# *Temperate ant communities under anthropogenic impact*

DISSERTATION

zur Erlangung des akademischen Grades eines

Doktors der Naturwissenschaften (Dr. rer. nat.)

in der Bayreuther Graduiertenschule für Mathematik und Naturwissenschaften (BayNAT)

der Universität Bayreuth

vorgelegt von

***Michael Erik Grevé***

aus *Alsfeld*

Bayreuth, 2019

This doctoral thesis was prepared at the department of Animal Ecology I at the University of Bayreuth from 03/2016 until 06/2019 and was supervised by Prof. Dr. Heike Feldhaar

This is a full reprint of the thesis submitted to obtain the academic degree of Doctor of Natural Sciences (Dr. rer. nat.) and approved by the Bayreuth Graduate School of Mathematical and Natural Sciences (BayNAT) of the University of Bayreuth.

Date of submission: 03.07.2019
Date of defence: 15.11.2019

Acting director: Prof. Dr. Markus Lippitz (since 01.10.2019)

Doctoral committee:

| | |
|---|---|
| Prof. Dr. Heike Feldhaar | (reviewer) |
| PD Dr. Elisabeth Obermeier | (reviewer) |
| Prof. Dr. Bettina Engelbrecht | (chairman) |
| PD Dr. Johannes Stökl | |

# Content

# Summary

European, temperate terrestrial ecosystems are shaped and managed by humans since millennia. While grasslands were consistently managed at low intensities over centuries, forest management changed multiple times over time and each change had an immense impact on the structure of forest ecosystems. Since the last decades, the management in both biomes is changing, but in opposite directions. Today, highly diverse grasslands are threatened by land-use intensification, while reciprocally, forests are transformed from intensively used even-aged monocultures to uneven-aged multi-species stands in order to promote biodiversity. How species communities are affected by management and how they respond to changes, are key questions in ecology. But especially for some keystone taxa such as ants which are known to be responsive to management, they are still not sufficiently understood. In grasslands for example, the underlying mechanisms leading to a decrease in species richness as well as changes in functional community composition remain elusive.

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.

In my first manuscript, I studied the direct and indirect effects of land-use intensification on ant communities in temperate grasslands which were sampled on 110 grassland plots in three regions in Germany. The sampled grasslands are used as meadows or pastures, being mown, grazed or fertilized at different intensities. I found that ant species richness, functional trait space of communities and abundance of nests decreased with increasing land-use intensity. The land-use practice most harmful to ants was mowing, followed by heavy grazing by cattle. Fertilization did not strongly affect ant species richness. Grazing by sheep increased ant species richness. The effect of mowing differed between species and most rare species occurred mainly in plots managed at low intensity. The results show that mowing less frequently or later in the season would retain a higher ant species richness – similarly to most other grassland taxa. The transformation from pastures to intensively managed meadows and especially mowing directly affects ants via the destruction of nests and indirectly via loss of grassland heterogeneity (reduced plant species richness) and increased soil moisture by shading of fast-growing plant species.

In my second manuscript, I explored 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. I 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. 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, which results in a higher temperature amplitude. Functional diversity, based on life-history traits, was affected positively by tree harvesting and negatively by structural complexity. This study shows that forest management practices in temperate forests strongly impact the 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 towards shade-intolerant tree species. To promote ant diversity as key taxon for maintaining ecosystem processes in forest ecosystems, I suggest integrating forest stands with more open and warmer conditions in future management strategies.

In my first two manuscripts, I could show that ant communities respond to changes in habitat structures and that species with certain (morphological and life-history) traits are more sensitive towards management intensification than others. Thus, the question arises whether traits can be used to predict how a species is affected by changes in habitat structures. Or in a broader view and based on other studies: how reliable are morphological traits as functional traits?

I try to answer this question in my third manuscript where I investigated the running speed of differently sized ants (body size and leg length) along a surface rugosity gradient which represents different habitat structures. In general, it is thought that leg length is a good predictor for running speed and by theory, similarly sized species should respond similarly towards changes. But the opposite was the case and leg length was not a good predictor for running speed. In addition, similar-sized species responded idiosyncratically to high surface rugosity, which might be related to species-specific habitat preferences. This hampers precise predictions on how species might respond to changing habitats, based on morphological traits exclusively. Based on the findings of all three manuscripts, it is possible to make predictions of how future management will change species communities, but species-specific forecasts remain difficult.

# Zusammenfassung

Die terrestrischen Ökosysteme werden in Europa seit Jahrtausenden vom Menschen bewirtschaftet und geformt. Während Wiesen und Weiden über Jahrhunderte durchgängig mit geringer Intensität bewirtschaftet wurden, veränderte sich die Forstwirtschaft mehrfach mit der Zeit und jede Veränderung hatte immensen Einfluss auf die Struktur und Ökosysteme der Wälder. In den letzten Jahrzehnten veränderte sich die Bewirtschaftung in beiden Biomen, allerdings in unterschiedliche Richtungen. Grasflächen, die eine enorme Diversität aufweisen, werden nun durch eine intensivierende Bewirtschaftung bedroht. Gleichzeitig werden Wälder von intensiv genutzten Monokulturen zu naturnäheren, baumartenreicheren Wäldern verändert, um die Biodiversität in ihnen zu schützen und zu erhöhen.

Wie Artgemeinschaften von Wald- und Landbewirtschaftung beeinflusst werden und wie sie auf daraus resultierende Veränderungen reagieren ist eine noch immer nicht ausreichend verstandene Grundfrage in der Ökologie. Dies gilt besonders für Schlüsselgruppen, wie etwa Ameisen von denen bekannt ist, dass sie auf Landnutzung reagieren. Welche genauen Mechanismen zu einer Reduzierung vom Artenreichtum oder zu Veränderungen in Artgemeinschaften führen, ist jedoch nicht ausreichend erforscht. Im Wald ist der Effekt von Forstwirtschaft auf Ameisen variabel und ist in den Tropen eher negativ und in der borealen Zone eher positiv. Welchen Effekt Forstwirtschaft in der gemäßigten Zone hat, ist bisher nicht bekannt.

In meinem ersten Manuskript erforsche ich die direkten und indirekten Effekte von intensivierter Landnutzung auf Ameisengemeinschaften in den gemäßigten Breiten, die auf 110 Grasflächen in drei Regionen in Deutschland gesammelt wurden. Diese Grasflächen werden als Wiesen und Weiden bewirtschaftet und verschieden intensiv gemäht, gedüngt und beweidet. Ich fand heraus, dass der Artenreichtum, die Variabilität der funktionellen Merkmale einer Gemeinschaft, sowie die Anzahl der Nester sich mit intensiverer Landnutzung verringert.

Häufiges Mähen hatte die stärksten, negativen Einflüsse, gefolgt von Überweidung durch Rinder. Düngung hatte keinen direkten Einfluss auf Ameisen. Beweidung durch Schafe erhöhte hingegen den Artenreichtum. Der Effekt vom häufigen Mähen variierte zwischen den Ameisenarten und besonders die seltenen Arten wurden zumeist nur auf wenig bewirtschafteten Flächen gefunden. Die Ergebnisse zeigen, dass Ameisen, ähnlich wie andere Organismengruppen im Grasland, von einer weniger häufigen oder eine zeitlich spätere Mahd stark profitieren würden. Die Umwandlung von Weiden in intensiv genutzte Fettwiesen sowie das Mähen hat direkte, negative Effekte durch die Zerstörung der Nester und indirekte Effekte

durch den Verlust von Heterogenität (durch reduzierte Pflanzen-Diversität) und einer höheren Bodenfeuchtigkeit durch schnellwachsende Grasarten.

In meinem zweiten Manuskript erforsche ich die direkten und indirekten Effekte von Forstwirtschaft auf den Artenreichtum und die funktionelle Diversität auf Ameisen in 150 Waldflächen, wieder aus drei Regionen in Deutschland. Ich analysiere den Effekt von 18 Variablen, unter anderem Forstwirtschaft, Waldstruktur, Diversität und Biomasse von Arthropoden, sowie auch abiotische Faktoren, auf die Ameisen-Diversität (Artenreichtum, Abundanz und funktionelle Diversität).

Die stärksten direkten Effekte von Forstwirtschaft auf die Anzahl an Ameisenarten und Individuen hat die Auswahl der Baumart, die im Wald vorherrscht. Dabei hatte den größten, positiven indirekten Effekt hat eine geringe Baumkronenabdeckung, etwa durch einen hohen Anteil an Eichen und Kiefern, die eine tagsüber erhöhte Temperatur im Wald ermöglichen. Das Ausdünnen des Waldes, sowie eine weniger komplexe Waldstruktur führte zu einer Erhöhung der funktionellen „life-history"-Diversität. Diese Studie zeigt, dass Forstwirtschaft einen starken Einfluss auf die Struktur von Ameisengemeinschaften hat. Dieser Einfluss kann sich positiv auf Ameisen auswirken, wenn er zu einem lichteren Wald führt, etwa durch das Herausnehmen von einzelnen Bäumen oder dem Anpflanzen von Lichtbaumarten. Um die Diversität von Ameisen und ihren Einfluss auf das Ökosystem Wald zu fördern, empfehle ich die Managementstrategien, die zu einem lichteren und wärmeren Wald führen.

In meinen ersten beiden Manuskripten konnte ich zeigen, dass Ameisengemeinschaften auf Änderungen in der Habitatstruktur reagieren und das Arten mit bestimmten (morphologischen sowie life-history) Merkmalen sensibler für Veränderungen sind als andere. Daraus resultierte die Frage ob man bestimmte Merkmalsausprägungen dazu nutzen kann um die Reaktion einer Art auf Veränderungen in der Habitatstruktur abzuschätzen. Oder grober gesagt: Kann man einem morphologischen Merkmal eine klare Funktion zuordnen?

Diese Frage versuche ich in meinem dritten Manuskript zu beantworten. In diesem vergleiche ich die Laufgeschwindigkeit verschieden großer Ameisenarten (Körpergröße und Beinlänge) auf unterschiedlich strukturierten Oberflächen, die verschieden komplexe Habitate darstellen sollen. Die Beinlänge eines Tieres ist generell als guter Prädikator für die Laufgeschwindigkeit angesehen und theoretisch sollten gleich große Arten auch ähnliche Reaktionen auf Veränderungen zeigen. Allerdings war das Gegenteil der Fall und die Beinlänge erwies sich als kein guter Prädiktor für Laufgeschwindigkeit. Zudem reagierten gleichgroße Arten sehr unterschiedlich auf zunehmende Oberflächenstruktur, die auf artspezifische Unterschiede in den bevorzugten Habitaten zurückzuführen ist. Diese Erkenntnis zeigt, dass es schwierig ist genaue Erwartungen zu formulieren wie ein Tier auf Habitatveränderung reagiert, wenn man nur dessen Morphologie betrachtet. Basierend auf den Erkenntnissen aller drei Manuskripte ist es möglich abzuschätzen wie zukünftige Bewirtschaftung Ameisengemeinschaften beeinflussen wird, jedoch sind artgenaue Vorhersagen nur schwer möglich.

# Introduction

## Grassland management in temperate Europe

European terrestrial ecosystems are shaped and managed by humans since millennia. Naturally, about 95% of the temperate forest zone of Central Europe would be covered by forest, dominated by deciduous trees, and only interrupted by marshes, bogs or rocky areas (Ellenberg 1996, Rüther and Walentowski 2008). But today, undisturbed regions with primeval forests are rare and very limited in size and the rest is covered with grassland, farmland, urban or rural areas.

Based on pollen studies, mankind started changing forest structures and progressively cutting down the closed forests to transform land into fields and meadows approximately 5000 years ago (Küster 1996, Rüther and Walentowski 2008). The created temperate grasslands were mostly managed by grazing of domestic livestock and haymaking (Poschlod and WallisDeVries 2002, Habel et al. 2013). The need for grazers to sustain temperate grasslands is the reason why this ecosystem is often named “semi-natural” (Hejcman et al. 2013).

Independently of their origin, temperate grasslands were managed at low intensities for millennia and accumulated a huge amount of biodiversity. Especially vascular plant species richness can be extremely high at small spatial scales with up to 76 species within on one square meter (Sammul et al. 2003) or 98 species on 10 square meters (Dengler et al. 2012). This exceeds plant diversity in any other ecosystem (at least at this small spatial scale) (Wilson et al. 2012). Along with plant diversity, temperate grasslands harbor a very high arthropod diversity, which relies on the vegetation as habitat and nutritional base of arthropod food webs (Murdoch et al. 1972, Tilman 1986). The grasslands were managed extensively for centuries as mostly unfertilized meadows with one or two cuts per year for haymaking, or as pastures for a low number of livestock like cattle or sheep. This extensive management is thought to be one of the main factors causing high plant species richness (Pärtel et al. 2005, Hejcman et al. 2013, Chytrý et al. 2015) and is needed for continuity of semi-natural grasslands to prevent scrub and tree encroachment and associated diversity declines (Ratajczak et al. 2012). Since terrestrial ecosystems are managed by mankind all over Europe and large parts of the temperate zone, it can be assumed that most of today's species communities are shaped or at least strongly influenced by human intervention. Overall, arthropod species are known to respond to environmental changes and react sensitively to changes in the management intensity or management type (Haddad et al. 2000, Morris 2000, Joern and Laws 2013).

## The effect of grassland management and its intensification on biodiversity

With the beginning of the 20th century, semi-natural grasslands across Europe were exposed to habitat destruction and fragmentation. This is due to the abandonment of traditional management practices (Hallanaro et al. 2002) and management intensification by additional fertilization or liming, increased number of cuts per year and higher stocking rates (Isselstein et al. 2005). With the improvement of the agronomic potential of grasslands, biodiversity decreased. Today, land-use change (the alteration from one land-use type to another), and land-use intensification (within one land-use type) have been identified as one of the most important drivers of global species loss (Sala 2000, Maxwell et al. 2016).

Beside the land-use intensification, the loss of semi-natural grasslands is immense. In Sweden for example, semi-natural grasslands used as pastures have been reduced by almost 90% over the past 80 years (Bernes 1994) and similar patterns can be found across Europe (Luoto et al. 2009). The risk is very clear and Habel et al. (2013) names European grasslands a “threatened hotspot of biodiversity”.

Overall, multiple studies found a significant and on-going loss of general insect species richness across Europe (Thomas et al. 2004, Conrad et al. 2006, Shortall et al. 2009, Habel et al. 2016). The threat reached even public attention with the study of Hallmann et al. (2017) who showed a biomass reduction of 75% in flying insects over 30 years in various sites in Germany. Habel et al. (2019) reviewed these studies and stated: “Agricultural intensification is the main driver of recent terrestrial insect decline, through habitat loss, reduced functional connectivity, overly intense management, nitrogen influx, and use of other fertilizers, as well as application of harmful pesticides”.

Figure 1. a) Meadow managed at high intensities, dominated by fast-growing plant species and a very low number of flowering plant species; b) Freshly mown high-intensity managed meadow without any remaining flowers; c) Example of overgrazing by a single horse, which result in similarly structured grassland as high mowing intensities.

In grassland ecosystems, increasing land use has been shown to reduce species richness and abundance of plants (Haddad et al. 2000, Harpole and Tilman 2007, Kleijn et al. 2009, Socher et al. 2012), as well as different arthropod groups (Hendrickx et al. 2007, Attwood et al. 2008, Simons et al. 2014, Allan et al. 2014, Chisté et al. 2016) and overall functional diversity of communities (Flynn et al. 2009, Birkhofer et al. 2015b, Blüthgen et al. 2016). However, generalizations are hard to make since, for example Simons et al. (2017) found no effects on taxonomic richness across groups with increasing land-use intensification. Likewise, Birkhofer et al. (2017) found no generally reduced trait diversity. However, both studies found that different taxa varied in their response to increased land use or different management practices. Importantly, the effects of each land-use component can differ in strength or direction (Socher et al. 2012, Simons et al. 2014, Gossner et al. 2016). Like already stated, the three management practices used in agricultural grasslands are mowing, fertilization and grazing (mostly by cattle and sheep), or a combination of them (Fischer et al. 2010).

The effects of grassland management can be direct, as a result of active management, or indirect as the response of species to the actual management. Direct effects are for example the killing of individuals by machines during mowing events (Thorbek and Bilde 2004, Humbert et al. 2010), which has direct negative effects on arthropod communities (Nickel and Hildebrandt 2003, Marini et al. 2007, Socher et al. 2012, Simons et al. 2017) or the plant removal, trampling and soil compression by grazers (Helden et al. 2010, van Klink et al. 2015).

The indirect effects of grassland management change grasslands in a more extensive manner: Fertilization and mowing are often highly correlated (Blüthgen et al. 2012) and high intensities of both support fast-growing, dominant grass species (Socher et al. 2012). These grass species outcompete other plants resulting in a decrease of plant diversity (Harpole and Tilman 2007) and the accompanying decrease of herbivorous and predatory arthropod diversity (Simons et al. 2014). Mowing has been demonstrated to have the strongest negative effects on multiple biotas (Gossner et al. 2016). In extremes, frequent mowing creates lawn-like grasslands with very reduced plant species richness and low number of flowers (Figure 1a, b) which harbour a low arthropod species richness, dominated by opportunists and disturbance-tolerant species (Di Giulio et al. 2001, Gossner et al. 2014, Simons et al. 2015).

Compared to mowing, grazers as selective feeders affect plants and the whole biotic environment in a much patchier manner and simplify or thin out vegetation and litter (Helden et al. 2010). Therewith, grazing can increase plant diversity if, for example dominant, fast-growing species are reduced by the grazers, which create gaps for less dominant species (Stewart and Pullin 2008). These effects can vary between the different types of livestock which differ in their feeding type and food preferences (Öckinger et al. 2006, Sjödin et al. 2008, Socher et al. 2013). At very high grazing intensities can have similar negative effects on species richness to mowing (Figure 1c).

Fertilization has negative effects on plant diversity since the mainly dominant, fast-growing plant species benefit of the increased nitrogen and other nutrients availability and outcompete less dominant plant species (Socher et al. 2013, Simons et al. 2014, Gossner et al. 2016)

## Forest management in temperate Europe

While 13% of the forests on the west coast of the United States and 40-52% of Canada are still natural (Parviainen et al. n.d., Heywood and Watson 1995), today, forests in Central Europe have been modified completely by mankind. Over centuries, the naturally broadleaved forests, which covered up to 95% of Central Europe, were managed with different strategies and for different purposes and their structures changed considerably over time (Rüther and Walentowski 2008, Leuschner and Ellenberg 2017). Today, only about 0.2% of the deciduous forests are in a relatively natural state (Hannah et al. 1995).

In temperate Europe, forest management started about 5000 years ago with coppicing, a strategy where trees are cut down to a stump but regrow with multiple stems (Rüther and Walentowski 2008). Large parts of European forests were managed this way for centuries which changed forest structures but maintained and supported mainly broad-leaved tree species. During the Middle Ages, coppicing with standards was established. Here, certain trees or tree species, oaks (*Quercus*) in particular, were excluded from coppicing and could grow old while other tree species were cut down. This management strategy was common in regions with dense settlement and livestock-keeping, as oaks provide e.g. food for pigs, and forests were thinned out over wide areas. At the same time, reforestation of deserted places started for which pioneer species with few demands like pine (*Pinus*) and spruce (*Picea*) trees were commonly chosen (Rüther and Walentowski 2008, Leuschner and Ellenberg 2017). Across Central Europe, in the Middle Ages, forests were used for multiple purposes, such as coppicing for firewood and tanning bark, together with the protection of old trees, which created a heterogeneous forest landscape.

In the 18th century, coppicing started to decline and the low-forest system (coppice forests) of the Middle Ages were replaced by a high-forest system which consists usually of large, mature trees with a closed canopy. Probably due to a lack of timber, forestry changed to economically more profitable management (Schelhaas et al. 2003, Rackham 2008), the age-class forests. This forest type consists of evenly aged, homogeneous, dense, single-species stands. The main tree species are conifers like *Pinus sylvestris*, *Picea abies* and the introduced Douglas fir *Pseudotsuga menziesii*, which can be harvested in shorter rotation cycles than most broad-leaved trees.

The gradual change from broad-leaved to conifer-dominated forests which stared in the Middle Ages was driven by the age-class forestry and in the 20th century, where large parts of Central European forests consist of coniferous monocultures. In 2012, European spruce (*Picea abies*) was the most common tree species in Germany with a percentage of 25.4% in all German forests, followed by Scots pine (*Pinus sylvestris*) with 22.3%, beech (*Fagus sylvatica*) with 15.4%, and 10.4% oaks (*Quercus robur* or *Q. patrea*) (Bundeswaldinventur 3).

