionally contributed to a decline of species associated with light forests.

Dung beetles (Scarabaeidae, Geotrupidae) and rove beetles (Staphylinidae) provide important ecosystem functions in forests (Symondson *et al.*, 2002; Nichols *et al.*, 2008). The majority of dung beetle species is linked to open and semi-open habitats (Buse *et al.*, 2018) and around half of Central European species are currently red-listed (Buse *et al.*, 2015). Hence,

dung-inhabiting beetles are commonly used bioindicators (Bohac, 1999; Spector, 2006). Most species of Aphodiinae (Scarabaeidae) feed and develop directly in the dung pile, while most of the Geotrupidae and Scarabeinae (Scarabaeidae) relocate dung into their underground nests to provision their offspring (Nichols *et al.*, 2008; Noriega *et al.*, 2021). *Via* these activities, they contribute to enhanced nutrient cycling, secondary seed dispersal or parasite and fly suppression (Nichols *et al.*, 2008; Maldonado *et al.*, 2019; Milotić *et al.*, 2019). The species-specific contribution to dung removal, strongly depends on species ecological and morphological traits, such as nesting strategy, foraging behaviour and body size (Milotić *et al.*, 2019; de Castro-Arrazola *et al.*, 2020; Tonelli *et al.*, 2020). Rove beetles are often the most numerous dung-inhabiting insects (Hanski & Hammond, 1986). Dung-associated rove beetles are mostly predators (and parasitoids) feeding on other dung-inhabiting insects, which makes them important biological control agents of *e.g.*, larvae of dung breeding pest flies (Maus *et al.*, 1998; Cabrera Walsh & Chani Posse, 2003). For instance, the large rove beetle species *Emus hirtus*, is a major predator in dung of various herbivores and preys on dung beetles in their galleries (Biel *et al.*, 2014). A minority of rove beetle species are phytosaprophagous-coprophagous (Freude, 2009). The maintenance of dung-inhabiting beetle functional diversity has hence recently become a conservation goal beyond the protection of taxonomic diversity (Barragán *et al.*, 2011; Milotić *et al.*, 2019).

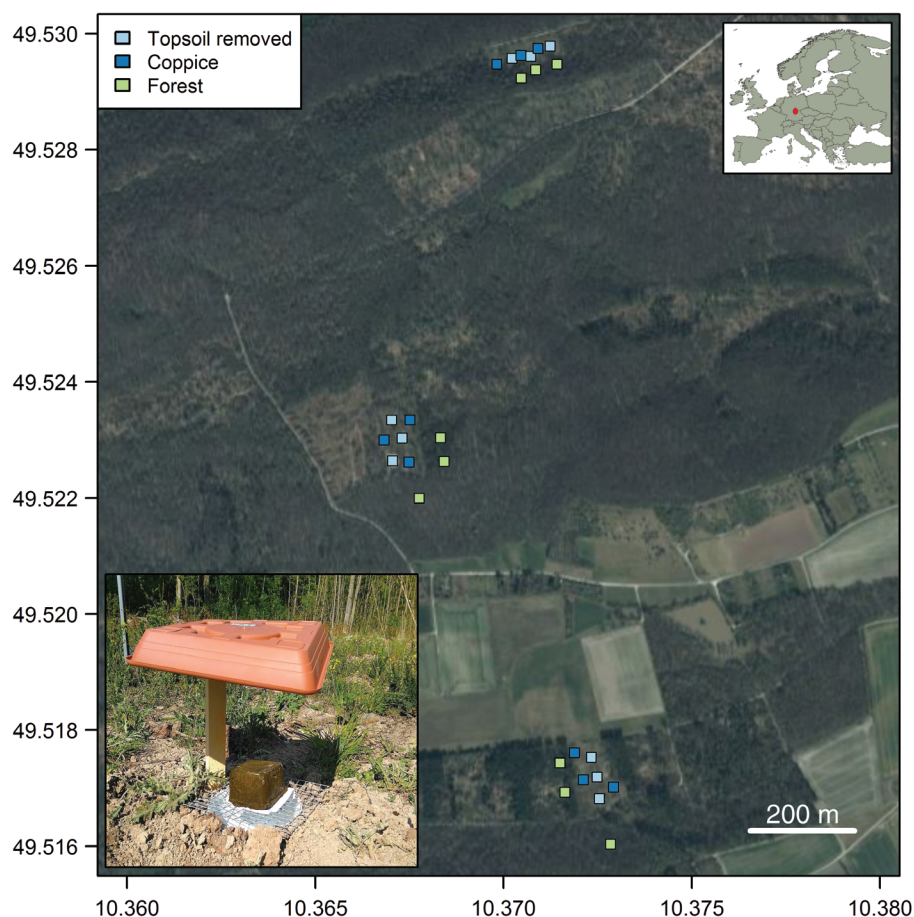
We applied experimental coppicing and topsoil removal to test if taxonomic and functional diversity of dung-inhabiting beetle communities can be promoted by forest opening and topsoil removal. Furthermore, we discussed the effects of experimental treatment on red-listed species.

