# Effect of forest management on temperate ant communities

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**Abstract.** Human management of ecosystems can have direct or indirect effects on species communities. How species communities are affected by management is a key question in ecology and nature conservation. As keystone taxon, changes in ant communities can have sustained consequences for entire ecosystems. In forests, management has been shown to have an overall negative effect on ant communities in tropical and a positive effect in boreal forests. However, in temperate forests, it is unclear what components of forest management affect ant communities and how. This study explores the direct and indirect effects of forest management on the taxonomic and functional diversity of ant communities in 150 temperate forest stands in three regions in Germany. Using a multi-model inference approach and structural equation models, we analyzed the effects of 18 variables, including variables of forest management, forest structure, arthropod diversity, and biomass, as well as abiotic factors, on ant species richness, abundance, and functional trait diversity (Rao's $Q$) based on morphological ($FD_M$) and life-history traits ($FD_{LH}$). In total, we found 28 ant species occurring on 120 plots. Main direct effects of forest management on ant abundance and species richness were caused by tree species selection, measured as dominant tree species. The main positive indirect effect was mediated by a reduced canopy cover with an increasing proportion of oak and pine, resulting in a higher temperature amplitude. Due to the low number of species in two regions, we analyzed functional diversity for the most ant species diverse region only. $FD_{LH}$ was affected positively by tree harvesting and negatively by structural complexity. $FD_M$ showed no response to forest management, potentially due to the low morphological diversity of temperate forest ants. Our results show that forest management practices in temperate forests strongly impact ant community structure. This can be beneficial for ants if management reduces the canopy cover, either by tree harvesting or by changing the tree species composition toward shade-intolerant tree species. To promote ant diversity as key taxon for maintaining ecosystem processes in forest ecosystems, we suggest to integrate forest stands with more open and warmer conditions in future management strategies.

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## INTRODUCTION

Land-use and management intensification is a major threat to biodiversity (Allan et al. 2014), leading to local species loss (alpha diversity; Newbold et al. 2015) and homogenization of communities (loss of beta diversity; Gossner et al. 2016) across trophic levels. In the

predominantly cultural landscapes of Europe, grasslands, croplands, and forests are the main land-use types which are managed at different intensities (Fischer et al. 2010). In temperate European managed forests, which cover more than 30% of the European land surface, native broad-leaved forests have partly been replaced by more productive conifer forests which also comprise shorter rotation cycles (Rüther and Walentowski 2008). This contributed to a decrease in species richness across multiple taxa (Paillet et al. 2010, Buse 2012) and to changes in structural and functional composition of arthropod communities (Finch and Szumelda 2007, Pohl et al. 2007, Gossner et al. 2013).

Traditionally, the major forest management system in Central Europe has been even-aged forestry (Fischer et al. 2010, Schall et al. 2018*a*). Resulting stands generally lack within-stand variability in tree age (low horizontal and vertical heterogeneity) and show low tree species diversity in comparison with natural and naturally regenerated forests (but see Commarmot et al. 2005, 2013). Reduced habitat heterogeneity is thought to negatively affect local biodiversity, in particular when tree species that do not naturally occur on a particular site (i.e., spruce or pine) were used (Chaudhary et al. 2016). Therefore, uneven-aged forests, showing high within-stand heterogeneity, are increasingly promoted in Europe. Moreover, admixing additional broad-leaved tree species, especially in conifer forests, is suggested to increase habitat heterogeneity and thus biodiversity in even-aged forests (Jäkel and Roth 2004). However, their positive effects on biodiversity have recently been questioned (Schall et al. 2018*a*).

Ants are keystone species in most terrestrial ecosystem (Folgarait 1998) and, in many cases, have been shown to respond to land-management practices (Underwood and Fisher 2006). Ants are sensitive to various types of forest management and disturbance (Vasconcelos 1999, Maeto and Sato 2004, Palladini et al. 2007, Ewers et al. 2015). While in tropical forests, disturbance or past forest management usually results in less diverse ant communities (Bihn et al. 2010), the impact of forest management in boreal and temperate forests is less clear but can increase ant abundance and diversity at a moderate management intensity as shown for boreal forests

(Punttila et al. 1994, Palladini et al. 2007, Véle et al. 2016). More intensive management measures such as clear-cutting can be detrimental to species if, for example, the food web is impaired (Sorvari and Hakkarainen 2007, 2009). In addition, abiotic factors affect ant communities. Warmer sites—that are usually more open—harbor more species than colder sites (Sanders et al. 2007), making temperature a good predictor for species richness across habitats (Del Toro 2013, Seifert 2017). Forest management can affect local microclimate by opening the canopy and thus increasing temperatures at the forest floor. This has been shown to increase ant abundances and ant species richness in managed or recovering forests (Punttila et al. 1994, Palladini et al. 2007, Graham et al. 2009). Like in other insects, development time of ants is faster with increasing temperatures (Kipyatkov and Lopatina 2015) and, especially in temperate and boreal regions, higher temperatures may thus result in faster colony growth.

An overall heterogeneous habitat provides both nest-site opportunities and suitable microhabitats (Kaspari 1996, Niemela et al. 1996) and thereby can increase species diversity (Niemela et al. 1996, Parui et al. 2015). Habitat heterogeneity (structural variation on a larger scale), nesting opportunities, food supply, and canopy coverage are highly affected by the tree species composition of forests. Forests differing in their tree species can host very different ant communities and ant species richness (Seifert 2017), with forest management indirectly affecting ants by a change in tree species composition.