These plantation-like even-aged forests are designed and managed to maximize productivity and forest attributes such as old trees, deadwood or gaps in the canopy are widely lacking. Due to the lack of small-scale disturbances, not enough light can reach the ground to enable the growth of understory, especially in spruce forests (Figure 2a). When the even-aged, commercial forests reach a certain rotation age, they are logged by clear-cutting which create large scale openings. This management system was established in large parts across Europe, but it turned out that even-aged forests in clear-cut systems are vulnerable to soil degradation, an infestation of pest insect or natural disturbances such as wind throw. As a result, foresters partly started to change management towards selective logging systems which maintained a permanent forest cover by removing only single trees in forest stands or by shelterwood cutting. Here, cohorts of even-aged trees are replaced by younger evenly aged cohort through repeated cuttings over decades (Schall et al. 2018). However, as these systems are based on monocultures, they do not differ fundamentally from even-aged clear-cut systems (Jacobson 2001).

Since the 1950s, alternative silvicultural strategies to the even-aged forest were developed, particularly in economically developed countries (Brukas and Weber 2009, Puettmann et al. 2015). The reasons for this change are manifold such as the public focus on environmental protection growing stronger, or the better understanding on the impact of forest management on biodiversity (Manolis et al. 2008, Bauhus and Schmerbeck 2010). In addition, alternative sources of income from landowners played an important role (Puettmann et al. 2015). In Germany, the decline of forests came to public perception when pest insects and windthrow damaged large forest areas in the 1980s. As a result, the close to nature forestry, which started in the 1950s (Jacobson 2001), increased in popularity and their guideline is integrated into the forest programs across Europe today (Pro Silva 2012). This management approach is characterized by uneven-aged forest stands with multiple tree species which differ in tree age and size. The applied methods try to sustain a continuous forest cover, avoidance of clear-cuts and using harvesting methods which do not harm the soil or stands (Pro Silva 2012). Forest regeneration and the transformation of even-aged monocultures to uneven-aged multi-species stands was promoted by planting seedlings or young trees under the canopy of the mature trees. This type of management resulted in an increased vertical heterogeneity and more complex stand structures with old-growth attributes such as deadwood or large veteran trees (Bauhus et al. 2009, Puettmann et al. 2015, Messier et al. 2015, Ehbrecht et al. 2017). Today, about 80% of oak and beech forests in Germany show two or more vertical layers and large parts of mature pine stands consist of regeneration layers of beech and oak trees (Bundeswaldinventur 3, Figure 2b).

Figure 2. a) Even-aged spruce forests stand with low light availability and plant growth on the ground; b) Adult pine trees with regeneration layers of beech.

## The effect of forest management on biodiversity

Although it is generally thought to be beneficial for biodiversity, little evidence for positive effects of uneven-aged forests compared to managed, even-aged forests was found. At smaller scales, unmanaged forests, in general, are said to contain more species than managed forests (Økland et al. 2003). In a review, Paillet et al. (2010) found a marginally negative effect of forest management on total species richness over multiple taxa, with more species in unmanaged forests. However, for plants, age-class managed forests harbor more species than unmanaged forests (Boch et al. 2013). Allegro and Sciaky (2003) and Fuller et al. (2008) found a shift in species communities from forest specialists to habitat generalists, but no negative effects of forest management on ground beetles richness when comparing poplar stands and natural woods in Italy, or comparing coniferous and broadleaved forests in the UK.

But overall, the effects of forest management on biodiversity are still under debate (Siitonen 2001) and different arthropod groups respond differently to forest management (Maleque et al. 2009). Low intensity, selective logging has little effects on ground-dwelling arthropods, but negative effects arise with increased management intensities (Oliver et al. 2000). Besides, the effects of tree harvesting can have time-delayed effects and e.g. ground-beetle species start disappearing two years after logging (Pohl et al. 2007).

Clear-cutting is known to be a very destructive management strategy since whole forest patches are removed (Punttila et al. 1991, Niemela 1997). It results in habitat loss of i.e. arboreal species (MacKay et al., 1991) and ground-dwelling species (Kaila et al. 1997, Andersson et al. 2012) due to drastically changed habitat conditions. Other management strategies which are less extensive, like selective logging or retention logging, are better for biodiversity conservation (Fedrowitz et al. 2014).

The main effects of forest management are via the change of forest structures and thus, different habitat heterogeneities and stand structural complexities. Analyzing this, various studies found a positive relationship between structural complexities and biodiversity (Tews et al. 2004, Hiroaki T. Ishii et al. 2004, Jäkel and Roth 2004). Forest structures shape biodiversity and even small-scale variations like leave sizes (Neuvonen and Niemelä 1981) lead to different shaped species communities. Halaj et al. (2000) manipulated the habitat complexity of Douglas-fir stands by removing needles and thinning branch axes and found an increased spider species richness and differently shaped communities in more complex habitats. In addition, these manipulations affected ground-dwelling, but not airborne arthropods (Halaj et al. 2000). Thus, different groups or taxa react differently to changes in forest structures, and the response of a single group can even vary between the different forest strata (Leidinger et al. 2019).

Currently, forests are managed to maintain a continuous canopy cover which includes, that trees are harvested before their half-life to reduce the risk of tree loss due to natural disturbances or fungal infestation (Knoke 2003). Overall, these production forests are low in structural diversity and thus, exhibit a lack of important resources for many species such as old trees, early successional stages and, especially deadwood, whose development is suppressed and which is regularly removed (Bauhus et al. 2009, Moning and Müller 2009, Meyer and Schmidt 2011, Larrieu et al. 2018).

Deadwood is a crucial component of forest ecosystems. Many forest arthropod species depend on deadwood (Lonsdale et al. 2008, Rondeux and Sanchez 2010), such as 56% of all forest Coleoptera in Germany (Köhler 2000). Thus, deadwood volume is widely used as an indicator of forest biodiversity (Lassauce et al. 2011) and an indicator for sustainable forest management (MCPFE 2003). Besides saproxylic arthropods (species which are directly or indirectly dependent on deadwood) also other organisms benefit of deadwood addition such as non-saproxylic epigeal arthropods (Seibold et al. 2016a), and small mammals (Fauteux et al. 2012). Besides the amounts of deadwood, also the diameter of dead trees is relevant and shapes species communities (Gossner et al. 2013).

Several studies have found, that biodiversity of saproxylic arthropods is higher in forests with less dense canopies where more light reaches the ground (Müller et al. 2010, 2015, Lachat et al. 2012, Horak et al. 2014, Seibold et al. 2016a). Seibold et al. (2016b) compared species communities on different amounts of deadwood between sunny and shady forest plots and concluded that habitat heterogeneity and canopy openness seem to be the major drivers of saproxylic beetle diversity in temperate forests. The light intensity in a forest stand has also been shown to be an important factor structuring Heteroptera communities (Gossner 2009), ground beetles (Humphrey et al. 1999) and to support plant diversity (Boch et al. 2013, Gao et al. 2014). This plant diversity enhances the vegetational structural complexity, which shapes vertebrate (Demarais et al. 2017) and invertebrate diversity (Jäkel and Roth 2004).

As mentioned above, current management strategies comprise the admixture of broad-leafed tree species in coniferous forest stands. But this strategy must be considered with caution. On the one hand, mixed tree stands harbor more species than pure coniferous stands (Jäkel and Roth 2004).On the other hand, thermophilic organisms like arthropods can face a decline as this succession results in higher canopy densities and thus less light availability (Horak et al. 2014). Recently, Schall et al. (2018) also showed that the current management strategies which result in multi-layered forests harbor less diverse communities than several single-species age-class forests and concludes that the heterogeneity between forest stands is more important than heterogeneity within a forest stand (Schall et al. 2018).

## The importance of functional (trait) diversity in biodiversity research

Multiple recent studies found a dramatic human-induced decline in arthropod biomass and arthropod diversity (Dirzo et al. 2014, Hallmann et al. 2017, Leather 2018). But what are the effects on an ecosystem if certain species get lost?

Species richness was the dominant measurement for biodiversity for centuries (Gaston 2000), but species do not equally contribute to all processes in an ecosystem (ecosystem functioning) (Diaz and Cabido 2001) which is why biodiversity research must go beyond the concept of species richness.

“Species are different, but they are not equally different” (Lefcheck et al. 2015). Thus, even within a species group, some species can vary significantly in morphology of life-history, while others show only minor differences. A common way to assess the dissimilarity between species is by collecting information or measuring their functional traits. These characteristics are relevant to define how species interact with the environment and with other species (Diaz and Cabido 2001) or after the definition of Tilman (2001) “those components of biodiversity that influence how an ecosystem operates or functions”. The variation of functional traits across organisms defines the functional diversity of a species community or a whole ecosystem. Thus, the more different species are in a community, the higher is its functional diversity. But functional diversity is not necessarily highly correlated with species richness, since communities can consist largely of generalists (low diversity) or can consist of species of which each is specialized in a different niche (high diversity). Hence, communities even with a relatively low number of species, can have a very high functional diversity (Andersen 2008, Stuart-Smith et al. 2013). In such functionally diverse but species-poor communities, the loss of a species with certain functional traits has more severe effects than in communities where multiple species have similar functional traits (strong niche overlap) or fulfill similar ecosystem functions. Those species-rich communities often have a high functional redundancy which buffers the loss of a species within a functional group without a loss of ecosystem functions.

In recent years, many comprehensive studies analyzed the effect of land-use intensification on species communities. Gossner et al. (2016) studied more than 4000 species belonging to 12 trophic groups and found that species communities are getting more similar with increasing land use. Thus, rare species with certain traits get lost and opportunists and generalists remain. These findings go in line with the study of Soliveres et al. (2016) who stated that locally rare species contribute significantly to grassland multifunctionality, and thus the preservation of multiple ecosystem functions and services (Hector and Bagchi 2007, Isbell et al. 2011). Gámez-Virués et al. (2015) found that grassland management filters species traits if it leads to a change in landscape heterogeneity. Especially feeding specialists require higher degrees of heterogeneity or different land cover types than generalists. As a result, they suggest that a grasslands can be managed also at higher intensities, if less managed grasslands are near (Gámez-Virués et al. 2015). Overall, across taxa, land-use intensification leads to a loss of rare (Simons et al. 2015) or specialized species (Winfree et al. 2011), but the effects can differ between taxonomic groups (Simons et al. 2017).

To increase the understanding how land-use intensification or changes in management affect species, more studies are needed which analyze changes in trait variation and community composition between different land-use types or management intensities. Birkhofer et al. (2015a) for example found that spiders are sensitive to grassland-management intensity. They showed that at high mowing intensities, rare species and at high grazing intensities, large species get lost. In addition, frequent cutting changes ground beetle communities as it led to a higher abundance of predaceous and omnivorous but a lower abundance of herbivorous species (Birkhofer et al. 2015a). Mangels et al. (2017) found that land-use intensification significantly reduced abundance and species richness as well as diversity of moths, an important pollinator and herbivore group in grasslands. With high mowing and fertilization intensities, rare species were replaced by highly reproductive habitat generalists. They conclude that the loss of plant trait diversity leads to a loss of herbivore diversity (Mangels et al. 2017), a finding which is supported by Gossner et al. (2014).

Thus, species communities change under management intensification. Thereby, specialists can be replaced by generalists, which results in a loss of (functional) diversity, although species richness does not decrease. Hence, to understand how management affects species communities, it is necessary to go beyond the species richness approach and to include the functional trait diversity of a community. But the use of traits requires a certain knowledge of the species, time and effort. Therefore, the best choice is to use a taxon, which species are well known, which plays a key role in its habitat and is known to be sensitive to management intensification, such as ants (Formicidae).

## Ants – ecosystem engineers and a key taxon in terrestrial ecosystems

Ants (Hymenoptera, Formicidae) encompass the dominant fraction of animal biomass (Wilson and Hölldobler 2005). They are one of the most abundant arthropod groups in terrestrial ecosystems and can, therefore, be regarded as a keystone taxon. They occur on every continent except Antarctica and currently, about 15000 species are described (Bolton et al. 2007). Overall, ant species richness declines with increasing latitudes and altitudes and is highest in tropical regions with more than 4100 species in the Neotropical region, 2900 species in the Indo-Australian Region or 2800 species in the Afrotropical Region. In the temperate region, ant species richness is lower, with fewer than 500 species in the USA or Europe (Folgarait 1998).

Ants are one of the most influential organisms in terrestrial ecosystems for many reasons. As ecosystem engineers, ants fulfill numerous ecosystem functions, which are mostly related to food consumption (Blüthgen and Feldhaar 2010). Ants are generalized scavengers (Hölldobler and Wilson 1990) and among the leading arthropod predators in most ecosystems (Way and Khoo 1992, Floren et al. 2002, Dejean et al. 2007). They affect the abundance and species composition of other organisms and can even shape the overall arthropod biodiversity of habitats by interference or intraguild predation (Laakso and Setälä 2000, Hawes et al. 2002). Simultaneously, they are prey for invertebrates (Gotelli 1996, Gastreich 1999) and vertebrates (Reiss 2001). Ants alter plant communities (and therewith the whole ecosystem) as they provide seed dispersal (Howe and Smallwood 1982, Boulay et al. 2007, Lengyel et al. 2009), and seed consumption (Dauber et al. 2006b, Parr and Gibb 2010, Blüthgen and Feldhaar 2010). They protect plants from herbivores (Heil and McKey 2003, Styrsky and Eubanks 2007, Rosumek et al. 2009) but also live in trophobiosis with herbivorous insects which they protect against predators and parasitoids (Buckley 1987, Styrsky and Eubanks 2007).

Most ground-dwelling ant species are "soil engineers" which affect the soil structure, mix and aerate soils through their tunneling (Folgarait 1998, Frouz and Jilková 2008, Ehrle et al. 2017). Ants modify the microbial community in the soil and add nutrients by importing resources into their nests (Folgarait 1998, Dauber and Wolters 2005, Frouz and Jilková 2008, Boots et al. 2012). Therewith, they directly or indirectly affect the availability of resources to other species (Folgarait 1998). These improvements of soil conditions even support greater plant diversity (Del Toro et al. 2012, Nemec 2014) and arbuscular mycorrhizal fungi (Dauber et al. 2008) and have the potential to even alter grassland productivity (Dean et al. 1997). Especially ant nest-mounts have improved drainage, less plant cover and changed alkalinity (King 1977). Therewith, nest mounts can be small islands for some plant species, which would otherwise be outcompeted by fast-growing plant species (Dean et al. 1997). Besides plants, ant-mounts are habitats for other taxa like threatened *Maculinea* butterfly (Thomas et al. 2009) or a variety of microorganisms (Boulton and Amberman 2006).

## Ants response to disturbance and management strategies

Ants are undoubtful a crucial part in most terrestrial ecosystems and are endorsed as biological indicators to estimate effects of land management, land use and success of restoration schemes (reviews Andersen and Majer (2004), Underwood and Fisher (2006), Crist (2009), Philpott et al. (2010)). Numerous studies tested the efficacy of ants as biological indicators across the world in warmer regions like Australia (Andersen et al. 2002, Andersen and Majer 2004), dry grassland in Argentina (Bestelmeyer and Wiens 2001a) or tropical forests (Roth et al. 1994, Perfecto and Snelling 1995, Perfecto et al. 1997), but in parts also in north-temperate cold biomes (Ellison 2012). For temperate regions, such insights are largely lacking. There is an extensive literature on responses of ant communities to different types of disturbance like agriculture, agroforestry, mining, fire, habitat fragmentation or ecosystem restoration which would go beyond the scope of this thesis and which was recently reviewed and partly listed by Andersen (2019). Here, most studies show a negative impact of human-made disturbance on ant species diversity across ecosystems. Although studies on restoration show how species communities or whole ecosystems recover from disturbances or human management, they do not show how communities respond to different management strategies.

Studies which analyzed the effects of management on ants mainly focused on grazing and logging as main management techniques in grassland and forest ecosystems (Underwood and Fisher 2006), although other management techniques are widespread.

Common techniques in current grassland management are grazing, mowing, and fertilization. The effect of grazing on ants has been shown to be highly variable and can differ between grassland types (Bestelmeyer and Wiens 2001b). In semi-arid rangelands with short histories of controlled grazing, such as in America and Australia, grazing by livestock can reduce ant species richness (Bestelmeyer and Wiens 1996, Andersen and Sparling 1997, Whitford et al. 1999, Woinarski et al. 2002, Boulton et al. 2005), has little effect (Whitford et al. 1999, Bestelmeyer and Wiens 2001b, Ehrle et al. 2017), or can even increase species richness (Bromham et al. 1999). Especially the intensity of grazing, and thus the type and the number of livestock can be decisive for the effect. While Majer and Beeston (1996) found more species in heavily grazed than in less grazed rangeland, Abensperg-Traun et al. (1996) found fewer ant species in highly disturbed Australian sites and suggested grazing and trampling to be the main factors of this reduction. The effects on ants can differ between the type of grazers. Sheep, for example, can have positive effects on ant abundance and biomass (Hutchinson and King 1980) while e.g. Beever and Herrick (2006) found more ant mounts in sites without grazing horses. In temperate grassland with long grazing history, the effect on ants is not sufficiently studied, but tends to be rather weak (Pihlgren et al. 2010).

Besides, it is poorly understood whether grazing has direct, indirect of even both effects on ants. Direct effects can be disturbance or even destruction of nesting sites by trampling of livestock, whereby the disturbance intensity will be highly dependent on the grazing intensity and livestock type. Indirect effects can be the increased structural heterogeneity due to selectively removed plant biomass and spotty fertilization by feces, plant species richness and the reduced plant ground cover (Calcaterra et al. 2010, Pihlgren et al. 2010, van Klink et al. 2015). While grazing of grasslands is very common (and relatively well-studied) across the globe (Hoffmann 2010), fertilization and mowing as management strategies are rather restricted to temperate grasslands.

The direct effects of fertilization might be the disturbance of nesting sites by heavy machinery, which may be needed to disperse fertilizer. But since this disturbance lasts just a short period and is rather spotty, the main effect of fertilization will be indirect. Pihlgren et al. (2010) found fewer ant species in fertilized than in non-fertilized meadows and attributed it to the enhanced growth of taller plant species. Those plant species reduce sun exposure and soil temperature, which can limit the occurrence of open-habitat specialized ant species.

In contrast to the trampling of livestock and the trajectories of heavy machinery, mowing affects the entire grassland patch. When grassland is mowed only a few centimetres above the soil surface nest mounds of ants may be mechanically destroyed which can result in a significant loss of brood and workers. Possible indirect effects of mowing on ant communities are the alteration of available food sources. Thus, mowing reduces the availability of resources associated with plant parts that are cut, such as floral and extrafloral nectar and the abundance of trophobionts associated with upper parts of the plants, such as aphids. When other arthropods are reduced in abundance due to mowing ants might be affected negatively as potential prey items may be lacking (Zechmeister et al. 2003, Socher et al. 2012). But studies on mowing effects on ants are rare and, to my knowledge, elucidate only the effects of low-intensity mowing. Pech et al. (2015) found a shift of species compositions with slightly more species in plots mown once or twice per year compared to unmown plots and Noordijk et al. (2010) found an increase of arthropod diversity (including ants) along a gradient from unmown to mowing twice a year. Other studies have focused on the time of mowing (Grill et al. 2008, Korösi et al. 2014) rather than on mowing intensity. E.g. Dahms, Wellstein, Wolters, & Dauber, (2005) found no effect of low-intensity mowing (once or twice per year) compared to other low-intensity management types (mown pastures, cattle pastures, and silage meadow). Although many studies already investigated the effects of mowing, fertilization, and grazing, it is still unclear how species communities change with increasing land-use intensity, how each management types affect ants, and which species are particularly vulnerable. Hence, several fundamental knowledge gaps still need to be filled. Therefore, in my **first manuscript**, I analysed the direct and indirect effects of the three main management components on temperate ant communities and investigated how ants react to land-use intensification.

Overall, it has been shown that ants are sensitive to various types of forest management and disturbance (Greenslade and Greenslade 1977, Majer 1983, Vasconcelos 1999, Oliver et al. 2000, Watt et al. 2002, Maeto and Sato 2004, Palladini et al. 2007, Yoshimura 2009, Philpott et al. 2010, Ewers et al. 2015). Forest management or, in particular, logging can range from low-intensity selective logging up to clear-cutting (high intensity). The effects on ants are therefore dependent on the logging intensity. Research on selective logging has so far been done mainly in tropical rainforests, where only weak effects on ant diversity were found (Vasconcelos et al. 2000, Kalif et al. 2001). Although the tropics are very species-rich with numerous specialized and therefore assumingly more sensitive species (Luke et al. 2014), the response to forest management is rather low (Lawton et al. 1998). Studies on the effects of clear-cutting on ants are mainly done in boreal or temperate forests, where clear-cutting is a widespread management technique. The effects of clear-cutting are variable and hard to generalize. Overall, it can increase ant abundance and diversity, if it reduces canopy cover and creates clearings which create habitats for "open-country" species (Punttila et al. 1994, Palladini et al. 2007, Babik et al. 2013, Véle et al. 2016, Tausan et al. 2017). Species which react more sensitively to forest management are wood ants (genus *Formica*). Clear-cutting or fragmentation causes population declines and a high nest-abandonment rate (Sorvari and Hakkarainen 2005, 2007), that leads to a more aggressive behavior between nests (Sorvari and Hakkarainen 2004), to changes in population structures (Punttila 1996) and lower variation in body size due to limit food availability (Herbers 1980, Deslippe and Savolainen 1995, Sorvari and Hakkarainen 2009).