## Methods

### *Study area and experimental design*

Our study was conducted near the city of Bad Windsheim in north-western Bavaria, Germany (49°32' N 10°23' E, around 350 m asl). In this area, the mean annual temperature was 9.2°C and the mean annual precipitation was 593 mm between 1991 and 2020 (station 'Kaubenheim', www.am.rlp.de). Forest stands in the study area are dominated by sessile and common oaks *Quercus petraea* (Matt.) Liebl. and *Quercus robur* L., with lower percentages of beech *Fagus sylvatica* L., Scots pine *Pinus sylvestris* L. and spruce *Picea abies* (L.) H. Karst., as well as a high variety of around 60 other tree and shrub species. Beside high-stem forests, the study area is partly managed as coppice with standards, thus promoting sun-exposed forest structures and *Q. petraea*. Forests are inhabited by wild ungulates (roe deer, wild boar) while the sampling area is embedded in a landscape with long grazing tradition of moving herds of sheep. The earliest signs of grazing in the area date back to 1365 (Schultheiß, 1963).

Coppicing in the above-described forests was applied in three randomized blocks of around 1.5 ha size each around Bad Windsheim in January 2019. Within each of the blocks, 10 cm of topsoil was removed on three patches of 20 × 20 m in size. Topsoil removal was performed by means of an excavator during daylight for several days in February 2019. The same plots were replicated in the coppiced area nearby without topsoil



**Figure 1** Experimental design to investigate the effects of coppicing and topsoil removal on communities of forest-dwelling dung beetles. Three experimental blocks were distributed to the forestry district of Bad Windsheim, where each experimental block contains three untreated forest plots, three coppices and three coppices with additional topsoil removal. The inset shows the baited pitfall trap used in our study. *Source of map:* Bing maps via openmaps.

removal and in adjacent forest (coppice with standards after 20 years without logging) serving as control, as it is the original forest, where coppicing and topsoil removal were applied. In total, we applied 27 plots (Fig. 1). The mean distance between plots was 640 m overall (60 m within blocks). On each plot, we exposed temperature loggers (model EL-USB-1, Easylog) from the beginning of April to the end of August 2020 and recorded the ground surface temperature every hour. We took one hemispherical photograph (Sigma EX DC 4.5 mm lens) in the middle of each plot and one in each corner in July 2020, resulting in five photographs per plot. These photographs were processed by means of the software HemiView (Version 2.1, Delta-T Devices) to yield the global site factor as a measure of solar radiation for each plot (Rich *et al.*, 1993). Total vegetation cover was assessed based on the sum of cover in moss, herb and shrub layer, surveyed on a 100 m<sup>2</sup> on each plot.