Forest management may also alter functional trait compositions of ant assemblages. Functional diversity is defined as the number and range of species functional traits (morphological, physiological, behavioral characteristics) in a community (Petchey and Gaston 2006). While often equated with species richness, studies also revealed great variation in functional diversity between communities with similar species number (Cadotte et al. 2011). Moreover, a high functional redundancy might ensure functional stability over time because functionally similar species with respect to their effects on ecosystem processes might respond differently to environmental changes (insurance hypothesis; Fonseca and Ganade 2001). The functional composition and diversity of

communities are commonly assessed using morphological and life-history traits in trait-based studies (Bihn et al. 2010, Silva and Brandão 2014, Simons et al. 2016). In ants, the effect of habitat complexity (structural complexity on a small scale like ground surface rugosity, percentage of grass cover, or leaf litter thickness) on morphological traits of ant communities has been well studied. Gibb and Parr (2013) provide support that habitat complexity can act as filter for species composition through their morphological traits. For example, ant leg length decreases with habitat complexity (Farji-Brener et al. 2004, Sarty et al. 2006, Wiescher et al. 2012) and larger body size can be beneficial in simpler habitats (Farji-Brener et al. 2004, Sarty et al. 2006). However, the correlations of body size and habitat complexity were not consistent (Gibb and Parr 2013). In addition, body size can be positively correlated with food supply (Johnson 2002), which can be limited by forest management if it effects the ant's main food sources (Sorvari and Hakkarainen 2009). Moreover, life-history traits can reveal changes within communities consisting of morphologically similar species.

To date, the response of ants to forest management has mainly been studied in the tropics (Vasconcelos 1999, Bihn et al. 2008, Klimes et al. 2012) and studies focusing on the responses of ant communities to habitat heterogeneity and complexity along environmental gradients were likewise conducted in warmer regions (Arnan et al. 2009, Blatrix et al. 2016). Although single studies on management-related questions regarding ground-dwelling (Tausan et al. 2017) and canopy (Dolek et al. 2009) ant communities exist, we still lack a more comprehensive understanding of the direct and indirect effects of forest management in temperate forests via changes in habitat heterogeneity, complexity, and microclimate (reviews: Underwood and Fisher 2006, Ellison 2015). Our study fills this gap by investigating ant communities in 150 German temperate forest stands with different forests management regimes. Specifically, we address the questions: (1) Does forest management affect the abundance, species richness, functional diversity, and composition of ant communities? (2) Are these changes mediated by a change in the environmental conditions, such as structural heterogeneity, microclimate, and food supply?

## Materials and Methods

### Study regions

The study was conducted within the framework of the Biodiversity Exploratories project (www.biodiversity-exploratories.de; Fischer et al. 2010). It comprises three different study regions across Germany: the UNESCO Biosphere Reserve Schorfheide-Chorin in the northeast (53°00′ N; 13°76′ E), the National Park Hainich and the surrounding Hainich-Dün region in the center (51°15′ N; 10°47′ E), and the UNESCO Biosphere Reserve Swabian Alb in the southwest (48°43′ N; 9°39′ E; henceforth "Schorfheide," "Hainich," and "Alb"). Beside the maximum distance of >600 km between the regions, the three regions differ in elevation (Schorfheide 3–140 m a.s.l., Hainich 285–550 m a.s.l., Alb 460–60 m a.s.l.), mean annual precipitation, and mean annual temperature (Schorfheide 520–580 mm and 8.0°–8.5°C, Hainich 500–800 mm and 6.5°–8°C, Alb 700–1000 mm and 6.0°–7.0°C). For additional details, see Fischer et al. (2010).

### Study sites and forest management types

In each region, 50 experimental forest plots (henceforth "plots") sized 1 ha (100 × 100 m) were installed. Each plot is located within a larger forest stand of the same management regime and thus represents one management unit. The plots differ in management type (unmanaged, even-aged, and uneven-aged forests) and intensity (Hessenmöller et al. 2011, Schall and Ammer 2013, Kahl and Bauhus 2014) as well as selected dominant tree species. Overall, plots comprise broad-leaved forests, dominated by European beech (*Fagus sylvatica*, all regions) and oaks (*Quercus petrea* or *Quercus robur*, Schorfheide only); mixed forests (broad-leaved coniferous at Schorfheide); and coniferous forests (Norway spruce [*Picea abies*] at Alb and Hainich and Scots pine [*Pinus sylvestris*] at Schorfheide), but not every management type can be found in every region. In unmanaged forests, management was ceased 20–70 yr ago. Even-aged forests comprise stands of different developmental stage (thickets, pole woods, immature timber, mature timber, thickets with shelterwood) that are spatially separated. Stands are regenerated in 80- to 160-yr intervals (for oaks, the rotation length exceeds 180 yr). In uneven-aged stands, single trees are

harvested selectively, resulting in a high within-stand variability of tree ages and thus high vertical heterogeneity (only in Hainich).

### Ant and other arthropod sampling

Sampling was conducted between May and October 2008. On each plot, three pitfalls with a funnel diameter of 15 cm were installed in three of four randomly selected plot corners (Lange et al. 2014). The pitfalls were emptied five times in intervals of five to six weeks. Due to trap losses, only two of the three traps were randomly chosen per sampling interval and analyzed.

All arthropod specimens were sorted to order level. All ants were identified to species level using Seifert (2007) and Radchenko and Elmes (2010) by the first author. Additionally, all Coleoptera, Araneae, Pseudoscorpiones, Opiliones, Hemiptera, Dermaptera, Mecoptera, Orthoptera, Dictyoptera, and Neuroptera were identified by taxonomic specialists (see *Acknowledgments*).

We calculated ant species richness as the number of ant species found per plot. Because ants recruit to food sources, we used the frequency of occurrence of a species in the pitfall traps as a measure of abundance rather than the number of individuals (maximum two traps × five sampling intervals = 10 per plot).

### Environmental variables

*Forest management variables.*—We define forest management as the decisions taken of a forest manager. In Central Europe, this comprises mainly three decisions: (1) the tree species selection, (2) the management system (even-aged, uneven-aged, unmanaged), and (3) the intensity of management.