As described above in detail, different forest management results in varying forest structures and complexities to which taxa respond differently. Thus, what can be expected for ants?

Only about 10% of the epigaic Central-European ant species nest occasionally in deadwood, and only 4% depend on deadwood as a nesting substrate (Seifert 2017). Therefore, the amount of deadwood might be less important for ants than for other taxa, unless they benefit from higher prey diversity (bottom-up effects). More important for ants might be the tree species or tree species diversity of which the forest consists, as tree species, differ in available potential niches and result in different microclimates. Seifert (2017) e.g. found more species in oak and pine forests than in beech or spruce dominated forests.

Management techniques such as clear-cutting, shelterwood systems or selective logging highly influence the canopy openness of forests. This has been shown to be important for ants, as studies found in woodland in Australia (Lassau and Hochuli 2004), in temperate conifer mountain forests (Arnan et al. 2009), and along an elevational gradient in a mountain region in South Africa (Munyai and Foord 2012), and southern France (Blatrix et al. 2016). Studies which were implemented in the temperate zone found more species in open habitats than in closed forests (Dolek et al. 2009, Graham et al. 2009, Bernadou et al. 2013, Del Toro 2013) which is rather not surprising since a high percentage of temperate ant species occur primarily in open habitats like grasslands (Seifert 2018, Del Toro et al 2013). A reduced canopy cover usually results in a warmer forest climate and a higher ground temperature. Ants are thermophiles and in temperate forests, warmer sites harbor more species than colder sites (Sanders et al. 2007). Thus, the temperature might be a good predictor for species richness (Del Toro 2013, Seifert 2017). But how are temperate ant communities affected by forest management and is it possible to assign changes to certain changes in forest structures or environmental conditions? In my **second manuscript**, I therefore explored 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.

## Morphological traits – a predictor for ant disturbance response?

Forest management and land use also affect the functional diversity of ant communities (even without noticeable changes in species richness). Functional diversity of communities' change if species with certain traits get lost or are replaced by other species with traits that are less affected by for example disturbance or changes in vegetation (Del Toro et al. 2013). Examples for such changes can be found in Punttila et al. (1994) where forest management weakened the dominance of *Formica aquilonia*, a suppressor of other species, which was beneficial for the less dominant *F. sanguinea*. Another example are the findings of Arnan et al. (2012), who showed that dominance hierarchies of Mediterranean ant communities are dependent on traits like thermal or moisture tolerance and dominant species are replaced by species which are e.g. adapted to lower temperatures.

To calculate functional diversity, a certain knowledge of the species is required, either about their lifestyle (life-history traits) or about their morphology (morphological traits). Although ants have been studied for decades to centuries, especially in the tropics, a high percentage of species are still undescribed (Folgarait 1998). To cope with this lack of knowledge, ants are often categorized in functional groups which are based on taxonomic relatedness, dominance hierarchies or habitat preferences (Andersen 1995). The occurrence or abundance of these functional groups is often the common "measurement" for ant functional diversity (e.g. Lassau & Hochuli 2004; Arnan, Cerdá & Retana 2012; Bernadou *et al.* 2013). Going beyond this "functional group approach" and combining morphological and functional traits enables a more detailed understandings of communities (Arnan et al. 2014, 2017, Silva and Brandão 2014)

Overall, trait-based approaches to understand species responses to their environment can substantially increase our understanding of ecological communities. Since as already stated, many ant species are still undescribed or weakly studied. Instead of species identities, it may be more useful to find general rules that can be assigned to species with certain functional traits rather than to specific species (McGill et al. 2006, Paine et al. 2015). Hence, an approach to investigate species communities is to analyze morphological traits (Bihn et al. 2010, Gibb and Parr 2013, Silva and Brandão 2014, Yates et al. 2014, Gibb et al. 2015) or easily measurable traits such as stable isotope signatures (Feldhaar et al. 2010, Pfeiffer et al. 2014)

Morphological traits of single species and trait compositions of species communities are for example often analyzed along environmental gradients (Arnan et al. 2014), between spatial scales (Yates et al. 2014) or differently structured habitats (Gibb and Parr 2010). For the latter, for instance, different habitat structures and complexities (e.g. desert vs. rainforest, shrubland vs. forests) can result in differently shaped species communities (Farji-Brener et al. 2004, Lassau and Hochuli 2004, Sarty et al. 2006, Schofield et al. 2016). Different habitat structures provide e.g. different food sources or nesting opportunities but also different microclimates and overall surface complexities. Radnan et al. (2018) found that ant body size declined with increasing surface complexity and suggested that larger ants are discouraged from foraging in complex habitats since smaller species can find food sources faster (exploitation competition). Generally, the effect of habitat complexity on the morphology of ant communities is well studies. For example, ant leg length decreases with habitat complexity (Parr et al. 2003, Farji-Brener et al. 2004, Sarty et al. 2006, Gibb and Parr 2010, 2013, Wiescher et al. 2012). Some studies found that larger body size can be beneficial in simpler habitats (Farji-Brener et al. 2004, Sarty et al. 2006), but the correlations of body size and habitat complexity are not consistent between continents (Gibb and Parr 2013). Nevertheless, findings of Gibb & Parr (2013) provide the support that habitat complexity filters species composition through their morphological traits.

Therefore, the question arises if a certain knowledge of a species, like its morphology, is enough to predict how it will respond to changes in habitat structures. Such knowledge could help to make precise and species-specific estimations of how habitat disturbances or management intensification affects species communities. In my **third manuscript**, I made a first attempt to answer this important but very extensive question. Based on the findings of Radnan et al. (2018), Farji-Brener et al. (2004), Sarty et al. (2006) and Kaspari and Weiser (1999), larger ant species should move faster in open, less structured habitats, while smaller species should be advantaged in more complex habitats, since their shorter legs enable movement through gaps between obstacles. Encouraged by the recent findings of Yanoviak et al. (2017), who found decreasing running speed of arboreal ants with increasing roughness of plant surfaces, I investigated the running speed of differently sized ants (body size and leg length) along a surface rugosity gradient which represents different habitat structures.

If habitat complexity filters species through their morphological traits, I predicted that larger species were fast on smooth surfaces but lost speed with increasing complexity, smaller species were less affected and most important, similarly sized species respond similarly to changes in surface complexity.

# Manuscripts of the thesis and overview of the main results

## Manuscript 1:

Heuss, L., **Grevé, M.E.**, Schäfer, D., Busch, V. & Feldhaar, H. (2019) Direct and indirect effects of land-use intensification on ant communities in temperate grasslands. *Ecology and Evolution*, 9:4013–4024.

In this manuscript, it was our aim to disentangle the direct and indirect effects of land-use intensification and its three main components, grazing, fertilization, and mowing, on ant species richness in 110 temperate grasslands in three regions in Germany. We found that a high land-use intensity had a significant negative effect on ant species richness, compared over all regions. Among the different land-use strategies, mowing had the strongest negative effect, followed by heavy grazing. Fertilization had no significant effect.

Ant species richness was directly negatively affected by a high mowing intensity and a high grazing intensity, as well as soil moisture. Besides, high mowing and grazing intensities resulted in a reduced plant species richness but a higher plant height. In contrast to grazing with cattle, grazing by sheep had significant positive effects on ant species richness.

We tested whether the ant community composition changes along a land-use intensity gradient and investigated which morphological and life-history (functional) traits are affected in communities when certain species disappear. We found that land-use intensity strongly impacted the occurrences of the different species. Very common species showed high tolerances to land-use intensification while the rarest species occurred mostly in low-intensity managed plots. Morphological trait spaces were not affected by land-use intensification, but at high management intensities, where species with rare life-history traits (like multiple nests in one colony) get lost. In addition, especially aboveground-nesting species were highly sensitive towards mowing.

## Manuscript 2:

**Grevé, M.E.**, Hager, J., Weisser, W.W., Schall, P., Gossner, M.M. & Feldhaar, H. (2018) Effect of forest management on temperate ant communities. *Ecosphere*, 9:e02303.

In this manuscript, we investigated ant communities in 150 German temperate forest stands with different forests management regimes and investigated 1) whether forest management affects the abundance, species richness, functional diversity, and composition of ant communities and 2) if these changes are mediated by a change in the environmental conditions, such as structural heterogeneity, microclimate and food supply. We found that ant species richness differed between forest types. Low species richness was found in spruce and beech forests and high species richness in oak and pine forests. Species richness was positively affected by pine as dominant tree species. Ant abundance was directly and negatively affected by spruce as dominant tree species.

The main indirect effects of forest management on ant abundance was a high temperature amplitude, and thus warmer forest climate, via a reduced canopy cover in oak and pine stands. Functional diversity could only be calculated for one of the three regions since the other two harbored a very low mean number of species. We could not find any direct or indirect effects of forest management on the functional diversity based on morphological traits. Based on life-history traits, functional diversity was the highest in open forests with a low structural complexity, which were dominated by pine trees.

## Manuscript 3:

**Grevé, M.E.**, Bláha, S., Teuber, J., Rothmaier, M. & Feldhaar, H. (2019) The effect of ground surface rugosity on ant running speed is species-specific rather than size dependent. *Insectes Sociaux* 33:355–364

In this manuscript, we asked the question whether morphological traits can be used to predict how a species is affected by increasing surface rugosity in differently complex habitats, or in a broader view tested the suitability of morphological traits as functional traits. Therefore, we measured intra- and interspecific variation in running speed of seven differently sized non-arboreal ant species along an increasing surface rugosity gradient.

We found that an increasing surface rugosity led to a decrease of running speed in all tested species but the response to increasing surface rugosity was idiosyncratic and highly species-specific. Running speed did not consistently rise with extending body size and leg length. In addition, similar sized species differed greatly in their response to changing surface rugosities. Thus, leg length was not a good predictor for running speed, which hampers precise predictions on how species might respond to changing habitats, based on morphological traits exclusively.

# Discussion

Central European temperate grasslands and forests are managed since millennia. With increasing human population size and a simultaneously increasing knowledge on the impact of management, management strategies have changed in recent years. These changes create new knowledge gaps, such as how certain species groups can be specifically supported and require additional research.

The impact of increasing land-use intensity on temperate grasslands communities was already investigated for plants and several arthropod groups (Socher et al. 2012, Simons et al. 2014, 2016, Gossner et al. 2016, Simons and Weisser 2017). Overall, land-use intensification threatens biodiversity and causes multitrophic homogenizations (Gossner et al. 2016). Unfortunately, ants as a key taxon in grasslands were not included in these studies. Thus, the question remained how increasing land-use intensity and the single land-use practices grazing, fertilization and mowing affect temperate ant communities.

This knowledge gap could be closed in Heuss and Grevé et al. (2019). Land-use intensification reduces ant species richness and diversity. Mowing was the most harmful practice, especially for aboveground-nesting ant species. In addition, high mowing intensities, combined with fertilization reduced the number of plant species and the shrub cover while simultaneously resulted in increased vegetation height. Hence, high mowing intensities have comprehensive effects on grasslands and reduce ant species richness and grassland structural diversity (Heuss and Grevé et al. 2019). Mowing has an immense negative impact on temperate ant communities (Heuss and Grevé et al. 2019), but assumingly, the effects are inconsistent among regions. Mowing affects aboveground-nesting species more than soil-nesting species (Heuss and Grevé et al. 2019). These aboveground nests serve as heat collectors for optimal larval development (Penick and Tschinkel 2008). In warmer climatic regions in which ant species do not build aboveground nests, mowing can be less detrimental.

Therewith ants respond similarly to multiple other groups such as plants, herbivores, secondary and tertiary consumers, and as such, all parts of the trophic pyramid of the grassland ecosystem (Gossner et al. 2016). To my knowledge, Heuss and Grevé et al. (2019) is the first study which covers a large gradient of land-use intensities in grasslands and which disentangles the effect of each management practices separately.

The effects of grazing for example are dependent on its intensity and can have both, positive and negative impacts on temperate ants (Heuss and Grevé et al. 2019). This fits the findings of several other studies across the world (positive: Majer and Beeston (1996); Bromham et al.

(1999); Bestelmeyer and Wiens (2001a); negative: Bestelmeyer and Wiens (1996); Andersen and Sparling (1997); Whitford et al. (1999); Woinarski et al. (2002); Boulton et al. (2005), or no effect: Arcoverde et al. (2017)).

More important than grazing itself are the resulting changes in the grassland structure. In a study on the effect of grazing on the structure and composition of ants between savanna and grasslands in subtropical Argentina, Calcaterra et al. (2010) found no direct effect of grazing on ants but the richness of ant species and functional groups was higher in the structurally more complex savannas. They also found that livestock grazing simplified vegetation structure by reducing overall plant height in both habitats. However, the grass cover variation did not explain the differences in overall species richness (see also Vasconcelos et al. (2008)), but the species group of hot-climate specialists gained distinctly. These species prefer open environments with sparse vegetation coverage as can be found in grazed sites (Andersen 1995). In grassland or savanna plots with a higher vegetation cover, hot-climate specialists are replaced by more shade tolerant, opportunistic species (Calcaterra et al. 2010). Such effects of grassland structures on species compositions can be found outside of the subtropical zone as well. In the semiarid Mediterranean region, hot-climate specialists are the dominant group in open habitats with low vegetation cover only and are otherwise replaced by opportunists and generalistic Myrmicinae in sites with higher plant densities (Reyes-López et al. 2003, Arnan et al. 2007).

Species belonging to the hot-climate specialists normally do not occur in the temperate region, but here, open habitats play an important role for other species as well. In Belgium, Dekoninck et al. (2007) showed that rare xerophilic ant species, preferring warm and dry habitats, occur in high numbers in calcareous grasslands, where vegetation is usually short. They assume that in grassland with the encroachment of tall grasses, the rare xerophilic ant species will be replaced by mesophilic, rather common species. Such xerophilic species belong largely to the genus *Formica* such as *F. clara*, *F. pratensis*, *F. rufibarbis* but also *Lasius alienus*. They will be superseded by less thermophilic ant species from woodlands and closed grassland vegetations like several *Myrmica* species (Dekoninck et al. 2007). This corresponds with the findings of Heuss and Grevé et al. (2019) in which thermophilic to xerophilic species occur in plots with low management intensities (mostly pastures with low vegetation height), while more shade-tolerant species were found in more intensively managed grassland plots (meadows, dominated by tall, fast-growing grass species).

But “grasslands” with limited plant cover are not necessarily the most ant species-rich grassland type. Indeed, the structural heterogeneity of grasslands is an important driver of ant species diversity. This heterogeneity can be due to a high plant species richness or due to e.g. shrub encroachment which will attract additional woody species as it was found across the world in Slovakia (Wiezik et al. 2013), Spain (Azcárate and Peco 2012), Ohio (Campbell and Crist 2017), and Australia (New 2000). But especially shrub encroachment should be limited since otherwise open-habitat grassland species will get lost (Dahms et al. 2010) (Figure 3c).

Figure 3. a) and b) Examples for extensively managed meadows with a high flower and ant diversity. c) Example for an abandoned meadow with early stages of shrub encroachment.

Now, that the effects of land use on ants are known, the question arises if current grassland conservation strategies are suitable to protect ant diversity. In Heuss and Grevé et al. (2019), we highly recommend reducing grassland management intensity, especially the number of mowing events per year. In addition, the transformation from pastures to high production meadows should be stopped. To preserve grassland biodiversity but also to maintain the productivity of grasslands, current grassland conservation strategies in Germany comprise a mosaic of grasslands which vary in management type and intensities within a landscape. This approach is supported by numerous scientific studies such as Kruess and Tscharntke (2002), Samways (2005), Cizek et al. (2012), Gámez-Virués et al. (2015), as well as Simons and Weisser (2017), who investigated how landscapes can be managed to maintain or increase productivity and protection of arthropods at the same time, using data from more than 1000 grassland arthropod species but unfortunately, does not include ants. Most arthropod species are highly mobile and find refuges in extensively used plots within this mosaic. But ants are quasi-sessile organisms, once the colony is established. Hence, their colony relocation into less intensively used plots is very unlikely. Furthermore, such a mosaic of different management types might not increase overall ant species richness at the landscape scale (Dauber and Wolters 2004). Grassland plots are often managed in a rotation system. The management intensity of so far extensively used plots will be increased, while management on so far high-intensity plots will be reduced. Being unable to move elsewhere quickly, ant species richness will therefore decrease in the newly intensively used plots. Dauber et al. (2006a) showed that the highest ant diversity occurs in plots with continuous, low-intensity land use. In contrast to plants, for which extensively used plots serve as seed banks (Kiehl et al. 2010), the recolonization of ants in former intensively used plots might be slow and highly variable (Dauber and Wolters 2005). Another currently used management strategy to protect arthropod diversity is mowing only parts of the grasslands and leave the rest undisturbed at first. However, this strategy does not protect ants.

A habitat type in which grassland management intensification should be particularly avoided is the ecotone of grasslands and forests. These ecotones are species-rich since they share ant communities from both biomes (Seifert 2017, 2018). Besides, the occurrence of grassland species can strongly influence forest communities. Wood ants (*Formica*) are one of the most influential groups in temperate forests (Frouz et al. 1997, Laakso and Setälä 2000, Domisch et al. 2008). However, they are more common at forest/grassland ecotones than in dense forests (Seifert 2018), since wood ants require and parasitize *Serviformica* nests which prefer grasslands. But especially *Serviformica* species are highly sensitive to grassland management and do not occur at high mowing intensities (Heuss and Grevé et al. 2019). Thus, grassland management can have a high impact on grassland and forest ant communities.

Forest management can positively affect temperate ant diversity (species richness and functional diversity) if it results in a reduced canopy cover and a lower structural complexity, e.g. through tree harvesting. Especially the selection of shade-intolerant tree species, which creates warm stand conditions, such as pines and oaks, leads to more diverse ant communities (Grevé et al. 2018). Interestingly, the forest types which reflect natural forests in Central Europe, uneven-aged and unmanaged beech forests, harbor significantly fewer species than managed forests (Grevé et al. 2018). These findings stand partly in contrast to the insights in Maeto and Sato (2004) and Yoshimura (2009), who found no differences in ant species richness between unmanaged forests and managed forests in temperate Japan. But the species compositions were differently structured, and the unmanaged forests were dominated by woodland specialists. While managed forests harbored mostly open-habitat specialists or habitat generalists (Maeto and Sato 2004, Yoshimura 2009).

Similar to Grevé et al. (2018), Guzmán-Mendoza and Castaño Meneses (2016), investigated ant communities in unmanaged forests, managed forests, and reforested forests in temperate Mexico. They found the highest species richness in the highly disturbed reforested forests and an overall high species turnover (few shared species) between the forest types. Hence, forest management in the temperate region strongly affects ant communities, leads to an increased species richness or at least to changes in species compositions.

A very important aspect or driver of these variations between ant communities is the change of the forest microclimate. Warmer forest climates increase the larval development of ants (Kipyatkov and Lopatina 2015) which may result in faster colony growth, especially in temperate and boreal regions.

Figure 4: Examples for a mixed coniferous-deciduous forest with a low canopy coverage and a high ant diversity. All pictures were made within a 500m x 500m area. After only 20 minutes of hand sampling, I could find 11 different ant species: *Lasius playthorax, Lasius brunneus, Formica polyctena, F. fusca, F. cunicularia, Camponotus ligniperda, Myrmica ruginodis, M. lobicornis, Tetramorium cf. caespitum*, *Temnothorax* unifasciatus and *T. nylanderi.*

A warmer microclimate via a reduced canopy cover has positive effects on ants in the European boreal (Punttila et al. 1994, Palladini et al. 2007) and temperate region (Dolek et al. 2009, Tausan et al. 2017, Grevé et al. 2018) (Figure 4). In the temperate part of the United States, studies investigated forests and adjacent open habitats and could highlight how important a high canopy openness and the consequently increased temperature can be for ant communities.

Del Toro et al. (2013) found a five times lower species richness in dark (hemlock-white) pine forest stands compared to open habitats. Forests with less dense canopies and open habitats were similarly diverse. Lessard et al. (2009) studied ant communities in oak forests in the southern Appalachians and stated a positive relation of species richness and within-site variation in ground temperature. Such a variation in ground temperature is assumingly a result of different canopy covers (Grevé et al. 2018). In addition, higher ground temperatures reduce soil moisture, which is beneficial for ground-dwelling ants as well (Seifert 2017).