#### *Beetle sampling and ecological traits*

In each of 27 plots, one dung-baited trap (Lobo *et al.*, 1988) was exposed for 1 week in three sampling campaigns, *i.e.*, May,

July and October in 2020, to cost-effectively cover the seasonal variability in the beetle community (Sladeczek *et al.*, 2013). A metal wire mesh (19 mm) carried the dung bait and was placed on the top of the 5 L bucket sunk in the soil with the upper edge levelled up to the soil surface. Traps were baited with homogenized fresh cattle *Bos primigenius f. taurus* (Linnaeus, 1758) dung collected from local cattle herds nearby, which were not treated with anthelmintics for at least 4 months. The size of the baits was standardized to 400 g. Baits were stored frozen prior to their exposition to avoid prior decomposition and thawed before use. All traps were filled with a saturated salt solution with detergent to preserve trapped specimens. In all sampling campaigns, traps were exposed for 1 week and collected from the field afterwards. All trapped beetles of the families Scarabaeidae, Geotrupidae and Staphylinidae were identified to the species level. Taxonomy follows Löbl and Löbl (2015, 2016).

We extended published information on morphological and ecological traits of dung beetles and rove beetles, which represent the body size, general lifestyle and reproductive characteristics of each species, based on Buse *et al.* (2018), Freude (2009), Assing and Schülke (2012), Meineke *et al.* (2017) and Lipkow (2011). For complete list of traits, see Tables S1 and S2.

### Data analysis

All statistical analyses were carried out in R version 4.0.2 (www.r-project.org). Prior to statistical analysis, all samples were accumulated to the plot level. First, we compared ground surface temperatures, global site factor, and vegetation coverage across treatments. Therefore, we modelled the mean hourly ground surface temperatures in all plots by generalized additive models with gaussian error distribution. We included the day-time within the respective treatment as smooth term, the Julian date as linear predictor and block and plot identity as random effect to control for repeated measurements. Global site factor and total vegetation cover were compared between treatments using linear mixed models for gauss-distributed data provided by the 'lme4' r-package (Bates *et al.*, 2015). The treatment (coppice/topsoil-removed/forest) was selected as response variable and the experimental block and plot was added as a random effect to account for the nested study design (Fig. 1).

We analysed species alpha diversity by comparing the mean number of species collected in managed and unmanaged plots by using generalized linear mixed models for poisson-distributed data (Bolker *et al.*, 2009). We selected the number of species as response variables and added the treatment as predictor. Additionally, we added the experimental block as a random effect. Pairwise comparisons between treatments in all models were conducted by means of multiple comparisons for parametric models with simultaneous adjustment of *p*-values based on the single-step method, provided by the function 'glht' from r-package 'multcomp' (Hothorn *et al.*, 2008). This model was repeated for the number of species of relocating dung beetle species (all species of the genus *Onthophagus* Latreille, 1802, *Anoplotrupes stercorosus* (Scriba, 1791), *Colobopterus erraticus* (Linnaeus, 1758) and *Sisyphus schaefferi* (Linnaeus, 1758)) and dwellers (*i.e.*, all others) (Buse *et al.*, 2018). To reveal single species which respond by changes in their abundance to the respective treatments, we repeated the poisson-linear mixed model for the abundance of each species separately as response variable. We selected the treatment as predictor, the experimental block as random effect and added an observation-specific random effect to account for possible poisson-overdispersion (Elston *et al.*, 2001). We estimated the degree of correlation of the model for alpha diversity residuals with geographic coordinates by means of spline correlograms (Bjørnstad & Falck, 2001), provided by the r-package 'ncl' to detect possible spatial auto-correlations. Based on 1000 bootstrap iterations, we did not detect any spatial dependency in our model outputs (Fig. S1).