As variable reflecting tree species selection, we used the *dominant tree species* of a stand (at least 50% ground cover area) and comprise pure stands (beech, oak, pine, spruce) as well as mixed stands with beech and pine trees. We did not use management system as management variable in our models as uneven-aged stands occurred only in one region (Hainich) and the differences in management systems are already covered by the component of forest management intensity. However, we tested the differences between seven different forest types, that is, beech unmanaged, beech

uneven-aged, beech even-aged, oak even-aged, spruce even-aged, pine even-aged, and pine–beech even-aged, separately.

As a measurement for forest management intensity, we used one parameter of the Forest Management Index of Kahl and Bauhus (2014), the proportion of harvested tree volume (*Iharv*). For the *Iharv*, a value of 0 means that no trees were harvested within the last 30–40 yr and 1 represents clear-cut sites (for differences between the regions and the forest types, see Appendix S1: Figs. S1, S2).

*Forest structure variables.*—A range of variables describing the forest structure were assessed based on a complete stand inventory (Schall et al. 2018b):

As a measure for stand age, the mean age of the dominant tree species was obtained from records of the respective forest administrations. The forest composition (stand purity) was defined as pure if the crown of the dominant tree species covered at least 80% of the ground area. Tree species richness and diversity (Shannon) were calculated based on data from forest inventory (Schall and Ammer 2013). Canopy cover (in %) was assessed by airborne LiDAR in summer 2008 and 2009 during leaf-on conditions (method explained in Hessenmöller et al. 2011). Stand structural complexity was measured at nine systematically distributed points using a terrestrial 3D laser scanner which was installed at a height of 130 cm. Based on the laser scans and their reflection, a three-dimensional distribution of biomass in space was measured and calculated in an index for stand structural complexity (Ehbrecht et al. 2017). As measurement for nest-site opportunities and suitable microhabitats, we used (1) dead wood volume, measured in $m^3$/ha for standing and lying trunks with a diameter >25 cm over the whole plot in 2012, and (2) leaf litter thickness, measured in each plot at 14 sampling points using a 15 × 15 cm metal frame and then averaged over the whole plot. This includes leaf litter as well as large organic material with a low level of decomposition.

*Forest biotic variables.*—Arthropod species richness and arthropod biomass were used as variables describing the potential food resources for ants. Both variables were calculated by considering all main ground-dwelling orders, except ants. Acarina and Collembola as small and mainly

soil-dwelling taxa were excluded. Dry mass of arthropod groups considered was calculated based on the body size using the power function from Rogers et al. (1976). Overall, the considered arthropod groups comprised more than one-third of individuals sampled in pitfall traps but a much higher proportion of biomass (due to the exclusion of abundant but small-bodied Acarina and Collembola).

*Forest abiotic variables.*—Each plot was equipped with a meteorological station measuring the air temperature in one-hour intervals. For our analyses, we used the minimum and maximum values per day between May and August 2009, the months of highest activity of ants (as proposed in Seifert 2017), at a height of two meters above ground to calculate the mean daily temperature amplitude. For the same time span, we measured ground temperature per plot at 10 cm above the ground. Soil moisture per plot was measured in percentage (% of volumetric water content) in 10 cm soil depth measured continuously at one point per plot and averaged for the whole period. We used 2009 data instead of 2008 data because of many data gaps in 2008 due to outages of the sensors. On 84 plots, climate data for at least 30 d (mean = 87 d/plot) over the whole sampling duration in both years were available. Here, we found strong correlations for temperature amplitude ($t_{82}$ = 17.82; $P$ > 0.001; $r$ = 0.89) and ground temperature ($t_{82}$ = 10.92; $P$ > 0.001; $r$ = 0.77) between 2008 and 2009. Due to these strong correlations, we are convinced that the results are not strongly biased using 2009 data.

### Ant functional diversity

*Morphological traits.*—For all ant species, we measured morphometric traits of one to six specimens for each plot (Leica M165 C binocular system and the software Leica Application Suite, Leica Mikrosysteme Vertrieb GmbH Mikroskopie und Histologie, Wetzlar, Germany). Of each ant, we measured the following traits: Weber's length (mesosoma length) and pronotum width as a measurement for body size; head length and width (both strongly correlate with body size [Gibb et al. 2017]) as proxy for the ants' diet as ants with larger heads can exert stronger forces on their mandibles (Weiser and Kaspari 2006); femur and tibia length, combined to leg length as a proxy for foraging

speed and distance (Feener et al. 1988); and eye size (eye length and eye width in frontal view) as this is used as an indicator of trophic position or diurnal activity in tropical ant species (Weiser and Kaspari 2006). Based on the measurements, we calculated the mean trait value for each trait and species per plot. We used the absolute Weber's length and calculated relative values (divided by Weber's length) of pronotum width, head length, and head width (for allometrically differences between species); leg length (femur length + tibia length); and eye size ($\pi/4$ × eye length × eye width − assuming elliptical eyes).

*Life-history traits.*—For all species, we extracted data of 10 different traits from two recent studies (Arnan et al. 2017, Seifert 2017) which are considered to reflect important parts of ant autecology. These traits comprise worker size, average colony size, assumed nutritional niche (these values are based mostly on assumptions by Seifert (2017), but also based on former published work), behavioral dominance, number of queens per nest, and nests per colony, as well as colony foundation type. The trait data and a more detailed description of the trait categories are provided in Appendix S1: Tables S2, S3.

### Trait processing

As a measurement of functional diversity of ants, we calculated Rao's quadratic entropy (Rao's $Q$; Botta-Dukát 2005). For the morphology-based Rao's $Q$ ($FD_M$), we used the traits Weber's length and all relative morphological trait values. For the life-history-based Rao's $Q$ ($FD_{LH}$), we used all life-history traits. Moreover, to test whether single traits respond to forest management, we calculated the community-weighted mean (CWM) by taking the mean trait value for a species weighted by its relative abundance within the community and the community-weighted variance (CWV) by calculating the variance within a trait for each species weighted by its relative abundance within the community. Rao's $Q$, CWM, and CWV were calculated separately per region based on the trait values which were measured from specimens found in that particular region.