Since forest management has positive effects on ants in cold and temperate regions if it results in a warmer forest climate, the question arises how ants respond to forest management in warmer regions. Surprisingly, the results of Azcárate et al. (2013) from Central Spain suggest similar patterns as found in colder regions. They analyzed the effects of forest paths in oak forests (*Quercus pyrenaica*) and coniferous forests (dominated by *Pinus sylvestris*) and found distinctively more species on the drove road than in the closed forests. The forest paths had a higher plant diversity than forests and were a habitat for more specialized ant species, such as granivores, scavengers and hot-climate and open-habitat specialists. Ant species occurring in the forests were mainly opportunists and generalists (Azcárate et al. 2013). In the subtropical woodland around Sydney, Australia, Lassau and Hochuli (2004) draw the same picture and showed that ant species richness was negatively associated with canopy cover.

Compared to the temperate zone, tropical rainforests are a hotspot of ant diversity and harbor numerous specialized species. Besides the immense loss of species and habitats due to extensive deforestation and transformation to arable land, outside protected areas, most tropical forests are exploited or managed by selective logging. Thereby, only trees of commercial value are harvested, and the forest is then left to regenerate. Overall, this sustainable use is less detrimental to the forest ecosystem and a meta-analysis of Putz et al. (2012) revealed that "85–100% of species of mammals, birds, invertebrates, and plants remain after logging" (Putz et al. 2012).

Vasconcelos et al. (2000) compared ground-living ants between undisturbed forests and forests which were selectively logged at different years in Amazonia. They found no significant differences in ant species richness between the treatments. However, compared to undisturbed forests, the managed forests showed a reduced canopy cover and different ant species compositions. Thus, rainforest management via selective logging has only minor effects on ground-living ants, if it does not lead to large scale disturbances and a high tree diversity remains (Leal et al. 2012). Furthermore, ant communities are able to recover and with increasing time after disturbance, species communities in disturbed and undisturbed forests become more similar (Ryder Wilkie et al. 2009, Bihn et al. 2010). But the effects of selective logging can differ between ground-living and arboreal ants. For the latter, logging can lead to a complete habitat loss which results in a lower number of arboreal species in secondary compared to primary rainforests (Klimes et al. 2012).

Another type of forest management is rainforest reforestation which has been shown to be very supportive for ant conservation. In Cameroon rainforests, Watt et al. (2002) found that even reforestation with a single tree species can recover large parts of the former ant diversity. If forests are reforested from pastures, ant communities are first intermediate between pastures and rainforests but become more similar to rainforest communities when the canopy cover increases (Piper et al. 2009, Lawes et al. 2017). Overall, ant communities in tropical forests respond to alterations of canopy cover with changes in community composition. But as opposed to colder regions, species diversity does not increase with canopy openness and species like specialized predators or tropical-climate specialists are replaced by more disturbance-tolerant species (Lawes et al. 2017). Nevertheless, tropical rainforest ant communities, similar to ants in colder bioregions are influenced by temperature (Mezger and Pfeiffer 2010, McGlynn et al. 2010, Dáttilo and Dyer 2014). Dröse et al. (2019) studied the drivers of ant communities in forest-grassland ecotones in South Brazil. Similar to forests and grasslands in colder regions, they found more ants in forests with higher temperatures at the forest ground and a low vegetation height in the grasslands (Dröse et al. 2019).

Summarized, an open canopy cover is a significant driver of ant diversity, particularly in less tropical regions. Keeping this in mind, current management strategies of forests in Central Europe must be reconsidered. The recommendation for forest managers in Grevé et al. (2018) to include more open and warmer stages in their management strategies to promote ants contradicts with current management strategies. These comprise the admixture of deciduous tree species in coniferous forest stands which increases structural complexity and add a second canopy layer. This second layer reduces the amount light reaching the ground and therewith result in colder ground temperatures. Thus, the management strategies of the last decades did not support ant diversity. However, facing climate change, forest management in Central Europe will undergo extensive restructuring. Future management strategies which are discussed, include an enhancement of tree species richness, the reduction of forest monocultures, and the promotion of light-demanding, or non-native tree species (Brang et al. 2014). Especially the promotion of light-demanding tree species can increase ant diversity in terms of species richness and even functional diversity (Grevé et al. 2018).

Functional diversity can among others, be based on morphological or life-history traits, or a combination of both. To understand how the diversity of an ecosystem, habitat, or population changes e.g. under management, it is very useful to include measurements of functional diversity in the analyses.

But functional diversity can only be calculated if communities consist of a sufficient number of species. However, especially in poor habitats, like spruce monocultures, ant communities often consist of a low number of species (Seifert 2017, Grevé et al. 2018) and measurements of functional diversity are difficult or even impossible. In Grevé et al. (2018) it was possible to use morphological traits to reveal regional differences between communities such as larger bodies or longer legs in formicine dominated communities, compared to mixed family communities. But the functional diversity, based on morphological traits, was not variable enough to find management related effects on the communities (Grevé et al. 2018). The cause for this lack of effects was the high morphological similarity between the occurring species.

If communities are diverse enough like in tropical or arid regions, the use of morphological traits can result in great insights like that ant species communities are shaped by habitat structures (Farji-Brener et al. 2004, Sarty et al. 2006, Wiescher et al. 2012, Gibb et al. 2015, Radnan et al. 2018). For example Gibb and Parr (2010) investigated the foraging efficiency of ant communities across the globe and found clusters of smaller species in complex habitats and a broad spread of body sizes in open habitats in South Africa (30 species). However, in Sweden (8 species) the body sizes were more evenly distributed since the species communities were similar in complex and open habitats (Gibb and Parr 2010). Thus, in less diverse communities, morphological trait variation can be too low to detect such variation (Grevé et al. 2018, Heuss and Grevé et al. 2019).

Another problem using morphological traits are my findings in Grevé et al. (2019), that the response of species to changes in e.g. habitat structure can be highly species-specific and not generalizable (Grevé et al. 2019). This hampers precise predictions on how species might respond to changing habitats, based on morphological traits only, since even similarly sized species can respond idiosyncratically if they have different habitat preferences or vary in other life-history traits (Grevé et al. 2019).

A great example for the comparison for a low morphological but high life-history trait diversity is the genus *Myrmica*. Most of the 20 species occurring in Germany have very similar shapes and the morphological distinction between species is often based on subtle differences in the shape of the scape or the petiole (Seifert 2018). Nevertheless, the species show high life-history variability. Within closely related species of for example the *Myrmica scabrinodis* species-group, species can vary distinctly in their temperature preference and therefore habitat preference (from cold to warm and wet to dry: *M. scabrinodis*, *M. sabuleti*, *M. specioides*) and differ e.g. in colony size, number of queens and competitive strength (Radchenko and Elmes 2010).

If an ant community is changing and one of these species is replaced by another, the life-history based functional diversity would change, while the morphological trait-based functional diversity would remain similar. Hence, investigating species-poor communities or communities which are consisting of many morphological similar species, a life-history approach to calculate functional diversity is more promising than a morphological trait approach (Grevé et al. 2018; Heuss and Grevé et al. 2019). But the usage of life-history traits requires a comprehensive knowledge of the studied species, which is often not available. To handle this problem, ants are commonly assigned to functional groups (Andersen 1997) and the diversity of the community is measured as the number of occurring functional groups and the number of species within each group (Bernadou et al. 2013, Del Toro et al. 2015). But this functional group approach is not useful for analyses of ants in Central Europe since the majority of the common species belong to the three largest genera, *Lasius*, *Formica* (incl. *Serviformica*) and *Myrmica* (Seifert 2018). Assigned to functional groups, *Lasius* and *Formica* (real wood ants) belong to the cold-climate specialists*, Serviformica* to the opportunists, and *Myrmica* belongs to the generalized Myrmicinae (Andersen 1997). Most other species are rare or only locally abundant (Seifert 2007). Especially cryptic species, like *Ponera*, are very rare or completely missing. Species with unique traits such as specialized predators do not occur, to my knowledge. Fortunately, the ant species in Europe are well studied and a variety of life-history traits can be found in the literature for many species (Arnan et al. 2017, Seifert 2017, 2018). Using a combination of taxonomic diversity (number of species) and functional diversity, based on life-history traits, we could show that grassland and forest management alter temperate ant communities (Grevé et al. 2018; Heuss and Grevé et al. 2019). Management in both biomes lead to changes in community compositions.

In the grassland, management intensification led to a loss of species richness and functional diversity. Low-intensity managed grasslands with low vegetation harbor species with a variety of (unique) life-history traits. They can be habitats for rare *Tapinoma* species, which belong to the subfamily Dolichoderine and which are highly dominant and abundant in warmer bioregions. They have a polygynous (multiple queens per nest) colony structure, forage preferably in the herb layer and are nectarivores (Seifert 2018). Another species which occurs only in dry, open habitats is *Lasius alienus*, which is a sister species of *L. niger* and does not differ much from *L. niger* but is less aggressive and is an important host for several butterfly species. Low-intensity managed grasslands harbor also species such as the aggressive, dominant, social-parasite species *Formica sanguinea* and their *Serviformica* hosts (Seifert 2018). In grasslands with at least some woody plants, *F. pratensis* can be found. This large species belongs to the wood ants, has a highly variable colony structure (monogynous or polygynous, single or grouped nests) and can build large aboveground nests with high population sizes (Seifert 2018). In Germany *F. pratensis* is highly threatened and protected by law. With their aboveground nests, they occur mainly in unmown grasslands (Heuss and Grevé et al. 2019).

However, a moderate land use which results in less dry grasslands via higher plant height can create suitable habitats for mesothermic ant species. Such a species is *Lasius flavus*, which are subterranean foragers, and alters grasslands via their aboveground nests and the movement of soil (Ehrle et al. 2017). However, with an increasing number of cuts per year, *L. flavus* stops occurring (Heuss and Grevé et al. 2019).

At high-intensity managed plots, formicine species which build huge colonies with multiple queens or aboveground nests are missing and only *Lasius niger* remains. This species is highly adaptive to most environments, strictly monogynous in older colonies, very aggressive and feeds on any available food source (Seifert 2018). Despite building partly aboveground nests, *L. niger* occurs in high densities so that mowing has weaker effects on them compared to more sensitive species. *Myrmica* species are less sensitive. While some species have narrow temperature and moisture preferences (see above), the three most common species *M. rubra*, *M. scabrinodis* and *M. ruginodis* show low sensitivities (Heuss and Grevé et al. 2019) and occur even in shady forests (Grevé et al. 2018). In forests, management intensification can have the opposite effect compared to grasslands. It can increase functional diversity, when it results in a lower canopy cover and a warmer forest climate (Grevé et al. 2018). Forests with low canopy cover are suitable habitats, especially for formicine species (Figure 4) which show high variation in life-history traits such as colony size, number of nests, number of queens, diet and behavioral dominance.

Ants are one of the most influential organisms in terrestrial ecosystems. As ecosystem and soil engineers, ants alter both, grasslands and forests and influence plant and animal communities. Therewith, ants are a great model organism to analyze a variety of ecological key questions, such as how communities are affected by management and how they respond to changes.

Overall, I could contribute significantly to the understanding of how ants react to current management practices in temperate grasslands and forests and could highlight the need for functional diversity analyses in biodiversity research. In addition, I strongly recommend the usage of life-history traits over morphological traits in the analyses in communities which show high morphological similarities (Grevé et al. 2018; Heuss and Grevé et al. 2019). Beside low variation, morphological traits may yield misleading results since similar shaped species can act idiosyncratic and highly species-specific (Grevé et al. 2019).

# List of publications

Heuss, L.*, **Grevé, M.E.***, Schäfer, D., Busch, V. & Feldhaar, H. (2019) Direct and indirect effects of land-use intensification on ant communities in temperate grasslands. Ecology and Evolution, 9:4013–4024.
* Authors contributed equally

**Grevé, M.E.**, Hager, J., Weisser, W.W., Schall, P., Gossner, M.M. & Feldhaar, H. (2018) Effect of forest management on temperate ant communities. Ecosphere, 9:e02303.

**Grevé, M.E.**, Bláha, S., Teuber, J., Rothmaier, M. & Feldhaar, H. (2019) The effect of ground surface rugosity on ant running speed is species-specific rather than size dependent. Insectes Sociaux, 33:355–364

# Manuscripts and declaration of own contribution

## Manuscript 1:

Authors: Lisa Heuss, Michael E. Grevé, Deborah Schäfer, Verena Busch, Heike Feldhaar

Title: Direct and indirect effects of land-use intensification on ant communities in temperate grasslands

Journal and status: *Ecology and Evolution*, 9:4013-4024
DOI: 10.1002/ece3.5030

Own contribution: concept and study design 0%, data acquisition 0%, analyses of samples 45%, data analyses and figures 45%, discussion of results 45%, manuscript writing 50%

HF conceived the study. LH did the field work. LH and MEG identified the ant species. DS and VB provided data and expertise. LH, MG, and HF analyzed the data and wrote the first version of the manuscript. Figures and tables were created by
LH and MEG All authors helped to improve the manuscript. LH and MEG are shared first authors. MEG is the corresponding author.

Received: 17 December 2018 | Revised: 7 February 2019 | Accepted: 11 February 2019

DOI: 10.1002/ece3.5030

ORIGINAL RESEARCH

WILEY Ecology and Evolution

# Direct and indirect effects of land-use intensification on ant communities in temperate grasslands

Lisa Heuss[1*] | Michael E. Grevé[1*] | Deborah Schäfer[2] | Verena Busch[3] | Heike Feldhaar[1]

[1]Animal Population Ecology, Animal Ecology I, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany

[2]Institute of Plant Sciences, University of Bern, Bern, Switzerland

[3]Institute for Landscape Ecology, Münster University, Münster, Germany

**Correspondence**
Michael E. Grevé, Animal Population Ecology, Animal Ecology I, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany.
Email: Michael.greve@uni-bayreuth.de

**Funding information**
Federal Ministry of Education and Research (BMBF), "Qualitätsoffensive Lehrerbildung", Grant/Award Number: 01JA160; German Research Foundation (DFG) Priority Program 1374 "Infrastructure- Biodiversity-Exploratories", Grant/Award Number: DFG-Ref no. FE631/7-1

## Abstract

Land-use intensification is a major driver of local species extinction and homogenization. Temperate grasslands, managed at low intensities over centuries harbored a high species diversity, which is increasingly threatened by the management intensification over the last decades. This includes key taxa like ants. However, the underlying mechanisms leading to a decrease in ant abundance and species richness as well as changes in functional community composition are not well understood. We sampled ants on 110 grassland plots in three regions in Germany. The sampled grasslands are used as meadows or pastures, being mown, grazed or fertilized at different intensities. We analyzed the effect of the different aspects of land use on ant species richness, functional trait spaces, and community composition by using a multimodel inference approach and structural equation models. Overall, we found 31 ant species belonging to 8 genera, mostly open habitat specialists. Ant species richness, functional trait space of communities, and abundance of nests decreased with increasing land-use intensity. The land-use practice most harmful to ants was mowing, followed by heavy grazing by cattle. Fertilization did not strongly affect ant species richness. Grazing by sheep increased the ant species richness. The effect of mowing differed between species and was strongly negative for *Formica* species while *Myrmica* and common *Lasius* species were less affected. Rare species occurred mainly in plots managed at low intensity. Our results show that mowing less often or later in the season would retain a higher ant species richness—similarly to most other grassland taxa. The transformation from (sheep) pastures to intensively managed meadows and especially mowing directly affects ants via the destruction of nests and indirectly via loss of grassland heterogeneity (reduced plant species richness) and increased soil moisture by shading of fast-growing plant species.

KEYWORDS
arthropods, Formicidae, grassland management, grazing, mowing, species homogenization

---

*Authors contributed equally.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2019 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

## 1 | INTRODUCTION

In temperate Europe, grasslands have been extensively managed over centuries by grazing and low-intensity mowing. These seminatural grassland ecosystems show a very high plant and animal diversity (Chytrý et al., 2015; Hejcman, Hejcmanová, Pavlů, & Beneš, 2013), but are threatened by increasing management intensity (or abandonment) over the last decades. A negative influence of increasing land use on species richness and abundance has already been documented for plants (Haddad, Haarstad, & Tilman, 2000; Harpole & Tilman, 2007; Kleijn et al., 2009; Socher et al., 2012), different arthropod groups (Allan et al., 2014; Chisté et al., 2016; Hendrickx et al., 2007; Simons et al., 2014), and on the overall functional diversity of communities (Birkhofer, Smith, Weisser, Wolters, & Gossner, 2015; Blüthgen et al., 2016; Flynn et al., 2009).

In Germany, about 28% of the agricultural land is used intensively as grassland, either as meadows or pastures (Statistisches Bundesamt, 2016). The three management practices used in agricultural grasslands are mowing, fertilization, and grazing (mostly by cattle and sheep). They differ in their effects on biodiversity in grasslands (Simons et al., 2014; Socher et al., 2012), and effects change along the management intensity gradient. Fertilization and mowing are often highly correlated (Blüthgen et al., 2012), and high intensities of both result in the homogenous vegetation structures and reduced plant diversity (Harpole & Tilman, 2007). This leads to overall multitrophic homogenization (Gossner et al., 2016) and therefore a decline in arthropod species richness and abundance (Haddad et al., 2009). Besides these indirect effects, mowing also has direct negative effects on arthropods (Marini, Fontana, Scotton, & Klimek, 2007; Nickel & Hildebrandt, 2003; Simons et al., 2017; Socher et al., 2012) as they are killed by machines (Thorbek & Bilde, 2004). In contrast, grazing affects the biotic environment by simplifying and thinning out vegetation and litter, which can, at a moderate level, increase plant diversity (Stewart & Pullin, 2008), an effect, that can vary between the different types of livestock (Socher et al., 2013). Thus, moderate grazing has a far less detrimental effect on arthropods than mowing and fertilization.

Ants are a key taxon in grasslands (reviewed in Wills & Landis, 2018). They are moderately diverse and can be highly abundant, making them important consumers and ecosystem engineers (Folgarait, 1998; Del Toro, Ribbons, & Pelini, 2012). Ants alter plant communities through predation of herbivorous insects (Sanders & van Veen, 2011), seed dispersal (Howe & Smallwood, 1982), and seed consumption (Dauber, Rommeler, & Wolters, 2006). Additionally, they build subterranean nests and thereby modify the soil structure, which increases plant diversity (Nemec, 2014; Del Toro et al., 2012) due to the creation of small islands for less competitive plant species, which would otherwise be outcompeted (Dean, Milton, & Klotz, 1997).

Land-use intensification may negatively affect ant species richness (Dauber & Wolters, 2004, 2005), abundance, and colony density (Diaz, 1991; Folgarait, 1998) and functional community composition (Dauber & Wolters, 2005) in temperate grassland both directly and indirectly. However, the underlying mechanisms leading to the decrease in ant species richness, abundance, and the effects on species with distinct functional traits and therefore functional community composition are currently not well understood. The impact of the different management practices such as mowing, fertilization, and grazing have not yet been elucidated.

*Mowing* affects the entire grassland patch and can have a direct negative effect on ant species building nest mounds, as especially the aboveground parts of the nest are destroyed during mowing. Ant species which differ in their trophic niche and foraging behavior (Blüthgen & Feldhaar, 2010) might be affected differently by land use as well. Indirect effects of mowing on ant communities are the alteration of available food sources and changes of microhabitats. Thus, mowing instantly reduces the availability of resources associated with plant parts that are cut, such as floral and extrafloral nectar, as well as the abundance of arthropods and therewith potential prey items and trophobionts may be lacking (Socher et al., 2012). To date, studies on mowing effects on ants are, to our knowledge, mainly elucidating effects of low-intensity mowing (max. two cuts per year). Pech, Dolanský, Hrdlička, and Lepš (2015), Noordijk et al. (2010), and Pérez-Sánchez, Zopf, Klimek, and Dauber (2017) found that different mowing regimes led to highly site-dependent responses of ants.

Direct effects of *fertilization* might be the disturbance of nesting sites by heavy machinery. However, the main effect of fertilization will be indirect. Pihlgren, Lenoir, and Dahms (2010) found fewer ant species in fertilized than in nonfertilized meadows and linked this to the enhanced growth of taller plant species. Such plant species reduce sun exposure and thus soil temperature, which can reduce the occurrence of ant species specialized to open habitats.

For *grazing*, positive (Bromham, Cardillo, Bennett, & Elgar, 1999), negative (Boulton, Davies, & Ward, 2005), and neutral (Bestelmeyer & Wiens, 2001; Whitford, Zee, Nash, Smith, & Herrick, 1999) effects have been found. However, grazing effects are to date not sufficiently studied in temperate grasslands with long grazing history (Pihlgren et al., 2010). Besides, it is poorly understood whether grazing affects ants directly due to the destruction of nesting sites by trampling of livestock or indirectly, through increased structural heterogeneity due to selectively removed plant biomass, localized fertilization by feces deposition, altered plant species richness, and reduced plant cover, which increases ground temperature (Boomsma & Van Loon, 1982).