We selected the distribution of functional traits in the functional space as a measure for functional diversity of dung beetle and rove beetle assemblages. Therefore, we used the abundance-weighted mean pairwise distances between co-occurring species in a functional space (Webb *et al.*, 2008). Gower distances were computed using the function 'daisy' in the r-package 'cluster' (Gower, 1971). However, the observed functional diversity can be correlated to the number of species in a local community. Thus, we used null models that standardize the observed functional diversity across multiple sampling locations to the diversity expected when species are randomly selected from a regional species pool (Gotelli, 2000). The regional species pool of the present study was defined as all species recorded within our plots. Resulting standardized functional

diversity values >0 indicate higher diversity per number of species than expected by chance and *vice versa* (Pausas & Verdú, 2010). Standardized functional diversity was modelled with the same model term as alpha diversity, but with a gaussian error-distribution.

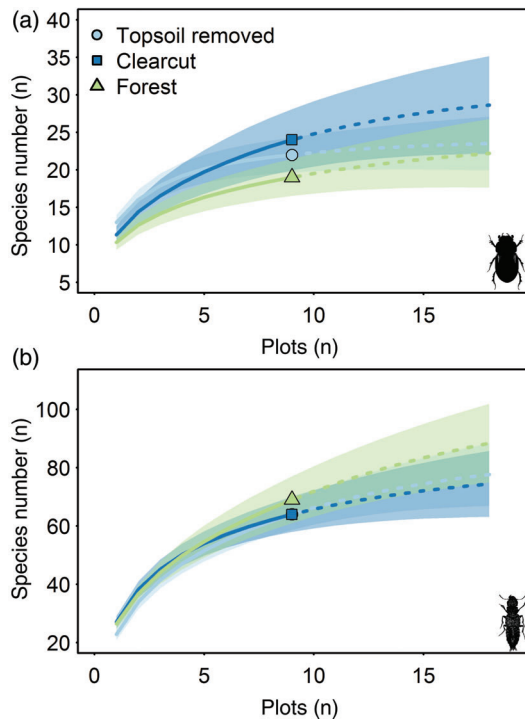
To analyse the effects of our experimental treatments on species communities, we used permutational multivariate analysis of variance (Legendre & Anderson, 1999), provided by the 'vegan' r-package (Oksanen *et al.*, 2020). Here, Bray-Curtis distances were used to derive the associated resemblance matrices. Community composition was visualized using non-metric multidimensional scaling (square root transformation, Wisconsin double standardization; Minchin, 1987). *P*-values were adjusted using Bonferroni correction for multiple testing due to pairwise comparisons among treatments.

In order to compare gamma-diversity among treatments, we used the analytical framework published by Chao *et al.* (2014), which is implemented in the r-package 'iNEXT' (Hsieh *et al.*, 2016). Here, species accumulation curves with confidence bands based on bootstrap replicates allow the comparisons of observed gamma diversity and sample coverage standardized by sampling effort. Pairwise dissimilarities within treatments were subjected to a multivariate homogeneity of group dispersions analysis (Anderson *et al.*, 2006), which was calculated by means of the function 'betadisper' in the 'vegan' r-package (Oksanen *et al.*, 2018). This analysis tests whether the average distance to the centroid of a given treatment ( $\beta$ -dispersion), differs between treatments. High  $\beta$ -dispersion indicates heterogeneous communities, while low  $\beta$ -dispersion indicates homogenous communities.

### Results

In total, we recorded 49 448 specimens belonging to 28 species of dung beetles (19 species of Scarabaeidae: Aphodiinae, eight species of Scarabaeidae: Scarabaeinae, one species of Geotrupidae), and 7573 specimens belonging to 99 species of rove beetles (Staphylinidae). See Table S3 for the complete list of species. Sample coverage analysis revealed high sample completeness for both groups around 90% (Fig. S2). The number of species per plot (alpha-diversity) did not differ among treatments, as indicated by generalized linear mixed models (Fig. S3, Table S4) and rarefaction-extrapolation curves, respectively (Fig. 2). However, the total number of species (gamma-diversity) of dung beetles in coppice was higher than that in forest (Fig. 2). The mean number of relocating and dwelling dung beetles did not differ among treatments (Table S4). Additionally, the highest temperature fluctuations were measured in topsoil-removed plots (8–30 °C), lesser in coppice (9–28 °C) and the lowest in forest (12–24 °C; Fig. 3a). Topsoil-removed plots received the highest amount of solar radiation, followed by coppice and forest (Fig. 3b, Table S5). Vegetation cover was significantly higher in coppice than in topsoil-removed plots (Fig. 3c, Table S6).