### Data transformation

We square-root-transformed the ant abundance, arthropod biomass, and the *Iharv*; we squared the temperature amplitude and transformed the

canopy cover to the power of four. For $FD_M$ and $FD_{LH}$, we log-transformed deadwood volume after adding 1 to each value because we had a few plots without deadwood. Since the continuous variables were measured at very different scales, we rescaled them to zero mean and unit variance using the decostand function (method standardize) of the R package vegan (Oksanen et al. 2016).

### Statistical analyses

All analyses were conducted in R (R Development Core Team 2016). To calculate trait measures, we used the FD package (Laliberté and Legendre 2010, Laliberté et al. 2014).

To test whether particular environmental variables affect measures of the ant communities, we used a multi-model inference approach as suggested in Grueber et al. (2011). We created a linear mixed-effect model using the R package lme4 (Bates et al. 2015) with different response variables and multiple predictor variables. We tested various variables for among-variable correlation and only chose variables with $r < 0.7$. If two variables had a higher correlation, we chose the variable with the predicted higher ecological importance.

The global model was calculated as the response variable against all above described predictor variables, with region as random factor (for multi-regional comparisons). An additional global model with region as fixed factor led to consistent results (provided in Appendix S1: Tables S6, S7, Fig. S3).

Then, we used the dredge function of the R package MuMIn (Bartón 2016) which generates a set of models with all possible combinations of predictor variables and weighted the models based on their Akaike information criteria for small samples sizes (AICc). We used all models with a ΔAICc < 2 and applied the model.avg function and subsequently the importance function which states the relative importance values of each variable calculated as the sum of AICc weights over all models in which the variable appears. Using these variables, we fitted a piecewise structural equation model (piecewise SEM) using the piecewiseSEM package (Lefcheck 2016) to test for direct and indirect effects of the most important variables (all variables selected by model averaging) on the response variable. The effects of a certain dominant tree species in the SEM were calculated in comparison with beech as dominant tree species, which is supposed to be the most natural state.

In the model for species richness, we additionally included ant abundance to test whether the effects on ant species richness are only driven by the effects on the ant abundance. Due to missing data of single variables, we had to exclude nine plots (four from Hainich and five from Schorfheide) from all analyses.

We compare the ant community composition between the regions we conducted a non-metric multidimensional scaling (NMDS) (two axes) on the Bray-Curtis distance matrix using the metaMDS function in the vegan package (Oksanen et al. 2016). To compare the trait space occupied by species among study regions, we additionally conducted an ordination analysis using all morphological and life-history traits. First, we used the Gower dissimilarity coefficient (Gower 1971) with Podani's (1999) extension to ordinal variables to create a distance matrix from our trait data (gowdis function in the FD package; Laliberté and Legendre 2010, Laliberté et al. 2014). Second, we performed a NMDS (two axes) on the Gower distance matrix using the metaMDS function in the vegan package (Oksanen et al. 2016). We tested for differences between regions in species composition and trait space using PERMANOVA (Adonis function, 1000 permutations). For illustration, traits were plotted post hoc using the envfit function with 1000 permutations.

## Results

### Ant species richness and community composition

Overall, we found 28 ant species on a total of 120 of the 150 plots sampled. No ants were found on 30 plots. Ant species richness differed strongly between the three regions (generalized linear model: $R_{137} = 161.29$; $P < 0.001$) with a low richness in Hainich (0–4 species per plot) and Alb (0–7 species per plot) and a comparatively high richness in Schorfheide (1–14 species per plot, Table 1; Appendix S1: Table S1). Ant species richness also differed between forest types. Low species richness was found in spruce and beech forests and high species richness in oak and pine forests (Fig. 1; Appendix S1: Table S4). Beside species richness, the regions hosted significantly different species compositions (PERMANOVA:

Table 1. Overview of the total number of ant species and the average number of species per plot sampled in the three regions.

| Region | Ant species richness | | Number of plots with ants for each management type | | | | | | |
| | Total species richness | Mean ± SD per plot | Beech EA | Beech UA | Beech UM | Oak EA | Pine EA | Pine–beech EA | Spruce EA |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Alb | 14 | 1.66 ± 1.39 | 28 (33) | 0 | 5 (5) | 0 | 0 | 0 | 10 (12) |
| Hainich | 7 | 0.8 ± 0.94 | 13 (20) | 7 (13) | 3 (13) | 0 | 0 | 0 | 4 (4) |
| Schorfheide | 23 | 6.8 ± 2.71 | 14 (14) | 0 | 7 (7) | 7 (7) | 15 (15) | 7 (7) | 0 |

*Note:* Moreover, the numbers of plots where ants were found and the overall number of plots per management type/region (in brackets) are shown (EA, even-aged; UA, uneven-aged; UM, unmanaged).

$F_2 = 7.01$, $P = >0.001$; Fig. 2). *Myrmica ruginodis* and *Lasius platythorax* were abundant in all three regions (Appendix S1: Table S1) and were the most common species in Hainich. *Formica pratensis, Camponotus herculaeanus,* and *Camponotus ligniperda* were exclusively found in the beech and spruce forests of the Alb. In the Schorfheide, wood ants (*Formica rufa* and *Formica polyctena*) as well as *Stenamma debile* and *Temnothorax crassispinus* were found in the majority of plots, but also additional *Myrmica* species and rare species such as *Polyergus rufescens* (Fig. 2; Appendix S1: Table S1).