In this study, we aim at disentangling the effects of the compound land-use intensity (LUI; Blüthgen et al., 2012) and its three main components, grazing, fertilization, and mowing, on ant species richness and abundance in temperate grasslands. We analyze the importance of both direct and indirect effects of land-use intensification and management type in temperate grasslands on ant community composition. We test whether the ant community composition changes along a land-use intensity gradient and investigate which morphological and life history functional traits are reduced in communities when certain species disappear.

## 2 | METHODS

### 2.1 | Study site

This study was performed within the framework of the Biodiversity Exploratories, which includes three study sites in Germany, the Schwäbische Alb, Hainich-Dün, and Schorfheide (Fischer et al., 2010) (www.biodiversity-exploratories.de). The three study regions reflect a gradient of increasing altitude and precipitation and decreasing annual man temperatures from northeastern to southwestern Germany (for detailed description of the regions see appendix). Each region (henceforth Alb, Hainich, and Schorfheide) comprises 50, relatively evenly distributed grassland plots of 50 m × 50m for comparative biodiversity studies along a land-use gradient. For additional details, see Fischer et al. (2010).

### 2.2 | Land-use intensity index

The sampled grasslands are managed by local farmers as meadows, pastures, or mown pastures (mown and grazed by livestock) at different intensities. Land-use intensities range from extensively used pastures to heavily fertilized meadows which are mown up to four times a year. Standardized interviews have been conducted every year to record the intensity and type of land use for every plot, considering *mowing intensity* (M), *fertilization intensity* (F), and *grazing intensity* (G ). Mowing is measured as the number of cuts per year (ranging from zero to three cuts per year). Fertilization intensity is measured as the amount of nitrogen (in kg) applied per hectare and year from chemical fertilizer, manure, or slurry. Grazing intensity includes information on livestock type (sheep, cattle, and/or horses), number of livestock units, and duration of the grazing period (in days). All three land-use components are integrated into the globally standardized land-use intensity measure LUI by averaging the three measures after standardizing to a common scale:

$$\mathrm{LUI}\,(i) = \sqrt{\frac{M\,(i)}{\mathrm{Mmean}} + \frac{F\,(i)}{\mathrm{Fmean}} + \frac{G\,(i)}{\mathrm{Gmean}}}$$

where Mmean, Fmean, Gmean are mean values for all plots of each region (Blüthgen et al., 2012). To quantify long-term land-use intensity, a mean LUI for the years 2011 to 2015 was calculated.

### 2.3 | Sampling design

Due to the presence of livestock or mowing activities, we conducted the sampling on 110 of the 150 plots (Table 1). Per 50 m × 50 m plot, we combined the three different sampling methods of pitfall trapping, hand sampling, and baiting in order to achieve a robust representation of ant species richness. Sampling was conducted in transects along all four edges of each plot, with transects of each edge being 50 m long and 2 m wide. In total, 12 pitfall traps were placed per plot along the transects (for detailed description see appendix). In 2014, we sampled pitfall traps in the regions Alb (June) and Hainich (August) and July 2015 in Schorfheide. In 2015 (Alb in May, Hainich in June, and Schorfheide in July), we walked the two-meter wide transects, collected all ants visible foraging on the ground or in vegetation. All visible ant nests were counted and sampled once on the same transects through walking along all four edges and searching for ant nests on the surface, as a measurement for ant abundance. In addition, 16 bait stations were placed along the edges (four per edge at a distance of 7.5, 17.5, 32.5, and 42.5 m from the corners of the plots). Bait stations were installed and monitored for one hour and contained artificial diet with different protein to carbohydrate ratios (for a detailed description see Supporting information Appendix S1). After collection, all ants were stored in ethanol to conserve them for further analysis. Ants were identified using Czechowski, Radchenko, Czechowska, and Vepsäläinen (2012), Radchenko and Elmes (2010), Seifert (2007), Seifert and Galkowski (2016), Seifert and Schultz (2009).

### 2.4 | Environmental variables

Biotic variables—Vegetation was sampled in 2015 from May to June. In a representative subplot of 4 m × 4 m, all vascular plant species were recorded, average vegetation height was measured, and the *coverage of herbs, shrubs, bryophytes*, and *litter* was estimated in percent. Aboveground community biomass (gram/m$^2$) was sampled at the same time by cutting the vegetation at a height of 2–3 cm in four 0.5 × 0.5 m subplots, dried, and weighed.

Abiotic variables—Each plot was equipped with a meteorological station measuring *ground temperature* (°C) at ten centimeters above the ground and *soil moisture* measured in percentage of volumetric

**TABLE 1** Overview over the three study regions. Stated is the number of sampled plots, range and mean number of ant species found, range of land-use intensity (LUI), and number of plots with different types of livestock

| | | Ant species | LUI | Livestock | | | |
|---|---|---|---|---|---|---|---|
| | | Min–Max | Min–Max | | | | |
| Region | Plots | Mean (SD) | Mean (SD) | None | Cattle | Sheep | Cattle & horses |
| Alb | 37 | 0–14<br>5.32 (SD 4.31) | 0.46–3.11<br>1.63 (SD 0.73) | 17 | 2 | 16 | 2 |
| Hainich | 33 | 0–15<br>6.39 (SD 3.65) | 0.65–3.05<br>1.52 (SD 0.64) | 5 | 13 | 15 | 0 |
| Schorfheide | 40 | 0–9<br>3.77 (SD 2.09) | 0.98–2.63<br>1.57 (SD 0.35) | 17 | 23 | 0 | 0 |

*Notes*. Plots with no livestock are managed as meadows (mown and fertilized at different intensities).

water content at ten centimeters depth. Temperature and moisture were measured continuously from May to August in 2014 and 2015 and then averaged over the whole period.

## 2.5 | Ant traits

We measured morphological traits for each species occurring on each plot under the binocular (Leica M165 C binocular system and the software "Leica Application Suite"). We measured up to ten individuals from different plots for each species and used trait means for the analyses. We measured the following traits: *Weber's length* (mesosoma length), *pronotum width*, *head length* and *width*, *femur*, and *tibia length* of the hind leg as well as *eye width*. We chose and measured traits as suggested by Parr et al. (2017) and references therein. For all traits, we calculated the relative values by dividing them by Weber''s length and used Weber's length as absolute values.

We extracted life history traits of all ant species mostly from Arnan, Cerdá, and Retana (2017) and partly from Seifert (2007, 2017). As traits, we used *behavioral dominance*, *number of queens per nest*, *number of nests*, *colony size*, and assumed *nutritional niche* (values for the latter are based mostly on expert knowledge by Seifert (2017), but also based on former published work). Further, we used the *foraging strata*, calculated from values a specific ant species is most likely found foraging on assumed by Seifert (2017). As a measurement of the ants´ size, we used the mean *Webers' length* per species. The trait data and a more detailed description of the trait categories are provided in the Supporting information Appendix: Tables S2, S3, and S4.

## 2.6 | Statistical analyses

We performed all statistical analyses using R (R Version 3.3.2, R Development Core Team, 2016). To analyze the effect of land-use intensity on ants, we created two generalized linear model (GLM, with Poisson error distribution) with number of ant species as the response variable in the first model (1) and the compound LUI and the region as predictor variables which were allowed to interact and the second model (2) with the three different land-use components (mowing-, grazing-, and fertilization intensity) as predictor variable (for *n* = 110 plots).

To analyze the direct and indirect effects of land use on ants, we used a multimodel inference approach and structural equation models (*SEM*). Since the continuous variables were measured at very different scales, we rescaled them to zero mean and unit variance using the "decostand"-function of the R package "vegan" (Oksanen, Blanchet, Kindt, Legendre, & O'Hara, 2016). We created a first global model (GM-1) (LME) with the number of ant species as response variable and the three land-use components as well as all environmental variables as predictor variables with the region as random factor over all plots (for *n* = 96). Due to missing data, we had to remove 14 plots from this analysis (Alb 8 plots, Hainich 1 plot, Schorfheide 5 plots). To reveal possible effects of the different livestock types on ants, we created a second global model which was similar to the first model but was restricted to only pasture and mown pasture plots (*n* = 61) and included the livestock type to the global model (GM-2). 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 $\Delta AIC_c < 2$ 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 R package "piecewiseSEM" (Lefcheck, 2016) to test for direct and indirect effects of the most important variables (all variables selected by model averaging) on the response variable. As suggested in Lefcheck (2016), we standardized the path regression coefficients by scaling them by mean and variance. The structure of both SEMs is described in the appendix. We could not perform the goodness-of-fit test (Fisher's C test) for both of our SEMs as they were both fully saturated, with each path being based on a plausible hypothesis.

To analyze the effect of land-use intensity on the number of sampled ant nests, we created two generalized linear model (GLM, with Poisson error distribution) with number of ant nests as response variable and (1) the compound LUI as predictor variable and (2) with the three different land-use components (mowing-, grazing-, and fertilization intensity) as predictor variables (for *n* = 110 plots for both). In order to study the effect of land-use intensification on the trait space of morphological and life history traits and to investigate which traits are affected, we performed an ordination analysis. We grouped land-use intensities into three categories (1/3 of the LUI each—low: LUI: <1.16 (*n* = 29 plots), medium: LUI: 1.17–2.33 (*n* = 69 plots), high: LUI > 2.34 (*n* = 12 plots)). Using the function "gowdis" in the package "FD" (Laliberté, Legendre, Shipley, & Laliberté, 2014; Laliberté & Legendre, 2010), we created a Gower distance matrix form the trait data. Subsequently, a nonmetric multidimensional scaling with two axes on the Gower distance matrix was performed using the "metaMDS" function in the R package "vegan" (Oksanen et al., 2016). The trait data were plotted post hoc with 1,000 permutations using the function "envit." Differences between the trait space of the LUI categories were tested with a PERMANOVA using "adonis" function with 1,000 permutations (*n* = 110 plots).

# 3 | RESULTS

Over all 110 plots, we found 31 ant species belonging to 8 genera. While the regions Alb and Hainich had a similar range of species numbers (Table 1), the region Schorfheide was less diverse. The regions differed in their land-use intensity. The gradient of land-use intensity was broader in the Alb and Hainich in comparison with Schorfheide where plots were mainly managed at a medium intensity (Supporting information Figure S1).

## 3.1 | Effects of land use on ant species richness

A high land-use intensity (LUI) had a significant negative effect on ant species richness, compared over all regions (GLM: $\chi_1^2 = 65.15$; $p < 0.001$, Figure 1). Among the regions, similar negative effects were found for the Hainich ($z = -4.54$; $p < 0.001$; Supporting information Figure S1) and Alb ($z = -7.55$; $p < 0.001$; Supporting information Figure S1), but not for the Schorfheide ($z = 2.06$; $p = 0.039$; Supporting information Figure S1) where we found positive effects. For the three land-use categories, the effect of mowing was the strongest (negative, GLM: $\chi_1^2 = 68.47$; $p < 0.001$; Supporting information Figure S2), followed by grazing (negative, GLM: $\chi_1^2 = 24.05$; $p < 0.001$; Supporting information Figure S2). Fertilization had no significant effect (GLM: $\chi_1^2 = 0.17$; $p = 0.68$; Supporting information Figure S2).

## 3.2 | Effects of environmental variables and land-use components on ant species richness

The first multimodel averaging approach revealed that seven of the twelve predictor variables (GM-1) were important for explaining ant species richness (Table 2a). The piecewise *SEM* on the drivers of ant species richness (Figure 2a) showed that a high mowing intensity ($\beta = -2.15$, standardized coefficient) and a high grazing intensity ($\beta = -0.67$, standardized coefficient) had direct negative effects. In addition, a high soil moisture had direct negative effects on ant species richness ($\beta = -0.10$, standardized coefficient). High mowing and grazing intensities had negative effects on plant species richness.

The second multimodel averaging approach (GM-2; only plots with livestock) revealed that six of the thirteen variables used were important for explaining ant species richness (Table 2b). The piecewise *SEM* (Figure 2b) showed the effect of land use including livestock type (compared with cattle as livestock) on ant species richness. In contrast to grazing with cattle, grazing by sheep had significant positive effects on ant species richness ($\beta = 1.11$, standardized coefficient). The mowing and fertilization intensity had indirect effects by influencing soil moisture, which had a negative effect on ant species richness ($\beta = -0.13$, standardized coefficient).

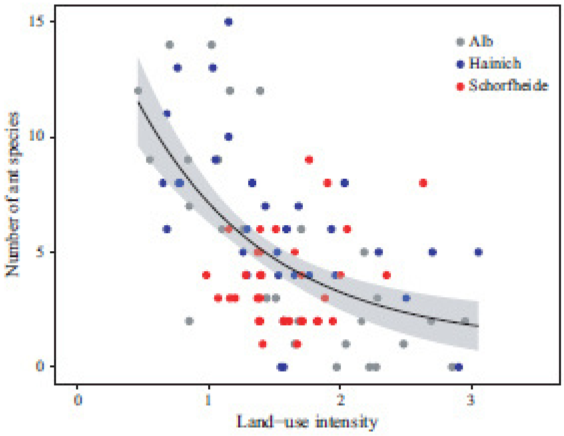

**FIGURE 1** Ant species richness along the land-use intensity gradient in the three study regions over all plots ($n = 110$). The black line represents the exponential function of a GLM for species number and increasing land-use intensity. The gray area represents the 95% confidence interval

## 3.3 | Effects of land use on ant species compositions

Land-use intensity strongly impacted the occurrences of the different species (Figure 3). Very common species (based on number of plots where these species occurred on) with high tolerance to different levels of land-use intensity were, for example, *Lasius niger*, *Myrmica rubra*, and *M. scabrinodis*. Other common species, like *Formica rufibarbis*, *F. cunicularia*, or *F. clara*, were rarely found on plots with high land-use intensity. Among the less common species, *Myrmica gallienii* or *Tetramorium caespitum* showed higher tolerances to high land-use intensity than for instance, *Lasius paralienus* or *Formica sanguinea*. The rarest species occurred mostly in low-intensity managed plots.

Since mowing was the land-use practice with the strongest negative effect on ant species richness, we additionally plotted the species occurrences along the number of cuts per year. This revealed that most *Formica* species and *Lasius flavus* were highly sensitive toward mowing while *Lasius niger* and most *Myrmica* species tolerated higher mowing intensities (Figure 4).

Ant abundance measured as the number of nests per plot was significantly negatively influenced by increased land-use (GLM: $\chi_1^2 = 9.29$; $p < 0.002$; Supporting information Figures S3, S4). Separately analyzed for the three land-use categories, we did not find significant effects for mowing (GLM: $\chi_1^2 = 2.32$; $p = 0.13$), grazing (GLM: $\chi_1^2 = 0.08$; $p = 0.78$), and fertilization (GLM: $\chi_1^2 = 2.29$; $p = 0.13$).

Land-use intensity also affected the functional trait space of ant communities. Overall, ant community functional trait space of morphological traits (PERMANOVA: $F_1 = 0.35$, $p = 0.72$, Figure 5a) and life history traits (PERMANOVA: $F_1 = 0.34$, $p = 0.78$) did not change significantly among plots managed at low, medium, and high land-use intensities. However, functional trait space for life history traits decreased strongly with increasing management intensity (Figure 5b). At high management intensities, species communities consist of species which foraged less in higher vegetation and had smaller and less polydomous colonies (Figure 5b). The morphological trait space did not differ between land-use intensities, since several species of the genera *Formica*, *Lasius*, and *Myrmica* occurred occasionally even at high intensities.

## 4 | DISCUSSION

We found a decrease in ant species richness, number of ant nests, functional trait space (life history traits), and a change of ant

**TABLE 2** Results of the multimodel averaging approach for ant species richness (a) for all plots ($n = 96$) and (b) for all plots with livestock ($n = 69$)

| (a) Variable | Importance (%) | N-containing models | (b) Variable | Importance (%) | N-containing models |
|---|---|---|---|---|---|
| Mowing intensity | 100 | 6 | Livestock | 100 | 6 |
| Grazing intensity | 100 | 6 | Soil moisture | 100 | 6 |
| Soil moisture | 100 | 6 | Mowing intensity | 71 | 4 |
| Plant species richness | 67 | 4 | Fertilization intensity | 43 | 3 |
| Vegetation height | 61 | 4 | Cover shrubs | 27 | 2 |
| Cover litter | 28 | 2 | Grazing intensity | 15 | 1 |
| Cover shrubs | 11 | 1 | | | |

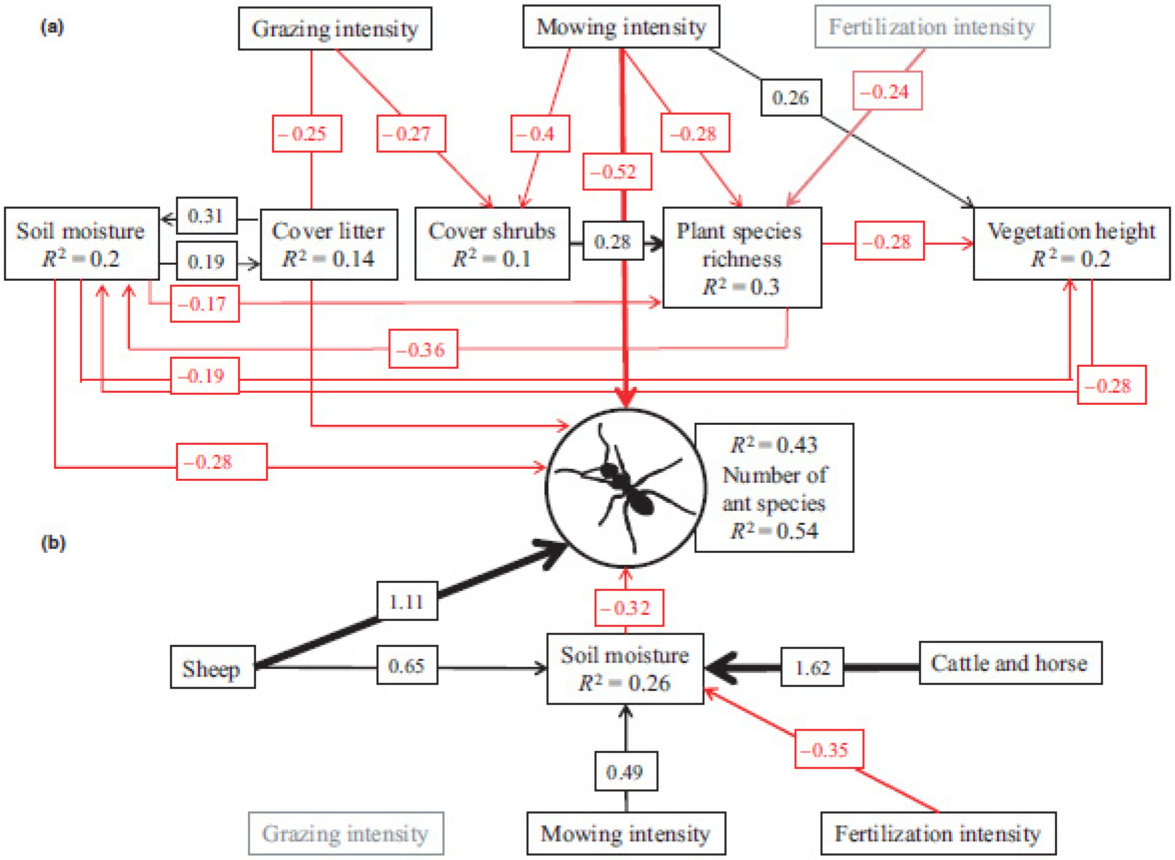

**FIGURE 2** Piecewise structural equation model showing direct and indirect effects of land use and environmental parameters on ant species richness (a) over all sampled plots ($n = 96$) and (b) only on pastures and mown pastures with the livestock type included ($n = 61$). Arrows represent significant ($p < 0.05$) unidirectional interactions between variables (black show positive, red negative interactions). We report the significant path coefficients as standardized effect sizes next to the arrows (all effect sizes are shown in Supporting information Table S5). $R^2$ values for component models are given in the boxes of their response variables

community composition with increasing land-use intensity. These negative effects were found for the regions Hainich and Alb, but not at the Schorfheide, where sampled grassland sites had a relatively narrow range of management intensities and ant species richness.

### 4.1 | Effects of land use on ant species richness

When comparing the three management practices, only mowing and grazing had significant, negative effects on ant species richness. The way in which mowing influences temperate ant communities is not well understood since former studies have focused on the time of mowing (Grill, Cleary, Stettmer, Bräu, & Settele, 2008; Korösi et al., 2014) rather than on mowing intensity. For example, Dahms, Wellstein, Wolters, and Dauber (2005) found no effect of low-intensity mowing (once or twice per year) compared with other low-intensity management types (mown pastures, cattle pastures, and silage meadow). Negative effects of intensive mowing were also found on the taxonomic richness of other groups including plants, fungi, arthropods, and vertebrates and overall herbivory (i.e., insects and slugs; Gossner, Weisser, & Meyer, 2014) and caused a decrease of mainly rare species in multiple arthropod taxa (Simons et al., 2015). The tremendous negative effect of mowing on ants becomes particularly clear by looking at the mean number of species per plot. Unmown plots had a mean species richness of 7.1 species, but the number decreased at plots mown once (4.1 species), twice (2.6 species), and three times per year (2.7 species). In our study, we found that ant species which are directly threatened by mowing were mainly species which build aboveground nests such as most *Formica* species and *Lasius flavus*. These species build large nests as "heat collectors" in which the brood is transferred for optimal larval growth (Penick & Tschinkel, 2008). The destruction of these nests through mowing with machines can lead to a significant loss of brood and workers. Further, since many species start their mating flights in June (Seifert, 2007), mowing in late spring or early summer can reduce the number of queens and males dramatically.