Five dung beetle species, namely, *Euorodalus paracoenus* (Balthasar & Hrubant, 1960), *Melinopterus prodromus* (Brahm, 1790), *Onthophagus fracticornis* (Preyssler, 1790), *Onthophagus ovatus* (Linnaeus, 1767), *S. schaefferi* and four rove beetle species, *Anotylus tetracarinatus* (Block, 1799), *Eurodotina inquinula* (Gravenhorst, 1802), *Atheta longicornis*

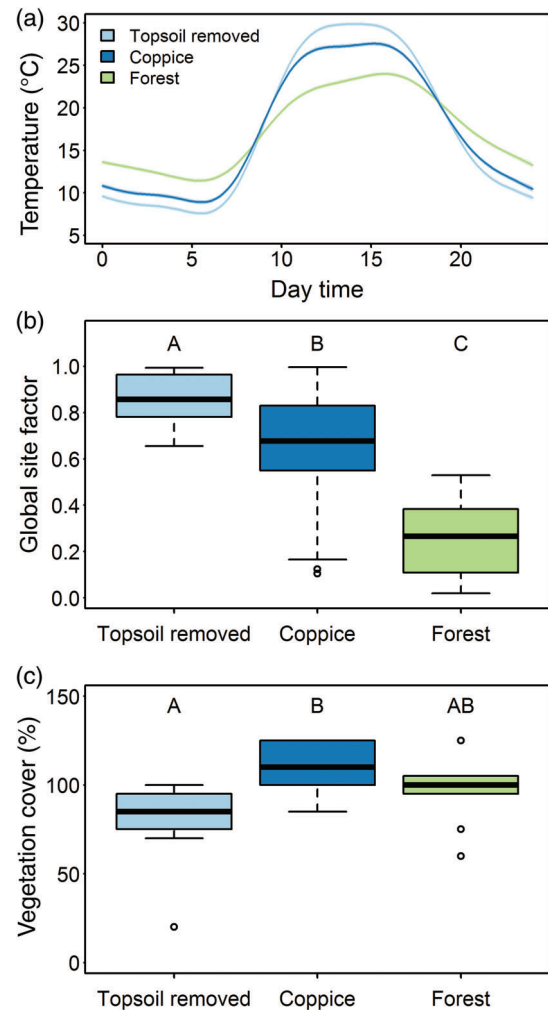


**Figure 2** Plot-based rarefaction (solid lines) and extrapolation (dotted lines, up to twice the sample size taken) of (a) dung beetles and (b) rove beetles sampled in baited pitfall traps on topsoil-removed plots, coppices and forest plots. Transparent shading indicates 95% confidence intervals based on 200 bootstrap replicates (see Fig. S2 for sample coverage).

(Gravenhorst, 1802), *Tinotus morion* (Gravenhorst, 1802), were significantly more abundant in coppices. One dung beetle (*E. paracoenosus*) and two rove beetle species (*Anotylus inustus* (Gravenhorst, 1806), *Aleochara curtula* (Goeze, 1777)) were significantly more abundant in topsoil-removed plots (Figs S4 and S5, Table S7). Also, several species were significantly more abundant in forest, while rarely present in coppiced and topsoil-removed plots, including *Anoplotrupes stercorosus*, *Limarus maculatus* (Sturm, 1800), *Volinus sticticus* (Panzer, 1798), *Acrolocha amabilis* (Heer, 1841), *Omalium rivulare* (Paykull, 1789), *Bisnius fimetarius* (Gravenhorst, 1802), *Platydracus chalcocephalus* (Fabricius, 1801), *Tachinus humeralis* Gravenhorst, 1802 and *Oxyroda acuminata* (Stephens, 1832).