## Effect of forest management and other variables on the ant community

The multi-model averaging approach revealed that 10 of the 18 variables were highly important for ant species richness (Table 2). The piecewise SEM on the drivers of ant species richness (Fig. 3) showed that species richness was positively affected by pine as dominant tree species ($\beta = 1.18$, standardized coefficient), the overall tree species richness ($\beta = 0.15$, standardized coefficient), and ant abundance ($\beta = 1.07$, standardized coefficient). Ant abundance was directly and negatively affected by spruce as dominant
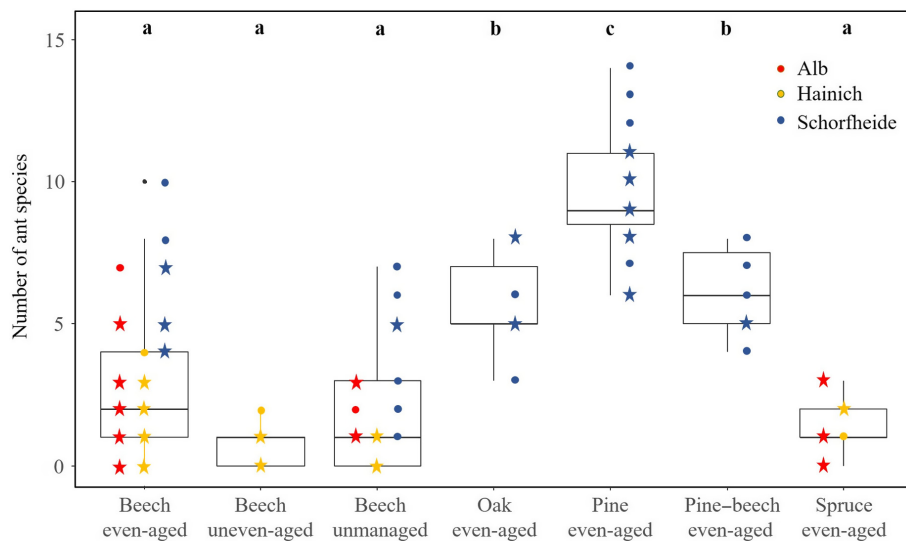


Fig. 1. Number of ant species found in the different management types ($n = 150$ plots). The forest types were defined by the dominant tree species (at least 50% ground cover area) and comprise pure stands as well as partly mixed stands of different broad-leaved and conifer species. Colored dots show the distribution of number of ant species per plot and region (Alb, red; Hainich, yellow; Schorfheide, blue). Asterisks represent multiple plots with the same number of species. Different letters above the boxplots indicate significant differences between the forest types based on Tukey's HSD pairwise comparisons.
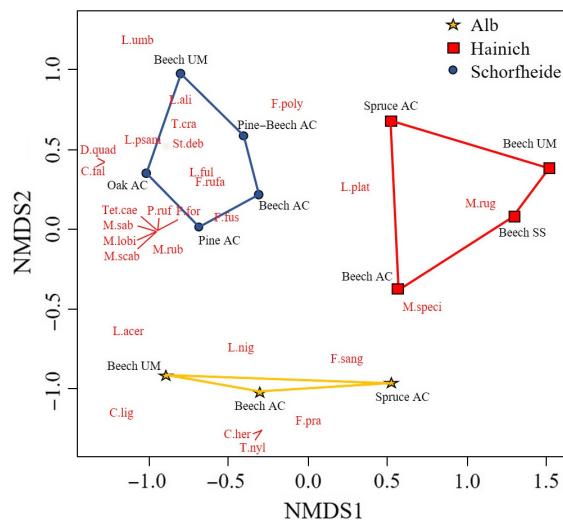
Fig. 2. Ordination plot illustrating the different ant species compositions between the different management types (EA, even-aged; UA, uneven-aged; UM, unmanaged) and the three different regions (different colors and shapes), based on based on species abundances. A non-metric multidimensional scaling (NMDS) was conducted based on a Bray-Curtis distance index (stress = 0.11). Species abbreviations are C.fal, *Camponotus fallax*; C.her, *Camponotus herculeanus*; C.lig, *Camponotus ligniperdus*; F.fus, *Formica fusca*; F.for, *Formica foreli*; F.poly, *Formica polyctena*; F.pra, *Formica pratensis*; F.rufa, *Formica rufa*; F.sang, *Formica sanguinea*; L.ali, *Lasius alienus*; L.ful, *Lasius fuliginosus*; L.nig, *Lasius niger*; L.plat, *Lasius platythorax*; L.psam, *Lasius psammophilus*; L.umb, *Lasius umbratus*; P.ruf, *Polyergus rufescens*; L.acer, *Leptothorax acervorum*; M.lobi, *Myrmica lobicornis*; M.rub, *Myrmica rubra*; M.rug, *Myrmica ruginodis*; M.sab, *Myrmica sabuleti*; M.scab, *Myrmica scabrinodis*; M.speci, *Myrmica specioides*; St.deb, *Stenamma debile*; T.cra, *Temnothorax crassispinus*; T.nyl, *Temnothorax nylanderi*; Tet.cae, *Tetramorium caespitum*; and D.quad, *Dolichoderus quadripunctatus*.

Table 2. Result of the multi-model averaging approach for ant species richness.

| Variable | Importance (%) | N-containing models |
|---|---|---|
| Arthropod species richness | 100 | 11 |
| Dominant tree species | 100 | 11 |
| Temperature amplitude | 100 | 11 |
| Tree species richness | 100 | 11 |
| Canopy cover | 90 | 10 |
| Arthropod biomass | 46 | 5 |
| Stand purity | 44 | 5 |
| Soil moisture | 21 | 3 |
| Leaf litter thickness | 15 | 2 |
| Tree species diversity | 6 | 1 |

*Note:* The relative importance values of each predictor variable were calculated as the sum of Akaike information criteria (AICc) weights with ΔAICc < 2 over all models in which the variable appears and the number of models which contained the respective variable is stated.

tree species (β = −1.12, standardized coefficient). The indirect effects of forest management on ant abundance were mediated by a negative effect of the proportion of pine, spruce, and oak as dominant tree species and stand purity on canopy cover, which in turn resulted in a higher temperature amplitude (β = 0.01, standardized coefficient) and thus in higher ant abundance. In addition, the proportion of pine affected arthropod species richness positively which in turn increased ant abundance (β = 0.02, standardized coefficient). The proportion of oak and tree species richness affected arthropod biomass negatively which in turn increase ant abundance (β = −0.05, standardized coefficient).