Effects of grazing on ants depended on grazing intensity as well as livestock type. High grazing intensity affected ant species richness negatively. However, in the present study pastures grazed at high intensity were only stocked with cattle. In comparison, grazing by sheep or cattle pastures with a low grazing intensity due to a short grazing duration and a low number of livestock showed a significantly higher ant species richness. Our study thus corroborates the findings of other studies where grazing by sheep had positive effects on ant abundance and biomass (Hutchinson & King, 1980) as well as other arthropods (Dennis et al., 2008; Simons et al., 2014; review: Scohier & Dumont, 2012). These positive effects may be mediated by higher habitat heterogeneity (Hoffmann & James, 2011) and a higher number of vascular plant species (Socher et al., 2013) on pastures grazed by sheep and generally pastures grazed at low intensity. Plant species richness is decreased on intensively managed, frequently mown plots which have higher percentages of fast-growing plant species (Socher et al., 2013), resulting in an increased average vegetation height.

Fertilization intensity only had an indirect effect on ants by altering plant communities. Nitrogen increases the plant growth, favoring especially fast-growing plant species (Socher et al., 2013), decreasing the sun exposure of the soil surface, and resulting in a higher soil moisture. This had a strong negative effect on ant species richness in our study sites, corroborating previous studies (Dahms et al., 2005; Pérez-Sánchez et al., 2017; Seifert, 2017).

Temperate ant species are thermophiles and prefer warm and dry habitats (Sanders, Lessard, Fitzpatrick, & Dunn, 2007) with a rather small range of soil moisture tolerated by most species (Seifert, 2017). However, the (ground) temperature was not among the most important variables in our analyses. This can be explained by the low temperature range among the plots (85% of plots had an average ground temperature between 16 and 18°C). Furthermore, the temperature measurement of ten centimeters above the ground might not directly represent the warm temperatures on sun-exposed ground. But since soil moisture and sun exposure should be correlated with each other, we assume that plots with a high soil

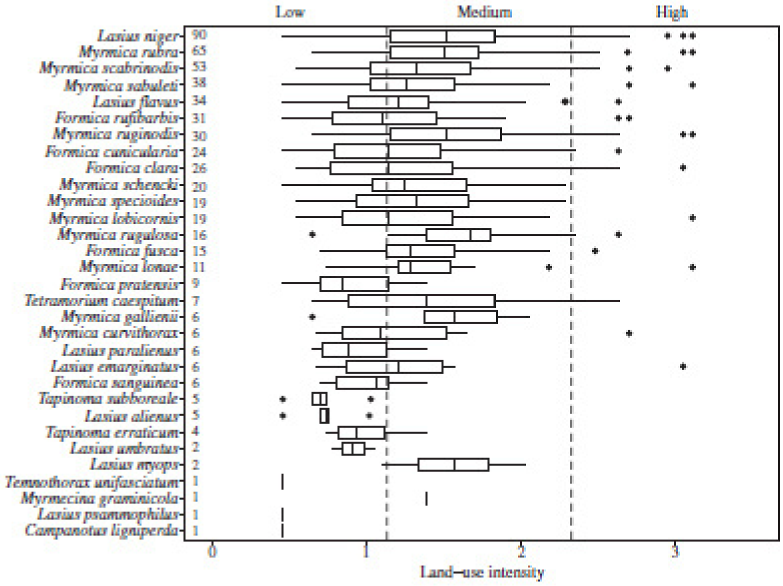

**FIGURE 3** Boxplot showing the occurrences of all ant species present in the three regions along the land-use intensity gradient, sorted by decreasing number of occurrences. The numbers on the left figure margin state the number of plots where the species occurred. Dashed lines show categories of low, medium, and high land-use intensity. Black dots indicate outliers

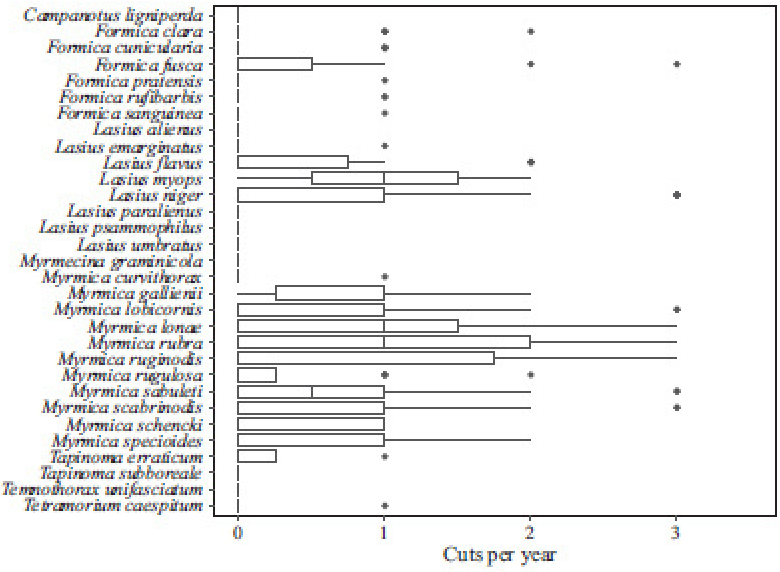

**FIGURE 4** Boxplot showing the occurrence of all ant species present in the three regions along the number of cuts per year, alphabetically ordered. Black dots indicate outliers

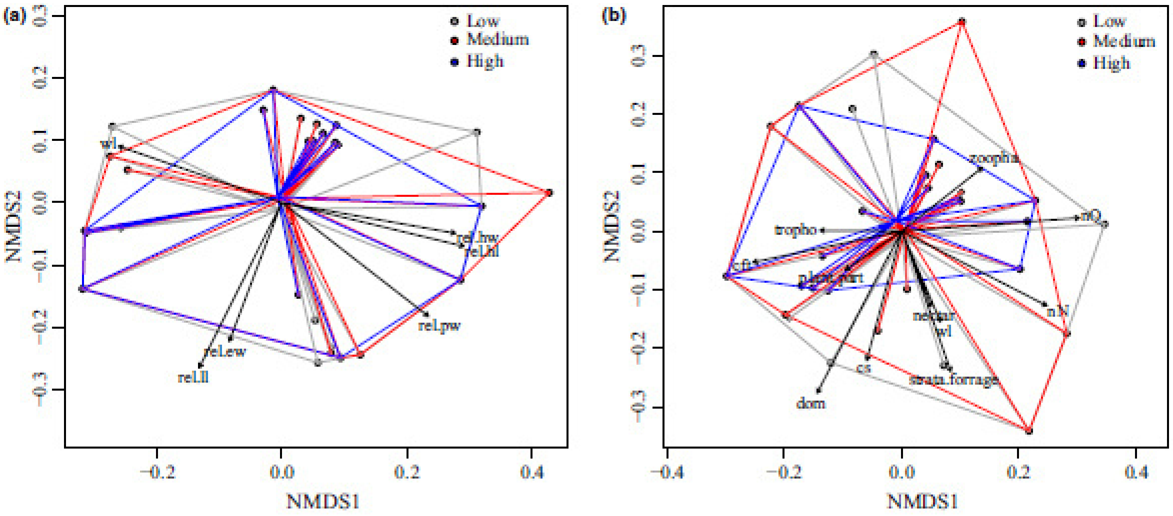

**FIGURE 5** Ordination plot showing the trait space covered by ant species occurring under low, medium, and high land-use intensity (different colors gray, red, and blue dots, respectively). For each, a nonmetric multidimensional scaling (NMDS) was conducted based on a Gower distance matrix. (a) Plot is based on morphological traits. Used morphological traits are as follows: Webers´ length (wl), relative leg length (rel.ll), relative pronotum width (rel.pw), relative head width (rel.hw), relative head length (rel.hl), relative eye width (rel. ew). (b) Plot is based on life history species traits. Used trait values are as follows: strata species is most likely to be found foraging (strata forage), assumed percentage animal diet of total food intake (zoopha), assumed percentage of nectar diet of total food intake (nectar), assumed percentage trophobiosis-based diet of total food intake (tropho), assumed percentage plant based diet of total food intake (plant), Weber´s length (wl), colony size ln transformed (cs), behavioral dominance (dom), number of queens per nest (nQ), number of nests per colony (nN), colony foundation type (cft)

moisture also have a lower ground temperature. Indeed, across Central Europe, Seifert (2017) found the highest average number of species in warm grassland with a good soil drainage (see also Dekoninck, Koninck, Baugnée, and Maelfait (2007)) and fewer ant species in more humid meadows or pastures.

Among the three study regions, the grassland plots in Schorfheide had the lowest mean soil moisture. However, overall species richness was relatively low in this region and decreased strongly with increasing soil moisture. Pastures in the Schorfheide were never grazed by sheep, which was where high ant species richness was found in the Alb and Hainich. Recently, Grevé et al. (2018) showed that forest plots at the Schorfheide are rather dry and species-rich, which implies a potentially large regional species pool. This suggests that a potential increase of ant species richness in grassland plots could be achieved by a change in the grassland management, shifting from cattle to sheep pastures.

### 4.2 | Effects of land use on functional trait space and ant community compositions

The functional trait space of ant communities decreased with increasing land-use intensity. At high land-use intensities, 14 of 31 species were absent and most others, such as *Formica* species, occurred only occasionally. The most common species on high-intensity plots were *L. niger*, *M. rubra*, and *M. scabriondis* which are widespread, very common in temperate grasslands, and known to be rather unaffected by grassland management (Dauber & Wolters, 2004, 2005; Grill et al., 2008; Seifert, 2017). Species disappearing first under increasing land-use intensity are open habitat specialists like *Tapinoma erraticum* and *T. subboreale* or the three species of the *Lasius paralienus*-complex: *L. alienus*, *L. paralienus*, and *L. psammophilus*, which require warm habitats with reduced plant cover such as nutrient-poor grasslands or sheep pastures (Seifert, 2007, 2017). Species communities in grasslands managed at high intensities, lacked species forming large and polydomous colonies or foraging higher up in the vegetation. Especially the meadow ant *Formica pratensis*, a key species in temperate European grasslands appears to be highly vulnerable. This species forms large, polydomous nests and is found primarily in grasslands with at least some woody plants (Seifert, 2007). High land-use intensities, and in particular a high mowing frequency, diminish the required structural and plant diversity in grasslands for such species and additionally lead to the destruction of nests.

Ant species living in intensively used grasslands must be disturbance-resistant, euryoecious and able to tolerate large climatic variations as the ground temperature increases, and soil humidity declines rapidly after mowing (Seifert & Pannier 2007). Beside *L. niger*, different *Myrmica* species can tolerate these climatic variations. Species of this genus can often tolerate dry and wet conditions and are dietary generalists (Radchenko & Elmes, 2010; Seifert, 2017). *Myrmica* species showed the highest tolerance to mowing, as these species build nests with a rather small nest mound and a larger part of the nest being underground (Radchenko & Elmes, 2010), making them less affected by mowing. However, in contrast to other genera like *Formica* and *Lasius*, *Myrmica* species are rather similar in shape and lifestyle, which results in a low functional trait space.

## 5 | CONCLUSIONS

To our knowledge, this is the first study analyzing the effect of land use in grasslands from low to high intensity, covering a large number of grassland plots and disentangling the effect of different management types (mowing, grazing and fertilization). Increasing land-use intensity reduced the number of ant species and the number of (aboveground) nests. In addition, it led to a reduced functional diversity and caused species community homogenization. Therefore, we can show a similar response of ants to higher land-use intensities as shown for multiple other groups such as plants, herbivores, secondary and tertiary consumers, and as such, all parts of the trophic pyramid of the grassland ecosystem (Gossner et al., 2016). To preserve species-rich grassland ant communities, we highly recommend reducing grassland management intensity, especially the number of mowing events per year. A transformation of nutrient-rich meadows with a low plant species richness and high soil moisture toward a nutrient-poor pasture with a higher diversity of plant species would be beneficial for ant species. Particularly low management intensities, as provided by sheep grazing, are a suitable method to increase habitat heterogeneity and maintain and fulfill the demands of specialized open habitat ant species.

### ACKNOWLEDGMENTS

We thank the farmers and landowners for providing their grasslands. We thank Markus Fischer, Valentin Klaus, Jens Nieschulze, and Ernst-Detlef Schulze for providing data which helped to facilitate this study. We thank the managers of the three Exploratories, Kirsten Reichel-Jung, Swen Renner, Katrin Lorenzen, Sonja Gockel, Kerstin Wiesner, and Martin Gorke for their work in maintaining the plot and project infrastructure; Christiane Fischer and Simone Pfeiffer for giving support through the central office; Michael Owonibi for managing the central database; and Markus Fischer, Eduard Linsenmair, Dominik Hessenmöller, Jens Nieschulze, Daniel Prati, Ingo Schöning, François Buscot, Ernst-Detlef Schulze, Wolfgang W. Weisser, and the late Elisabeth Kalko for their role in setting up the Biodiversity Exploratories project. We thank Markus Fischer for the Scientific Writing Workshop. We thank the two unknown reviewers for their helpful comments on the manuscript, and we thank the project DEAL for the payment of the article publication charge. The work has been funded by the German Research Foundation (DFG) Priority Program 1374 "Infrastructure-Biodiversity-Exploratories" (DFG- Ref no. FE631/7-1). MEG has been funded by the Federal Ministry of Education and Research (BMBF), "Qualitätsoffensive Lehrerbildung," support code 01JA160. Fieldwork permits were issued by the responsible state environmental office of Baden-Württemberg, Thüringen, and Brandenburg (according to § 72BbgNatSchG).

### CONFLICT OF INTEREST

None declared.

### AUTHOR CONTRIBUTIONS

HF conceived the study. LH did the field wk. LH and MEG identified the ant species. DS and VB provided data and expertise. LH, MG, and HF analyzed the data and wrote the first version of the manuscript. All auths helped to improve the manuscript

## DATA ACCESSIBILITY

This work is based on data elaborated by several projects of the Biodiversity Exploratories program (DFG Priority Program 1374). Part of the data used are available on the Biodiversity Exploratories Information System (http://doi.org/10.17616/R32P9Q) at https://www.bexis.uni-jena.de/PublicData/PublicData.aspx (IDs: 23986, 1000). However, to give data owners and collectors time to perform their analysis the data and publication policy of the Biodiversity Exploratories include by default an embargo period of three years from the end of data collection/data assembly which is valid for the remaining data (IDs: 19809). These datasets will be made publicly available at the same data repository.

## ORCID

*Michael E. Grevé* https://orcid.org/0000-0003-2782-6577

*Heike Feldhaar* https://orcid.org/0000-0001-6797-5126

## REFERENCES

Allan, E., Bossdorf, O., Dormann, C. F., Prati, D., Gossner, M. M., Tscharntke, T., ... Fischer, M. (2014). Interannual variation in land-use intensity enhances grassland multidiversity. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 308–313. https://doi.org/10.1073/pnas.1312213111

Arnan, X., Cerdá, X., & Retana, J. (2017). Relationships among taxonomic, functional, and phylogenetic ant diversity across the biogeographic regions of Europe. *Ecography*, *40*, 448–457. https://doi.org/10.1111/ecog.01938

Bartón, K. (2016). MuMIn: Multi-Model Inference. R package version 1.15.6. https://CRAN.R-project.org/package=MuMIn

Bestelmeyer, B. T., & Wiens, J. A. (2001). Ant biodiversity in semiarid landscape moisaics: The consequence of grazing vs. natural heterogenity. *Ecological Applications*, *11*, 1123–1140.

Birkhofer, K., Smith, H. G., Weisser, W. W., Wolters, V., & Gossner, M. M. (2015). Land-use effects on the functional distinctness of arthropod communities. *Ecography*, *38*, 889–900. https://doi.org/10.1111/ecog.01141

Blüthgen, N., Dormann, C. F., Prati, D., Klaus, V. H., Kleinebecker, T., Hölzel, N., ... Weisser, W. W. (2012). A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. *Basic and Applied Ecology*, *13*, 207–220. https://doi.org/10.1016/j.baae.2012.04.001

Blüthgen, N., & Feldhaar, H. (2010). Food and shelter: How resources influence ant ecology. In L. Lach, C. L. Parr, & K. L. Abbott (Eds.), *Ant ecology* (pp. 115–136). New York, NY: Oxford University Press.

Blüthgen, N., Simons, N. K., Jung, K., Prati, D., Renner, S. C., Boch, S., ... Gossner, M. M. (2016). Land use imperils plant and animal community stability through changes in asynchrony rather than diversity. *Nature Communications*, *7*, 10697.

Boomsma, J. J., & Van Loon, A. J. (1982). Structure and diversity of ant communities in successive coastal dune valleys. *Journal of Animal Ecology*, *51*, 957–974. https://doi.org/10.2307/4016

Boulton, A. M., Davies, K. F., & Ward, P. S. (2005). Species richness, abundance, and composition of ground-dwelling ants in Northern California grasslands: Role of plants, soil, and grazing. *Environmental Entomology*, *34*, 96–104. https://doi.org/10.1603/0046-225X-34.1.96

Bromham, L., Cardillo, M., Bennett, A. F., & Elgar, M. A. (1999). Effects of stock grazing on the ground invertebrate fauna of woodland remnants. *Austral Ecology*, *24*, 199–207. https://doi.org/10.1046/j.1442-9993.1999.00963.x

Chisté, M. N., Mody, K., Gossner, M. M., Simons, N. K., Köhler, G., Weisser, W. W., & Blüthgen, N. (2016). Losers, winners, and opportunists: How grassland land-use intensity affects orthopteran communities. *Ecosphere*, *7*, e01545.

Chytrý, M., Dražil, T., Hájek, M., Kalníková, V., Preislerová, Z., Šibík, J., ... Vymazalová, M. (2015). The most species-rich plant communities in the Czech Republic and Slovakia (with new world records). *Preslia*, *87*, 217–278.

Czechowski, W., Radchenko, A., Czechowska, W., & Vepsäläinen, K. (2012). The ants of Poland with reference to the myrmecofauna of Europe. In W. Czechowski, A. Radchenko, W. Czechowska, & K. Vepsäläinen (Eds.), *Fauna Poloniae (New Series)*. Warszawa, Poland: Natura Optima dux Foundation.

Dahms, H., Wellstein, C., Wolters, V., & Dauber, J. (2005). Effects of management practices on ant species richness and community composition in grasslands (Hymenoptera: Formicidae). *Myrmecologische, Nachrichten*, 9–16.

Dauber, J., Rommeler, A., & Wolters, V. (2006). The ant *Lasius flavus* alters the viable seed bank in pastures. *European Journal of Soil Biology*, *42*, S157–S163.

Dauber, J., & Wolters, V. (2004). Edge effects on ant community structure and species richness in an agricultural landscape. *Biodiversity and Conservation*, *13*, 901–915.

Dauber, J., & Wolters, V. (2005). Colonization of temperate grassland by ants. *Basic and Applied Ecology*, *6*, 83–91. https://doi.org/10.1016/j.baae.2004.09.011

Dean, W. R. J., Milton, S. J., & Klotz, S. (1997). The role of ant nest-mounds in maintaining small-scale patchiness in dry grasslands in Central Germany. *Biodiversity and Conservation*, *6*, 1293–1307.

Dekoninck, W., De Koninck, H., Baugnée, J. Y., & Maelfait, J. P. (2007). Ant biodiversity conservation in Belgian calcareous grasslands: Active management is vital. *Belgian Journal of Zoology*, *137*, 137–146.

Del Toro, I., Ribbons, R. R., & Pelini, S. L. (2012). The little things that run the world revisited: A review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). *Myrmecological News*, *17*, 133–146.

Dennis, P., Skartveit, J., McCracken, D. I., Pakeman, R. J., Beaton, K., Kunaver, A., & Evans, D. M. (2008). The effects of livestock grazing on foliar arthropods associated with bird diet in upland grasslands of Scotland. *Journal of Applied Ecology*, *45*, 279–287. https://doi.org/10.1111/j.1365-2664.2007.01378.x

Diaz, M. (1991). Spatial patterns of granivorous ant nest abundance and nest site selection in agricultural landscapes of Central Spain. *Insectes Sociaux*, *38*, 351–363. https://doi.org/10.1007/BF01241871

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., ... Weisser, W. W. (2010). Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. *Basic and Applied Ecology*, *11*, 473–485. https://doi.org/10.1016/j.baae.2010.07.009

Flynn, D. F. B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B. T., Lin, B. B., ... DeClerck, F. (2009). Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, *12*, 22–33. https://doi.org/10.1111/j.1461-0248.2008.01255.x

Folgarait, P. (1998). Ant biodiversity to ecosystem functioning: A review. *Biodiversity and Conservation*, *7*, 1121–1244.