Functional diversity of dung beetles was highest in forest, lower in topsoil-removed plots, and coppice hosted the functionally least diverse community (Fig. 4a). Functional diversity of rove beetles was increased by both, coppicing and topsoil removal, compared to forest control (Fig. 4b, Table S8).

Communities of dung beetles found in coppice and topsoil-removed plots were similar but differed from communities found in forest (Fig. 5a, Table S9). Communities of rove beetles differed among all three experimental treatments (Fig. 5b, Table S9). Beta-diversity of dung beetles did not differ between any pair of treatments (Table S10). However, beta-diversity of rove beetles was lower in forest compared to coppice (Table S10).

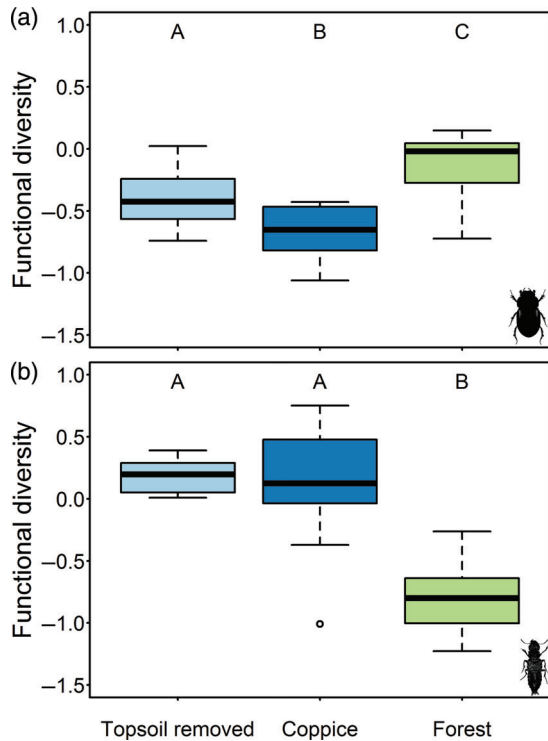


**Figure 3** (a) Mean hourly ground surface temperatures in study treatments. Temperature loggers (model EL-USB-1, Easylog) from the beginning of April to the end of August 2020 and recorded the ground surface temperature every hour, (b) global site factor, indicating the amount of solar radiation, (c) total vegetation cover based on the sum of cover in moss, herb and shrub layer on a 100 m<sup>2</sup> plot. Uppercase letters indicate statistically significant differences (see Tables S5 and S6 for statistical details).