### Ant functional diversity

Due to a very low species richness in the regions Alb and Hainich (Table 1), we analyzed the $FD_M$ and the $FD_{LH}$ for the more diverse region Schorfheide only. There, we could not find any direct or indirect effects of forest management on the $FD_M$ (see Appendix S1: Table S5, Fig. S4). For the $FD_{LH}$, the multi-model averaging approach revealed that nine of 18 variables were important (Table 3).

The piecewise SEM on the drivers of ant functional diversity showed a strong positive direct effect of the percentage of harvested tree volume (*Iharv*) on $FD_{LH}$ (Fig. 4; β = 4.97, standardized coefficient). In contrast, the proportion of pine reduced stand structural complexity which in turn positively affected $FD_{LH}$ (β = −0.91, standardized coefficient). Thus, open forests with a low structural complexity have the highest ant $FD_{LH}$. Besides, soil moisture had a positive effect (β = 0.18, standardized coefficient) on $FD_{LH}$.

When analyzed across the three regions, we did not find effects of forest management on the CWMs and CWVs of the single morphological traits. Despite the large difference in ant species
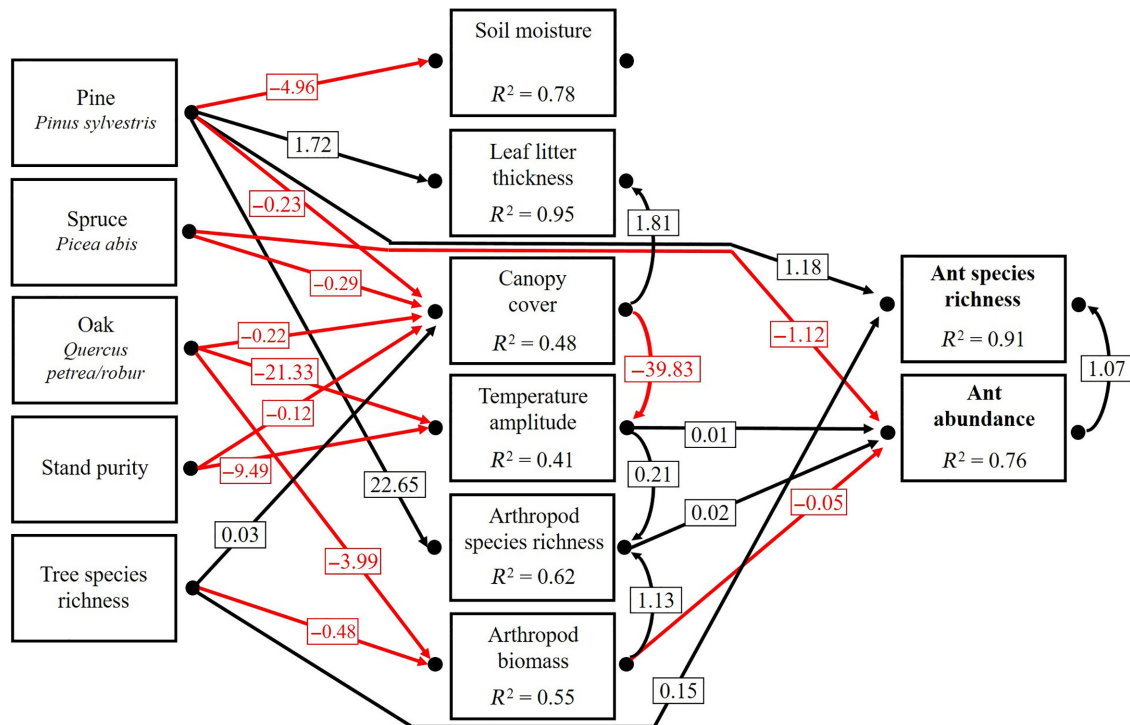
Fig. 3. Final piecewise structural equation model ($n$ = 141 plots) exploring the direct and indirect effects of forest management on ant species richness. Boxes represent measured variables. Arrows represent significant ($P < 0.05$), unidirectional relationships among variables. Black represents positive and red represents negative relationships. We report the path coefficients as standardized effect sizes next to the arrows. $R^2$ values for component models are given in the boxes of their response variables. Variables on the left reflect forest management decisions, and variables in the middle are expected to be affected by forest management.

Table 3. Result of the multi-model averaging approach for the functional diversity based on life-history traits ($FD_{LH}$).

| Variable | Importance (%) | N-containing models |
|---|---|---|
| Stand structural complexity | 93 | 16 |
| Percentage harvested tree volume (Iharv) | 73 | 13 |
| Dominant tree species | 69 | 12 |
| Canopy cover | 58 | 9 |
| Soil moisture | 56 | 9 |
| Arthropod biomass | 53 | 9 |
| Leaf litter thickness | 34 | 6 |
| Tree species richness | 22 | 4 |
| Tree species diversity | 4 | 1 |

*Note:* The relative importance values of each predictor variable were calculated as the sum of Akaike information criteria (AICc) weights with ΔAICc < 2 over all models in which the variable appears and the number of models which contained the precise variable is stated.