Gossner, M. M., Lewinsohn, T. M., Kahl, T., Grassein, F., Boch, S., Prati, D., ... Allan, E. (2016). Land-use intensification causes multitrophic homogenization of grassland communities. *Nature*, *540*, 266–269. https://doi.org/10.1038/nature20575

Gossner, M. M., Weisser, W. W., & Meyer, S. T. (2014). Invertebrate herbivory decreases along a gradient of increasing land-use intensity in German grasslands. *Basic and Applied Ecology*, *15*, 347–352. https://doi.org/10.1016/j.baae.2014.03.003

Grevé, M. E., Hager, J., Weisser, W. W., Schall, P., Gossner, M. M., & Feldhaar, H. (2018). Effect of forest management on temperate ant communities. *Ecosphere*, *9*, e02303.

Grill, A., Cleary, D. F. R., Stettmer, C., Bräu, M., & Settele, J. (2008). A mowing experiment to evaluate the influence of management on the activity of host ants of *Maculinea* butterflies. *Journal of Insect Conservation*, *12*, 617–627. https://doi.org/10.1007/s10841-007-9098-1

Haddad, N. M., Crutsinger, G. M., Gross, K., Haarstad, J., Knops, J. M. H., & Tilman, D. (2009). Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters*, *12*, 1029–1039. https://doi.org/10.1111/j.1461-0248.2009.01356.x

Haddad, N. M., Haarstad, J., & Tilman, D. (2000). The effects of long-term nitrogen loading on grassland insect communities. *Oecologia*, *124*, 73–84. https://doi.org/10.1007/s004420050026

Harpole, W. S., & Tilman, D. (2007). Grassland species loss resulting from reduced niche dimension. *Nature*, *446*, 791–793. https://doi.org/10.1038/nature05684

Hejcman, M., Hejcmanová, P., Pavlů, V., & Beneš, J. (2013). Origin and history of grasslands in central Europe - A review. *Grass and Forage Science*, *68*, 345–363. https://doi.org/10.1111/gfs.12066

Hendrickx, F., Maelfait, J. P., Van Wingerden, W., Schweiger, O., Speelmans, M., Aviron, S., … Bugter, R. (2007). How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *Journal of Applied Ecology*, *44*, 340–351. https://doi.org/10.1111/j.1365-2664.2006.01270.x

Hoffmann, B. D., & James, C. D. (2011). Using ants to manage sustainable grazing: Dynamics of ant faunas along sheep grazing gradients conform to four global patterns. *Austral Ecology*, *36*, 698–708. https://doi.org/10.1111/j.1442-9993.2010.02205.x

Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, *13*, 201–228. https://doi.org/10.1146/annurev.es.13.110182.001221

Hutchinson, K. J., & King, K. L. (1980). The effects of sheep stocking level on invertebrate abundance, biomass and energy utilization in a temperate, sown grassland. *The Journal of Applied Ecology*, *17*, 369. https://doi.org/10.2307/2402333

Kleijn, D., Kohler, F., Baldi, A., Batary, P., Concepcion, E., Clough, Y., … Verhulst, J. (2009). On the relationship between farmland biodiversity and land-use intensity in Europe. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 903–909. https://doi.org/10.1098/rspb.2008.1509

Korösi, Á., Szentirmai, I., Batáry, P., Kövér, S., Örvössy, N., & Peregovits, L. (2014). Effects of timing and frequency of mowing on the threatened scarce large blue butterfly - A fine-scale experiment. *Agriculture, Ecosystems and Environment*, *196*, 24–33. https://doi.org/10.1016/j.agee.2014.06.019

Laliberté, A. E., Legendre, P., Shipley, B., & Laliberté, M. E. (2014). FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. R package:0–12.

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*, 299–305. https://doi.org/10.1890/08-2244.1

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579.

Marini, L., Fontana, P., Scotton, M., & Klimek, S. (2007). Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. *Journal of Applied Ecology*, *45*, 361–370. https://doi.org/10.1111/j.1365-2664.2007.01402.x

Nemec, K. T. (2014). Tallgrass prairie ants: Their species composition, ecological roles, and response to management. *Journal of Insect Conservation*, *18*, 509–521. https://doi.org/10.1007/s10841-014-9656-2

Nickel, H., & Hildebrandt, J. (2003). Auchenorrhyncha communities as indicators of disturbance in grasslands (Insecta, Hemiptera) - A case study from the Elbe flood plains (northern Germany). *Agriculture, Ecosystems and Environment*, *98*, 183–199. https://doi.org/10.1016/S0167-8809(03)00080-X

Noordijk, J., Schaffers, A. P., Heijerman, T., Boer, P., Gleichman, M., & Sýkora, K. V. (2010). Effects of vegetation management by mowing on ground-dwelling arthropods. *Ecological Engineering*, *36*, 740–750. https://doi.org/10.1016/j.ecoleng.2010.01.003

Oksanen, J., Blanchet, F., Kindt, R., Legendre, P., & O'Hara, R. (2016). Vegan: community ecology package.

Parr, C. L., Dunn, R. R., Sanders, N. J., Weiser, M. D., Photakis, M., Bishop, T. R., … Gibb, H. (2017). GlobalAnts : A new database on the geography of ant traits (Hymenoptera: Formicidae). *Insect Conservation and Diversity*, *10*, 5–20.

Pech, P., Dolanský, J., Hrdlička, R., & Lepš, J. (2015). Differential response of communities of plants, snails, ants and spiders to long-term mowing in a small-scale experiment. *Community Ecology*, *16*, 115–124. https://doi.org/10.1556/168.2015.16.1.13

Penick, C. A., & Tschinkel, W. R. (2008). Thermoregulatory brood transport in the fire ant, *Solenopsis invicta*. *Insectes Sociaux*, *55*, 176–182. https://doi.org/10.1007/s00040-008-0987-4

Pérez-Sánchez, A. J., Zopf, D., Klimek, S., & Dauber, J. (2017). Differential responses of ant assemblages (Hymenoptera: Formicidae) to long-term grassland management in Central Germany. *Myrmecological News*, *25*, 13–23.

Pihlgren, A., Lenoir, L., & Dahms, H. (2010). Ant and plant species richness in relation to grazing, fertilisation and topography. *Journal for Nature Conservation*, *18*, 118–125. https://doi.org/10.1016/j.jnc.2009.06.002

R Development Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. 0:{ISBN} 3-900051-07-0.

Radchenko, A. G., & Elmes, G. W. (2010). *Myrmica ants (Hymenoptera: Formicidae) of the Old World*. Page Fauna Mundi. Warsaw, Poland: Natura Optima Dux Foundation.

Sanders, D., & van Veen, F. J. F. (2011). Ecosystem engineering and predation: The multi-trophic impact of two ant species. *Journal of Animal Ecology*, *80*, 569–576. https://doi.org/10.1111/j.1365-2656.2010.01796.x

Sanders, N. J., Lessard, J. P., Fitzpatrick, M. C., & Dunn, R. R. (2007). Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography*, *16*, 640–649. https://doi.org/10.1111/j.1466-8238.2007.00316.x

Scohier, A., & Dumont, B. (2012). How do sheep affect plant communities and arthropod populations in temperate grasslands? *Animal*, *6*(7), 1129–1138.

Seifert, B. (2007). *Die Ameisen Mittel- und Nordeuropas*. Tauer: Lutra.

Seifert, B. (2017). The ecology of Central European non-arboreal ants – 37 years of a broad-spectrum analysis under permanent taxonomic control. *Soil Organisms*, *89*, 1–67.

Seifert, B., & Galkowski, C. (2016). The Westpalaearctic *Lasius paralienus* complex (Hymenoptera: Formicidae) contains three species. *Zootaxa*, *4132*, 44–58.

Seifert, B., & Pannier, L. (2007). A method for standardised description of soil temperatures in terrestrial ecosystems. *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, *78*, 151–182.

Seifert, B., & Schultz, R. (2009). A taxonomic revision of the *Formica rufibarbis* FABRICIUS, 1793 group (Hymenoptera: Formicidae). *Myrmecological News*, *12*, 255–272.

Simons, N. K., Gossner, M. M., Lewinsohn, T. M., Boch, S., Lange, M., Müller, J., … Weisser, W. W. (2014). Resource-mediated indirect effects of grassland management on arthropod diversity. *PLoS ONE*, *9*(9), e107033.

Simons, N. K., Gossner, M. M., Lewinsohn, T. M., Lange, M., Türke, M., & Weisser, W. W. (2015). Effects of land-use intensity on arthropod species abundance distributions in grasslands. *Journal of Animal Ecology*, *84*, 143–154. https://doi.org/10.1111/1365-2656.12278

Simons, N. K., Lewinsohn, T., Blüthgen, N., Buscot, F., Boch, S., Daniel, R., … Weisser, W. W. (2017). Contrasting effects of grassland management modes on species-abundance distributions of multiple groups. *Agriculture, Ecosystems and Environment*, *237*, 143–153. https://doi.org/10.1016/j.agee.2016.12.022

Socher, S. A., Prati, D., Boch, S., Müller, J., Baumbach, H., Gockel, S., … Fischer, M. (2013). Interacting effects of fertilization, mowing and grazing on plant species diversity of 1500 grasslands in Germany differ between regions. *Basic and Applied Ecology*, *14*, 126–136. https://doi.org/10.1016/j.baae.2012.12.003

Socher, S. A., Prati, D., Boch, S., Müller, J., Klaus, V. H., Hölzel, N., & Fischer, M. (2012). Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. *Journal of Ecology*, *100*, 1391–1399. https://doi.org/10.1111/j.1365-2745.2012.02020.x

Statistisches Bundesamt. (2016). Statistische Jahrbuch 2016.

Stewart, G. B., & Pullin, A. S. (2008). The relative importance of grazing stock type and grazing intensity for conservation of mesotrophic 'old meadow' pasture. *Journal for Nature Conservation*, *16*, 175–185. https://doi.org/10.1016/j.jnc.2008.09.005

Thorbek, P., & Bilde, T. (2004). Reduced numbers of generalist arthropod predators after crop management. *Journal of Applied Ecology*, *41*, 526–538. https://doi.org/10.1111/j.0021-8901.2004.00913.x

Whitford, W. G., Van Zee, J., Nash, M. S., Smith, W. E., & Herrick, J. E. (1999). Ants as indicators of exposure to environmental stressors in North American desert grasslands. *Environmental Monitoring and Assessment*, *54*, 143–171.

Wills, B. D., & Landis, D. A. (2018). The role of ants in north temperate grasslands: A review. *Oecologia*, *186*, 323–338. https://doi.org/10.1007/s00442-017-4007-0

## SUPPORTING INFORMATION

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

**How to cite this article:** Heuss L, Grevé ME, Schäfer D, Busch V, Feldhaar H. Direct and indirect effects of land-use intensification on ant communities in temperate grasslands. *Ecol Evol*. 2019;9:4013–4024. https://doi.org/10.1002/ece3.5030

## Supporting information Appendix S1

# Direct and indirect effects of land-use intensification on ant communities in temperate grasslands

Lisa Heuss [1+], Michael E. Grevé [1+*], Deborah Schäfer[2], Verena Busch[3], Heike Feldhaar[1]

[1] Animal Population Ecology, Animal Ecology I, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany

[2] University of Bern, Institute of Plant Sciences, Altenbergrain 21, 3013 Bern, Switzerland

[3] Münster University, Institute for Landscape Ecology, Heisenbergstr. 2, 48149 Münster, Germany

[+] Authors contributed equally

* Corresponding author: Michael.greve@uni-bayreuth.de

Detailed description of the three study areas

The biosphere reserve Schwäbische Alb is located in the low mountain ranges of south-west Germany (48°43'N 9°37'E; 6-7 °C mean annual temperature, 700-1000 mm mean annual rainfall, elevation of 460-860 m a.s.l., and a spatial extent of 420 km$^2$). The national park of Hainch-Dün and its surrounding areas is located in central Germany (51°20'N 124 10°41'E, 6.5-8°C, 500-800 mm, 285–550 m a.s.l., 1300 km$^2$). The biosphere reserve Schorfheide-Chorin is situated in the lowlands of north-eastern Germany in a young glacial landscape with many wetlands (53°02'N 13°83'E, 8-8.5 °C, 500-600 mm, 3-140 m a.s.l., 1300 km$^2$). The study areas have a latitudinal distance of around 600 km between Alb and Schorfheide

Detailed description of pitfall trap sampling

Three pitfalls were placed on each side of the plot at 12.5 m, 25 m, and 37.5 m from the corner. As pitfalls, plastic cups (Ø = 70 mm) were placed in the soil with the opening at surface level and filled with a solution of water, salt, and soap (200 g salt, 1 ml soap per liter water). Pitfalls were collected on the third day after installation.

Detailed description of baiting

Four bait stations were placed on each side at 7,5 m, 17,5 m, 32,5 m and 42,5 m from the corners. As baiting station we used petri dishes (Ø = 90 mm) with a round filter paper and placed five baits made from an artificial diet (based on whey protein, caseinate, egg powder, sucrose, agar, and water, Table S1) on each filter paper that contained different protein to carbohydrate ratios (1:1, 1:2.5, 1:5, 1:7.5 and 1:10; protein:carbohydrate) to attract all ants feeding on different food sources. Baits were comprised of whey and casein protein as protein source and sucrose and carbohydrate source dissolved in water and gelled with agar to produce homogenous cubes of approximately 1 cm$^3$. We counted all ants at these baiting stations 30 minutes and 60 minutes after placing them in the field.

Table S1. Artificial diet used for bait stations

| Proportion P:C | Whey protein (g) | Caseinat (g) | Egg powder (g) | Succrose (g) | Vitamines (g) | Benzoat (g) | Agar (g) | Water (ml) |
|---|---|---|---|---|---|---|---|---|
| 1:1 | 33.5 | 30.52 | 11 | 60.0 | 2 | 1 | 8 | 600 |
| 1:2.5 | 17.82 | 16.24 | 11 | 85.71 | 2 | 1 | 8 | 600 |
| 1:5 | 9.11 | 8.3 | 11 | 100.0 | 2 | 1 | 8 | 600 |
| 1:7.5 | 5.52 | 5.03 | 11 | 105.88 | 2 | 1 | 8 | 600 |
| 1:10 | 3.57 | 3.25 | 11 | 109.09 | 2 | 1 | 8 | 600 |

## Detailed description of SEMs

To analyze all direct and indirect effects of land-use components and environmental variables, which were found to be affecting ant species richness, we used structural equation modeling. First for all sampled plots (n=96) and second for only grazed plots (n=61) to analyze the effects of different livestock types separately. The region was used as random effect. The structure of each linear model within the SEM is: LME (response variable ~ all possible predictor variables added up by +, region as random effect)

Structure of the first SEM over all 96 plots:

SEM1= (

lme (Number of ant species ~ Mowing intensity + Fertilisation intensity + Grazing intensity + Soil moisture + Number of vascular plants + Mean vegetation height (cm) + Cover of litter (%) + Cover of shrubs (%), random = ~ 1 | Region),

lme (Number of vascular plants ~ Mowing intensity + Fertilisation intensity + Grazing intensity + Soil moisture + Cover of litter (%) + Cover of shrubs (%), random = ~ 1 | Region),

lme (Mean vegetation height (cm) ~ Mowing intensity + Fertilisation intensity + Grazing intensity + Soil moisture + Number of vascular plants + Cover of litter (%) + Cover of shrubs (%), random = ~ 1 | Region),

lme (Cover of litter (%) ~ Mowing intensity + Fertilisation intensity + Grazing intensity + Soil moisture + Number of vascular plants + Mean vegetation height (cm) + Cover of shrubs (%), random = ~ 1 | Region),
lme (Soil moisture ~ Mowing intensity + Fertilisation intensity + Grazing intensity +Number of vascular plants + Mean vegetation height (cm)+ Cover of litter (%)+ Cover of shrubs (%), random = ~ 1 | Region),
lme (Cover of shrubs (%) ~ Mowing intensity + Fertilisation intensity + Grazing intensity + Soil moisture, random = ~ 1 | Region))

Structure of the second SEM including only pasture- and mown pasture-plots.

SEM2 = (
lme (Number of ant species ~ Soil moisture + Livestock type + Mowing intensity + Fertilisation intensity + Cover of shrubs (%) + Grazing intensity + pH, random = ~ 1 | Region),
lme (Soil moisture ~ Livestock type + Mowing intensity + Fertilisation intensity + Cover of shrubs (%)+ Grazing intensity, random = ~ 1 | Region),
lme (Cover of shrubs (%)~ Soil moisture + Livestock type + Mowing intensity + Fertilisation intensity + Grazing intensity, random = ~ 1 | Region))

Table S2. Ant species found in Alb, Hanich and Schorfheide with the trait values used for the calculation of $FD_{LH}$. Trait information marked with * are taken from Seifert (2007, 2017) and marked with + are taken from Arnan et al. (2017). Abbreviations: strata forage, vertical strata where species is most likely to be found foraging (calculation and trait data see Table S3); zoopha, assumed percentage animal diet of total food intake; nectar, assumed percentage of nectar diet of total food intake; tropho, assumed percentage trophobiosis based diet of total food intake; plant, assumed percentage plant based diet of total food intake; WL = Weber's length; CS =colony size ln transformed; Dom = behavioral dominance, nQ = number of queens per nest, nN = number of nests per colony; CFT= colony foundation type. Data type and additional information on the traits are provided in Table S3.

| Species | Zoopha* | Nectar* | Tropho* | Plant part* | WL | Dom+* | CS+* | nQ+* | nN+* | CFT+* | Strata forage* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Campanotus ligniperda* | 0.27 | 0.05 | 0.63 | 0.05 | 3.83 | 1 | 7.82 | 0.5 | 0 | 1 | 1.99 |
| *Formica clara* | 0.6 | 0.05 | 0.29 | 0.06 | 2.26 | 1 | 8.52 | 0 | 0 | 1 | 0.93 |
| *Formica cunicularia* | 0.58 | 0.05 | 0.32 | 0.05 | 1.92 | 0 | 7.24 | 0 | 0.5 | 1 | 1.05 |
| *Formica fusca* | 0.5 | 0.1 | 0.35 | 0.05 | 1.95 | 0 | 9.1 | 1 | 1 | 1 | 1.08 |
| *Formica pratensis* | 0.14 | 0.02 | 0.55 | 0.02 | 2.71 | 1 | 11 | 1 | 1 | 0 | 0.97 |
| *Formica rufibarbis* | 0.59 | 0.05 | 0.31 | 0.05 | 2.27 | 0 | 6.91 | 0 | 0 | 1 | 1.04 |
| *Formica sanguinea* | 0.48 | 0.02 | 0.48 | 0.02 | 2.61 | 1 | 9.21 | 0.5 | 0 | 0.5 | 1.24 |
| *Lasius alienus* | 0.39 | 0.18 | 0.37 | 0.06 | 1.15 | 1 | 9.47 | 0 | 0 | 1 | 0.76 |
| *Lasius emarginatus* | 0.45 | 0.05 | 0.44 | 0.06 | 1.32 | 1 | 9.21 | 0 | 0 | 1 | 1.49 |
| *Lasius flavus* | 0.2 | 0 | 0.8 | 0 | 1.32 | 0 | 9.21 | 0.5 | 0 | 1 | -2.08 |
| *Lasius myops* | 0.2 | 0 | 0.8 | 0 | 0.85 | 0 | 8.52 | 0 | 0 | 1 | -2.08 |
| *Lasius niger* | 0.34 | 0.05 | 0.56 | 0.05 | 1.23 | 1 | 9.21 | 0 | 0 | 1 | 1.05 |
| *Lasius paralienus* | 0.39 | 0.19 | 0.36 | 0.06 | 1.11 | 1 | 9.21 | 0 | 0 | 1 | 0.76 |
| *Lasius psammophilus* | 0.35 | 0.14 | 0.5 | 0.01 | 1.0 | 0 | 10.43 | 0 | 1 | 1 | 0.53 |
| *Lasius umbratus* | 0.2 | 0 | 0.8 | 0 | 1.32 | 0 | 8.01 | 0.5 | 0 | 0 | -2.08 |
| *Myrmecina graminicola* | 0.99 | 0 | 0 | 0.01 | 0.95 | 0 | 4.61 | 0.5 | 0 | 0 | -1.36 |
| *Myrmica curvithorax* | 0.56 | 0.04 | 0.35 | 0.05 | 1.45 | 1 | 6.68 | 0 | 0 | 1 | 0.12 |
| *Myrmica gallienii* | 0.6 | 0.06 | 0.32 | 0.02 | 1.61 | 1 | 6.72 | 1 | 0 | 1 | 0.27 |
| *Myrmica lobicornis* | 0.72 | 0.04 | 0.2 | 0.04 | 1.53 | 0 | 5.63 | 0.5 | 0 | 0.5 | -0.26 |
| *Myrmica lonae* | 0.54 | 0.04 | 0.35 | 0.07 | 1.51 | 0 | 8.01 | 1 | 0 | 0.5 | 0.42 |
| *Myrmica rubra* | 0.48 | 0.05 | 0.37 | 0.1 | 1.51 | 0 | 8.01 | 1 | 1 | 0.5 | 0.66 |
| *Myrmica ruginodis* | 0.53 | 0.02 | 0.3 | 0.15 | 1.69 | 0 | 7.6 | 0.5 | 0 | 0.5 | 0.77 |
| *Myrmica rugulosa* | 0.64 | 0.08 | 0.25 | 0.03 | 1.45 | 0 | 7.6 | 1 | 1 | 0.5 | 0.13 |
| *Myrmica sabuleti* | 0.51 | 0.07 | 0.37 | 0.05 | 1.46 | 0 | 8.01 | 1 | 0 | 0.5 | 0.54 |
| *Myrmica scabrinodis* | 0.51 | 0.06 | 0.4 | 0.03 | 1.43 | 0 | 7.31 | 0.5 | 0 | 0.5 | 0.34 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Myrmica schenki* | 0.58 | 0.1 | 0.27 | 0.05 | 1.57 | 0 | 5.87 | 0.5 | 0 | 0.5 | 0.29 |
| *Myrmica specioides* | 0.51 | 0.05 | 0.41 | 0.03 | 1.37 | 0 | 7.31 | 1 | 0 | 0.5 | 0.22 |
| *Tapinoma erraticum* | 0.6 | 0.13 | 0.2 | 0.07 | 0.96 | 1 | 8.16 | 1 | 1 | 0 | 0.95 |
| *Tapinoma subboreale* | 0.6 | 0.13 | 0.2 | 0.07 | 0.88 | 0 | NA | 1 | 1 | 0 | 0.95 |
| *Temnothorax unifasciatum* | 0.8 | 0.15 | 0.05 | 0 | 0.72 | 0 | 5.78 | 0 | 0 | 1 | 0.8 |
| *Tetramorium caespitum* | 0.26 | 0.04 | 0.35 | 0.35 | 0.94 | 1 | 9.21 | 0 | 0 | 1 | -0.73 |