## Discussion

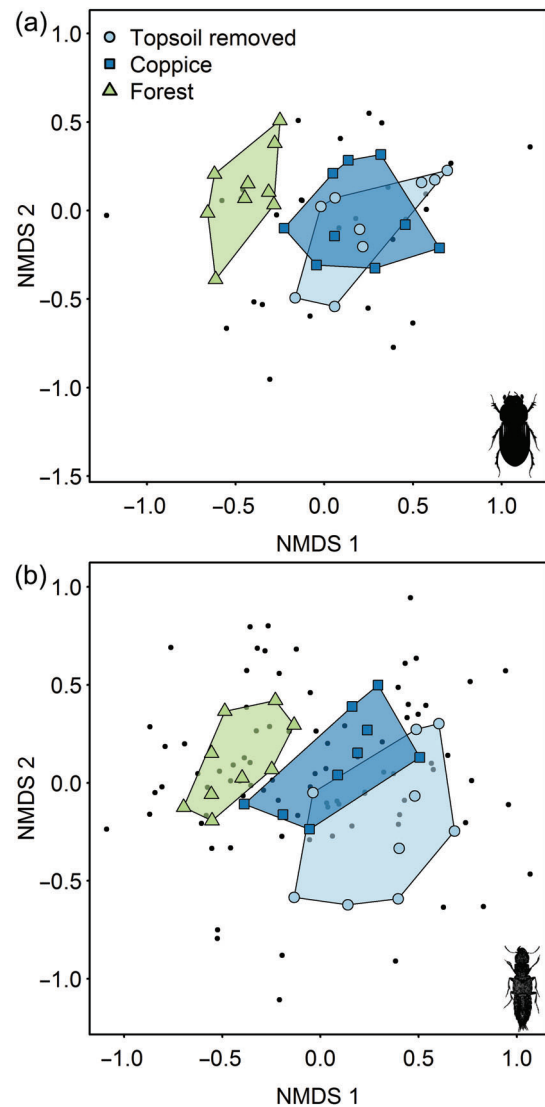
The total number of dung beetle species was higher in coppice and topsoil-removed plots compared to forest control plots. However, the mean number of dung and rove beetle species per plot did not statistically differ among treatments. Functional diversity of rove beetles was increased by coppicing and topsoil removal, while dung beetles had highest functional diversity in forest, followed by topsoil-removed and coppice, respectively. Species communities of rove beetles differ in all pairwise comparisons and their beta-diversity were higher in coppices compared to untreated forest control plots.

Topsoil removal can eliminate nitrogen and exposes large patches of bare soil (Jentsch *et al.*, 2009). As the bare ground usually absorbs more heat, the surface gets warmer and drier



**Figure 4** Functional diversity, measured as standardized mean pairwise distances between co-occurring species in the functional space, of (a) dung beetles and (b) rove beetles sampled in baited pitfall traps on topsoil-removed plots, coppices and forest plots. Uppercase letters indicate statistically significant differences.

than on sites with forest litter (Sayer, 2006). Warmer, drier and sun-exposed patches inside a forest matrix might enable the co-existence of open habitat and forest species on small spatial scales (Warren & Büttner, 2008). This is confirmed by our temperature data (Fig. 3a), revealing large differences in temperature amplitudes among our treatments, with the greatest differences in topsoil-removed plots and the lowest in forest. After topsoil removal, biological communities usually tend to shift towards less nutrient demanding, xero/thermo/heliophilic species or species of initial succession stages (Jentsch *et al.*, 2009; Kiehl *et al.*, 2010; Tropek *et al.*, 2017; Volf *et al.*, 2018). In our study, dung beetles of conservation concern, *i.e.*, *E. paracoenus* and *S. schaefferi* (Fig. S4) were predominantly caught in coppices and topsoil-removed plots (Table S3). *Onthophagus illyricus* (Scopoli, 1763) and *Onthophagus medius* (Kugelann, 1792), both are species of conservation concern, were exclusively found on managed plots. Also, we found significantly higher abundances of *E. paracoenus* and *Anotylus inustus* on topsoil-removed plots than in coppiced and forest plots. Both species prefer warm habitats (Assing & Schülke, 2012; Buse *et al.*, 2018) and likely benefitted from warmer microclimate in topsoil-removed plots. Also, high, yet not significant, abundances of the ball-rolling dung beetle, *S. schaefferi*, were found in topsoil-removed plots. Patches of bare soil and low vegetation cover are critical for survival of many threatened organisms including plants (Česonienė *et al.*, 2019), bees (Heneberg *et al.*, 2016), and spiders (Krause *et al.*, 2011), as well as ground



**Figure 5** Non-metric multidimensional scaling of species (black dots) of (a) dung beetles and (b) rove beetles from baited pitfall traps in topsoil-removed plots, coppice and forest plots (symbols). Polygons depict minimum convex hulls encompassing all plots of a respective treatment to indicate beta-dispersion.

beetles (Volf *et al.*, 2018; Růžičková & Hykel, 2019). Our results indicated that bare soil, created by topsoil removal, is important also to some dung-inhabiting beetles. Hence, measures ensuring the presence of insolated patches of bare soil would benefit a wide array of specialized organisms and should be considered as a conservation measure for sustainable forest management (Borchard *et al.*, 2014; Buckley, 2020). For practical applications further studies are needed to evaluate different patch sizes. Here, we show that already small patches of 400 m<sup>2</sup> are sufficient to support species of conservation concern.