richness and community composition (Fig. 2) among regions, the trait space covered by the species in the three regions did not significantly differ, neither for the morphological traits (PERMANOVA: $F_2 = 1.52$, $P = 0.19$) nor for the life-history traits (PERMANOVA: $F_2 = 0.48$, $P = 0.82$). The NMDS of the morphological trait space (Fig. 5) shows that the ant communities at Alb and Schorfheide had an approximately similar sized trait space with centroids laying close together. Both communities, however, contained a few species with exclusive morphological trait compositions. The trait space in the species poor region Hainich can be seen as a subset of the trait space covered by the species in Schorfheide. Nevertheless, the species communities at the Alb consisted of larger species with relatively larger eyes and longer legs, while species at the
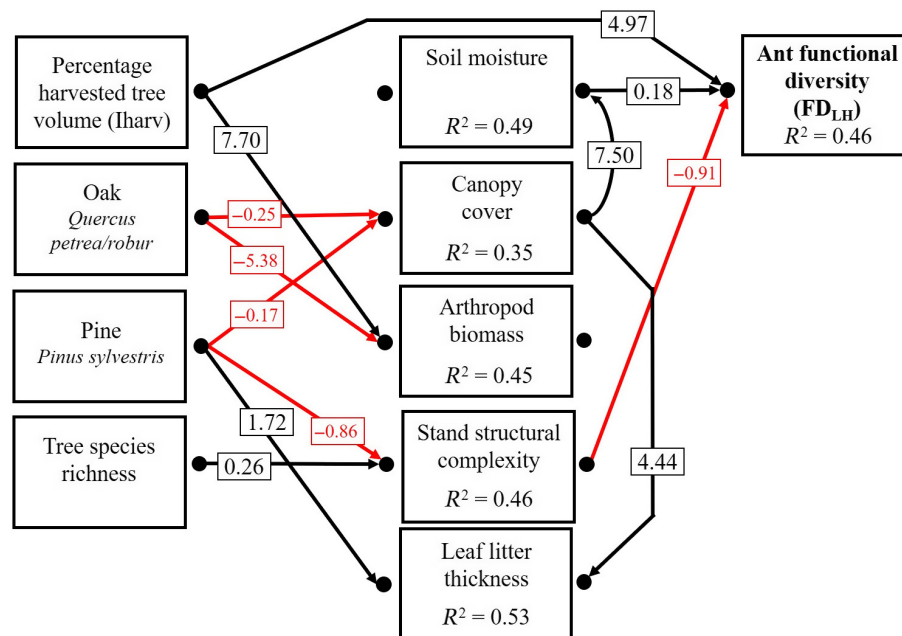
Fig. 4. Final piecewise structural equation model ($n$ = 45 plots) exploring the direct and indirect effects of forest management on the functional diversity based on life-history trait ($FD_{LH}$) at the Schorfheide. Boxes represent measured variables. Arrows represent significant ($P < 0.05$), unidirectional relationships among variables. Black represents positive and red represents negative relationships. We report the path coefficients as standardized effect sizes next to the arrows. $R^2$ values for component models are given in the boxes of their response variables.
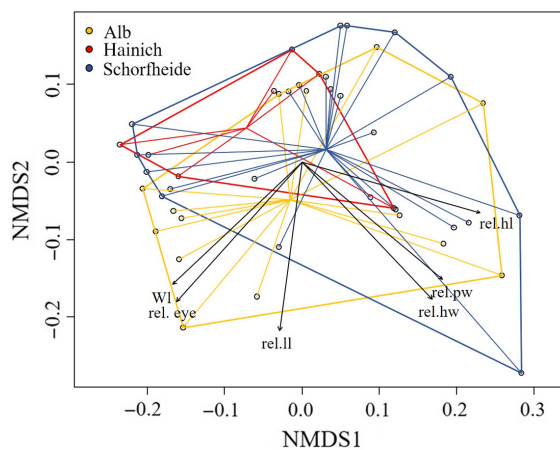


Fig. 5. Ordination plot showing the trait space covered by the ant species sampled the three different regions (different colors), based on morphological species traits. A non-metric multidimensional scaling (NMDS) was conducted based on a Gower distance matrix (stress = 0.05). The morphological traits are Wl, Weber's length; rel.ll, relative leg length; rel.pw, relative pronotum width; rel.hw, relative head width; rel.hl, relative head length; and rel. eye, relative eye size.

Schorfheide had relatively larger heads (Fig. 5). The communities at the Alb mainly consisted of formicinae ants (10 of 14 species) including large *Formica* and two *Camponotus* species. Large Formicinae were also found at the Schorfheide but the communities also contained distinctly more small myrmecine and formicine species (Appendix S1: Table S1) which had relatively larger heads and relatively shorter legs. Results based on life-history traits showed similar results, with less exclusive trait space covered by the species at Alb (Fig. 6).

## DISCUSSION

Our main result is that forest management positively affected the abundance, species richness, and functional diversity of ant communities in temperate forests. This was mainly a consequence of reduced canopy cover and stand structural complexity through tree harvesting and selection of shade-intolerant species, which resulted in warmer stand-scale conditions.
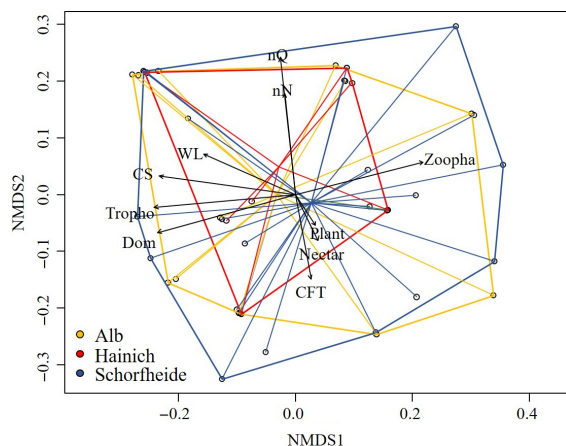
Fig. 6. Ordination plot showing the trait space covered by the ant species sampled the three different regions (different colors), based on life-history species traits. A non-metric multidimensional scaling (NMDS) was conducted based on a Gower distance matrix (Stress = 0.17). The life-history traits are CS, colony size; WL, Weber's length; Zoo, percentage zoophagous diet of total food intake; Nectar, percentage nectar diet of total food intake; Troph, percentage trophobiosis-based diet of total food intake; Plant, percentage plant-based diet of total food intake; Dom, behavioral dominance, nQ, number of queens per nest; nN, number of nests per colony; and CFT, colony foundation type.