Beta dispersion analyses revealed larger turnover of rove beetle species within coppices (Table S10) compared to forest control plots, *i.e.*, coppicing seems to create largely heterogeneous habitat conditions for rove beetles. The more heterogeneous

habitat could be created by the simultaneous presence of legacies from the original forest, such as solitary standing trees, and the exposition of bare soil e.g., due to logging operations. This assumption is supported by higher beta-diversity in coppices, observed for plants (Kopecký *et al.*, 2013; Bartha *et al.*, 2020), birds (Battisti & Fanelli, 2011; Mentil *et al.*, 2018), butterflies, amphibians, reptiles and small mammals (Buckley, 2020). More heterogenous habitats, *i.e.*, more niches, in coppice and topsoil-removed plots may also support a higher functional diversity of rove beetles (Fig. 4b).

Untreated forest plots hosted dung beetle communities with typical forest species, such as the relocating species *Anoplotrupes stercorosus*, *Onthophagus verticicornis* (Laicharting, 1781), *O. coenobita* (Herbst, 1783) and the dung-dwelling species *Acrossus depressus* (Kugelann, 1792), *Limarus maculatus* and *Volinus sticticus* (Buse *et al.*, 2018). The dung-relocating (tunnelling) beetles are particularly important for dung removal in forests (Buse & Entling, 2020). This might also be reflected by higher functional diversity of dung beetles in forests, compared to coppice or topsoil-removed plots (Fig. 4a). Here, the lack of very large relocators in coppice and topsoil-removed plots could contribute to decreased functional diversity. However, an additional topsoil removal might promote higher abundances of other functionally distinct species, such as *S. schaefferi*, the only roller in our study.

#### Recommendations for management

Coppicing and topsoil removal had distinct effects on species communities of dung beetles and rove beetles. The effects of additional topsoil removal on the taxonomic diversity of dung and rove beetle communities were relatively small, compared to the effects of coppicing alone. However, additional topsoil removal buffered the slightly negative effects of coppicing on the functional diversity of dung beetles (Fig. 4a). Coppices showed significantly higher abundances of species of high conservation value, such as *E. paracoenosus* and marginally significant also *S. schaefferi*. Those species, together with other protected or rare invertebrates, birds and plants related to coppices (Benes *et al.*, 2006; Spitzer *et al.*, 2008; Buckley, 2020), justify continuous coppicing. By contrast, the abandonment of coppicing or coppice conversion to high forest might lead to local disappearance of light-demanding organisms (Kopecký *et al.*, 2013; Buckley, 2020). Shade-tolerant species would remain largely unaffected since their required habitat remains available in currently most preferred closed-canopy high-stand forests (Buckley, 2020). However, the benefits of topsoil removal should be carefully weighed against its potentially high costs. Other measures creating bare soil patches, such as prescribed burning, might be a suitable substitute for topsoil removal to create patches of bare soil. We presented the short-term biological response, while topsoil removal might result in a delayed succession of the respective plots, which may maintain open forest for a longer-time span.

#### Conclusions

Dung and rove beetles contribute to nutrient cycling and provide important ecosystem services in forests, such as dung

removal and pest control. However, numerous species, including red-listed species, depend on open patches within a forest matrix. Our results demonstrate that taxonomic and functional diversity of those species can be promoted by coppicing, and additional topsoil removal. A mosaic of coppice and bare-soil-rich patches can hence promote landscape-level gamma diversity of dung and rove beetles within forests.

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#### Data availability statement

Data available on request from the authors.

#### Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

#### Appendix S1. Supporting Information

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