## Effects of forest management on ant abundance and species richness

The dominant tree species at each plot strongly affected ant species richness and abundance. Both richness and abundance were low in beech and spruce forests and high in oak and pine forests (Fig. 1). As spruce forests occurred not in the same regions as pine and oak forest, this comparison might be biased by regional differences in ant communities in our study. However, our results underpin the findings of Seifert (2017) that beech and spruce forests are species poor while oak and pine forests are generally species rich. Different forest and management types show great differences in forest structure and canopy cover. Especially pine- and oak-dominated forests have a more open canopy (lower canopy cover) than beech-dominated forests (Appendix S1: Fig. S5). A low canopy cover increases ants species richness in the temperate zone (Gotelli and Ellison 2002, Arnan et al. 2009, Dolek et al. 2009, Tausan et al. 2017), and our

results clearly support this (Figs. 1, 3). The most likely underlying mechanism is an increased temperature amplitude with decreased canopy cover. In forests with an open structure light can reach the ground and heat it up. Since ants are thermophiles, an increase in the ground temperature could accelerate development of brood in ground nests and thus increase colony growth (Kipyatkov and Lopatina 2015) and promote foraging activity (Cerdá et al. 1998, Lessard et al. 2009, Blatrix et al. 2016). Hence, forest management has positive effects on temperate ant communities if it promotes more open canopies and thus a warmer forest climate. More open canopies are realized in even-aged management systems which include more open developmental stages (Schall et al. 2018a), and by using tree species such as pine and oak which form a less dense canopy. In contrast, management systems that lead to a high vertical structuring and high canopy cover throughout a rotation period such as uneven-aged (selection) beech management systems result in a low ant species richness (Fig. 1). The small gaps created by single-tree harvesting are closed by the surrounding trees very fast (Juchheim et al. 2017), resulting in a closed canopy across time and space. A rather surprising result is the very low importance of deadwood and leaf litter thickness for the ant communities. Both variables were expected to offer nesting opportunities or suitable microhabitats. We assume that either the forests provide sufficient nesting opportunities independently of our measured amounts or we did not consider the relevant variable.

Like ants, overall arthropod species richness benefited from warm forest climate due to a low canopy cover. Previous studies on different taxa already showed that temperature is a crucial, positive driver of arthropod species richness in temperate forests (Topp 2003, Gossner 2009, Müller et al. 2015, Seibold et al. 2016). This is because the metabolism of arthropods is temperature-dependent (Danks 2007, Sformo et al. 2010). However, the magnitude of the response to decreased canopy cover might depend on the taxon, stratum, and spatial scale of openings (Goßner et al. 2006). Some taxa, such as ground-dwelling beetles, might not be affected by canopy openness (Lange et al. 2014). Thus, generalizing assumptions for a highly diverse group

like arthropods might be difficult. Nevertheless, the preference of many arthropod taxa for more open forest habitats might also be a relic of the past history of temperate forests where the grazing of large herbivores resulted in less dense forests (Vera 2000).

We could not find an indication that the higher arthropod biomass in our systems supports ant abundance and species richness through higher supply of food resources. Thus, overall arthropod biomass and ants most likely responded to forest management similarly without an indication of a direct trophic interaction.

### Effects of forest management on functional diversity

$FD_{LH}$ was positively affected (increasing community trait diversity) by tree harvesting and negatively by a high structural complexity. Hence, our results support the assumption that low structural complexity can increase the diversity of woodland ants (Bernadou et al. 2013). Harvesting substantial amounts of tree volume leads to an open forest structure and thins out the canopy cover, which in turn facilitates a warmer forest climate. Thus, with canopy openness, we found a common main driver of ant $FD_{LH}$, species richness, and abundance.

A positive correlation between ant functional diversity and ant species richness was recently found in eastern North American forests (Del Toro et al. 2015) and across the biogeographic regions of Europe (Arnan et al. 2017). However, the latter study showed that ant functional diversity in Continental Europe is in general relatively low. This low diversity is also noticeable in our study since the regions did not differ in morphological and life-history-based trait spaces despite the significant differences in the number of species. The lack of a positive relationship between species richness and trait spaces underscores the low functional variability of ant communities in temperate Central Europe.

Overall, we showed that management in temperate forest can result in an increase in ant species richness and functional diversity via indirect effects of canopy openness resulting in warmer forest climate and a less complex forest structure. When going further poleward from temperate forest to boreal forests and the taiga, forest management can likewise have positive effects with

managed, as well as early successional forests harboring more species than mature forests since they have a lower canopy coverage and are thereby more suitable for less shade-tolerant species (Punttila et al. 1991, 1994, Schall et al. 2018a).

In contrast, in the warmer climate of tropical and subtropical forests, ants are not limited by low temperatures. In tropical forests, management results in tremendous species loss and a significant reduction in functional diversity by reducing habitat complexity (Bihn et al. 2010, Klimes et al. 2012, Solar et al. 2016). In Mediterranean forests, studies on direct forest management effects are rare, but changes in associated variables like a reduction in high vegetation/ canopy cover can either support species richness (Blatrix et al. 2016) or do not change species richness but change species composition toward more dominant species and functionally more diverse communities (Retana and Cerda 2000, Arnan et al. 2012). Thus, predictions on the effect of forest management on Mediterranean ant communities are still ambiguous.

## Conclusion

With this study, we contribute significantly to the understanding of how ants react to current management practices in temperate forests, which lacked so far for this biogeographic region. We show that forest management practices in temperate forests shape ant community structures and can be beneficial when they lead to a less dense forest structure with a lower canopy cover and warmer forest climate. This can be achieved by increasing the proportion of shade-intolerant tree species with a less dense crown or by tree harvesting. We therefore encourage forest managers to include more open and warmer stages in their management strategies to promote ants as ecologically important group in forest ecosystems, but also other organisms.

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## Supporting Information