Table S3. Description of the different traits for the calculation of the life history trait analyses

| Trait | Data type | States |
|---|---|---|
| CS | Continuous | Mean colony size (log transformed) |
| WL | Continuous | Mean Weber´s length of worker (mm) |
| Zoo, Nectar, Troph, and Plant | Continuous | Assumed relative percentage of animal-, nectar-, trophobiosis- or plant-based diet. All summed to 100 %. Values are partly assumed by Seifert (2017), but also based on very detailed food analyses* |
| Dom | Binary | (0) Subordinate; (1) Dominant |
| nQ | Ordinal | (0) Monogyny; (0.5) Monogyny or polygyny; (1) Polygyny |
| nN | Ordinal | (0) Monodomy; (0.5) Monodomy or polydomy; (1) Polydomy |
| CFT | Ordinal | (0) Dependent colony founding; (0.5) Dependent and independent colony founding; (1) Independent colony founding |
| Strata.forage | Continuous | Positive values for higher probability of species found foraging above ground, negative values for foraging under the surface. |

Arnan, X., Cerdá, X., & Retana, J. (2017). Relationships among taxonomic, functional, and phylogenetic ant diversity across the biogeographic regions of Europe. *Ecography*, *40*(3), 448–457. https://doi.org/10.1111/ecog.01938

Seifert, B. (2017). The ecology of Central European non-arboreal ants – 37 years of a broad-spectrum analysis under permanent taxonomic control. *Soil Organisms*, *89*(April), 1–67.

Table S4. Foraging strata calculated as the sum of the probability of worker to forage in different vertical strata, where the value for each strata is multiplied by a specific factor, based on predictions of Seifert (2017). Deep soil - foraging in deeper soil at depths of at least 10 cm; top soil - foraging in top soil including the root layer of herbs in depths < 10 cm; moss litter-foraging in the moss and litter layer; free surf = foraging on free, above-ground surfaces except of those on herbs, shrubs and trees; herb = foraging in the herb layer; shrub tree =foraging on shrubs and trees, higher than 2 meters.

| Species | Strata.forage | deep soil (multiplied by -3) | top soil (multiplied by -2) | moss litter (multiplied by -1) | free surf (multiplied by 1) | herb (multiplied by 2) | shrub tree (multiplied by 3) |
|---|---|---|---|---|---|---|---|
| *Campanotus ligniperda* | 1.99 | 0.03 | 0.06 | 0.01 | 0.21 | 0.07 | 0.62 |
| *Formica clara* | 0.93 | 0.01 | 0.09 | 0.03 | 0.6 | 0.24 | 0.03 |
| *Formica cunicularia* | 1.05 | 0.01 | 0.11 | 0.02 | 0.45 | 0.36 | 0.05 |
| *Formica fusca* | 1.08 | 0.01 | 0.14 | 0.05 | 0.33 | 0.3 | 0.17 |
| *Formica pratensis* | 0.97 | 0.01 | 0.15 | 0.03 | 0.45 | 0.2 | 0.16 |
| *Formica rufibarbis* | 1.04 | 0.01 | 0.1 | 0.02 | 0.5 | 0.32 | 0.05 |
| *Formica sanguinea* | 1.24 | 0.01 | 0.1 | 0.02 | 0.53 | 0.09 | 0.26 |
| *Lasius alienus* | 0.76 | 0.03 | 0.22 | 0.04 | 0.31 | 0.18 | 0.22 |
| *Lasius emarginatus* | 1.49 | 0.01 | 0.07 | 0.03 | 0.4 | 0.18 | 0.31 |
| *Lasius flavus* | -2.08 | 0.16 | 0.78 | 0.05 | 0.01 | 0 | 0 |
| *Lasius myops* | -2.08 | 0.16 | 0.78 | 0.05 | 0.01 | 0 | 0 |
| *Lasius niger* | 1.05 | 0.02 | 0.16 | 0.04 | 0.34 | 0.19 | 0.25 |
| *Lasius paralienus* | 0.76 | 0.03 | 0.22 | 0.04 | 0.31 | 0.18 | 0.22 |
| *Lasius psammophilus* | 0.53 | 0.04 | 0.29 | 0.04 | 0.21 | 0.2 | 0.22 |
| *Lasius umbratus* | -2.08 | 0.16 | 0.78 | 0.05 | 0.01 | 0 | 0 |
| *Myrmecina graminicola* | -1.36 | 0.05 | 0.36 | 0.54 | 0.05 | 0 | 0 |
| *Myrmica curvithorax* | 0.12 | 0.02 | 0.25 | 0.1 | 0.48 | 0.15 | 0 |
| *Myrmica gallienii* | 0.27 | 0.01 | 0.18 | 0.23 | 0.32 | 0.21 | 0.05 |
| *Myrmica lobicornis* | -0.26 | 0.02 | 0.15 | 0.39 | 0.39 | 0.05 | 0 |
| *Myrmica lonae* | 0.42 | 0.02 | 0.1 | 0.26 | 0.37 | 0.18 | 0.07 |
| *Myrmica rubra* | 0.66 | 0.02 | 0.15 | 0.19 | 0.26 | 0.19 | 0.19 |
| *Myrmica ruginodis* | 0.77 | 0.01 | 0.15 | 0.18 | 0.26 | 0.18 | 0.22 |
| *Myrmica rugulosa* | 0.13 | 0.02 | 0.17 | 0.19 | 0.52 | 0.1 | 0 |
| *Myrmica sabuleti* | 0.54 | 0.02 | 0.1 | 0.21 | 0.4 | 0.2 | 0.07 |
| *Myrmica scabrinodis* | 0.34 | 0.02 | 0.18 | 0.15 | 0.42 | 0.2 | 0.03 |
| *Myrmica schencki* | 0.29 | 0.02 | 0.15 | 0.2 | 0.41 | 0.22 | 0 |
| *Myrmica specioides* | 0.22 | 0.02 | 0.18 | 0.18 | 0.42 | 0.2 | 0 |
| *Tapinoma erraticum* | 0.95 | 0 | 0.09 | 0.1 | 0.4 | 0.4 | 0.01 |
| *Tapinoma subboreale* | 0.95 | 0 | 0.09 | 0.1 | 0.4 | 0.4 | 0.01 |
| *Temnothorax unifasciatum* | 0.8 | 0 | 0.06 | 0.24 | 0.24 | 0.46 | 0 |
| *Tetramorium caespitum* | -0.73 | 0.17 | 0.34 | 0.03 | 0.43 | 0.03 | 0 |

Table S5. Path coefficients (and standard error (SE)) of all unidirectional relationships among variables of both piecewise SEM, shown in Fig. 2a and 2b. Significance: p< 0.05: *; p< 0.01: ** p< 0.001: ***

| Response | Predictor | Coefficient | SE | P-value | Significance |
|---|---|---|---|---|---|
| First SEM over all 96 plots: | | | | | |
| Number of ant species | Mowing intensity | -0.52 | 0.12 | < 0.001 | *** |
| | Soil moisture | -0.28 | 0.08 | 0.002 | ** |
| | Grazing intensity | -0.25 | 0.10 | 0.012 | * |
| | Vegetation height | -0.18 | 0.11 | 0.088 | |
| | Cover litter | 0.14 | 0.11 | 0.208 | |
| | Cover shrubs | 0.08 | 0.08 | 0.349 | |
| | Plant species richness | 0.10 | 0.11 | 0.390 | |
| | Fertilization intensity | -0.06 | 0.10 | 0.514 | |
| Plant species richness | Cover shrubs | 0.28 | 0.07 | < 0.001 | *** |
| | Fertilization intensity | -0.24 | 0.09 | 0.009 | ** |
| | Mowing intensity | -0.28 | 0.11 | 0.013 | * |
| | Soil moisture | -0.17 | 0.08 | 0.031 | * |
| | Grazing intensity | -0.17 | 0.09 | 0.063 | |
| | Cover litter | -0.03 | 0.10 | 0.736 | |
| Vegetation height | Plant species richness | -0.28 | 0.11 | 0.012 | * |
| | Soil moisture | -0.19 | 0.08 | 0.026 | * |
| | Mowing intensity | 0.26 | 0.12 | 0.031 | * |
| | Cover litter | 0.17 | 0.11 | 0.118 | |
| | Cover shrubs | -0.08 | 0.08 | 0.322 | |
| | Grazing intensity | 0.06 | 0.10 | 0.543 | |
| | Fertilization intensity | 0.00 | 0.10 | 0.994 | |
| Cover litter | Soil moisture | 0.19 | 0.08 | 0.021 | * |
| | Vegetation height | 0.16 | 0.10 | 0.117 | |
| | Fertilization intensity | -0.14 | 0.09 | 0.128 | |
| | Grazing intensity | -0.14 | 0.09 | 0.141 | |
| | Mowing intensity | 0.14 | 0.12 | 0.222 | |
| | Cover shrubs | 0.04 | 0.08 | 0.628 | |
| | Plant species richness | 0.01 | 0.11 | 0.900 | |
| Soil Moisture | Plant species richness | -0.36 | 0.14 | 0.011 | * |
| | Cover litter | 0.31 | 0.13 | 0.023 | * |
| | Vegetation height | -0.28 | 0.13 | 0.035 | * |
| | Fertilization intensity | -0.17 | 0.12 | 0.165 | |
| | Grazing intensity | -0.16 | 0.12 | 0.201 | |
| | Cover shrubs | 0.05 | 0.11 | 0.635 | |
| | Mowing intensity | 0.07 | 0.15 | 0.664 | |
| Cover shrubs | Mowing intensity | -0.40 | 0.15 | 0.007 | ** |
| | Grazing intensity | -0.27 | 0.12 | 0.036 | * |
| | Soil moisture | 0.02 | 0.11 | 0.818 | |
| | Fertilization intensity | 0.02 | 0.12 | 0.882 | |
| Second SEM including only pasture- and mown plots: | | | | | |
| Number of ant species | Sheep | 1.11 | 0.25 | < 0.001 | *** |
| | Soil moisture | -0.32 | 0.11 | 0.004 | ** |
| | Mowing intensity | -0.23 | 0.14 | 0.111 | |
| | Cover shrubs | 0.11 | 0.09 | 0.243 | |

| | | | | | |
|---|---|---|---|---|---|
| | Fertilization intensity | -0.10 | 0.12 | 0.372 | |
| | Grazing intensity | -0.09 | 0.11 | 0.427 | |
| | Cattle and horses | -0.03 | 0.58 | 0.961 | |
| Soil Moisture | Mowing intensity | 0.49 | 0.17 | 0.006 | ** |
| | Fertilization intensity | -0.35 | 0.14 | 0.019 | * |
| | Cattle and horses | 1.62 | 0.71 | 0.027 | * |
| | Sheep | 0.65 | 0.31 | 0.042 | * |
| | Cover shrubs | 0.08 | 0.12 | 0.536 | |
| | Grazing intensity | -0.01 | 0.15 | 0.969 | |
| Cover shrubs | Sheep | 0.38 | 0.32 | 0.245 | |
| | Mowing intensity | -0.22 | 0.19 | 0.249 | |
| | Grazing intensity | -0.17 | 0.16 | 0.304 | |
| | Soil moisture | 0.10 | 0.15 | 0.502 | |
| | Cattle and horses | -0.08 | 0.80 | 0.924 | |
| | Fertilization intensity | 0.00 | 0.17 | 0.985 | |

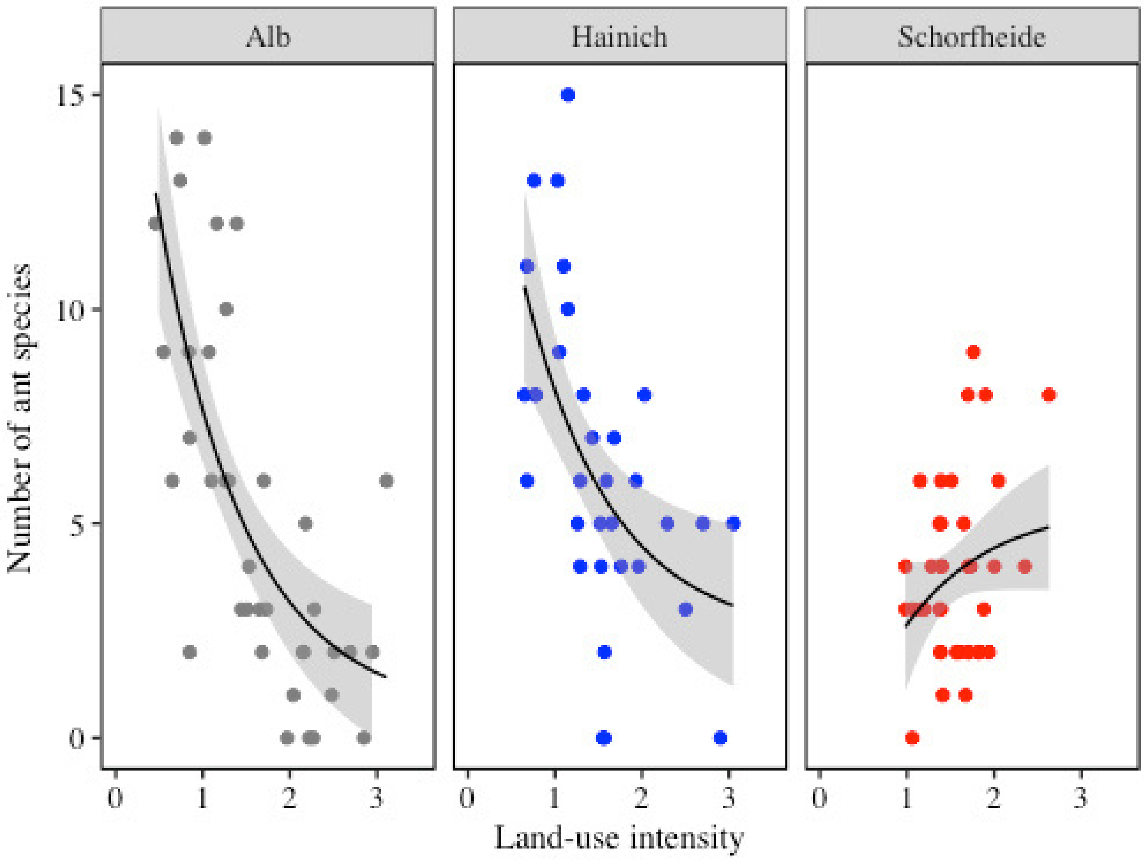

Fig. S1. Number of collected ant species along the land-use gradient for each of the three study regions.The black lines represent the exponential function of a GLM for species number and increasing land-use intensity. The grey areas represent the 95 % confidence intervals.

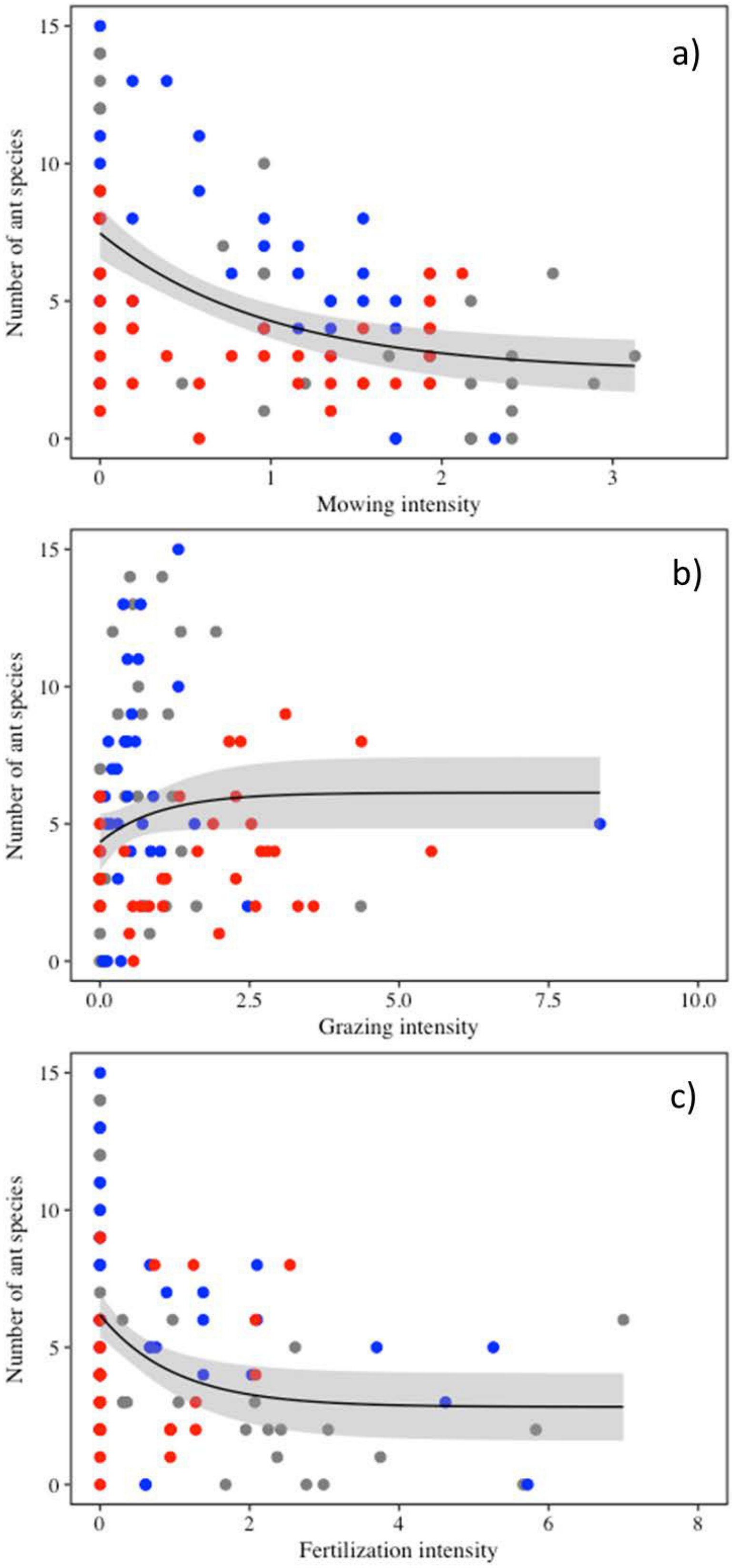

Fig. S2. Effects of mowing (a), grazing (b) and fertilization (c) intensity on number of ant species, grey for Alb, blue for Hainich and red for Schorfheide. The black line represents the exponential function of a GLM for species number and the land-use type. The grey areas represent the 95 % confidence intervals.

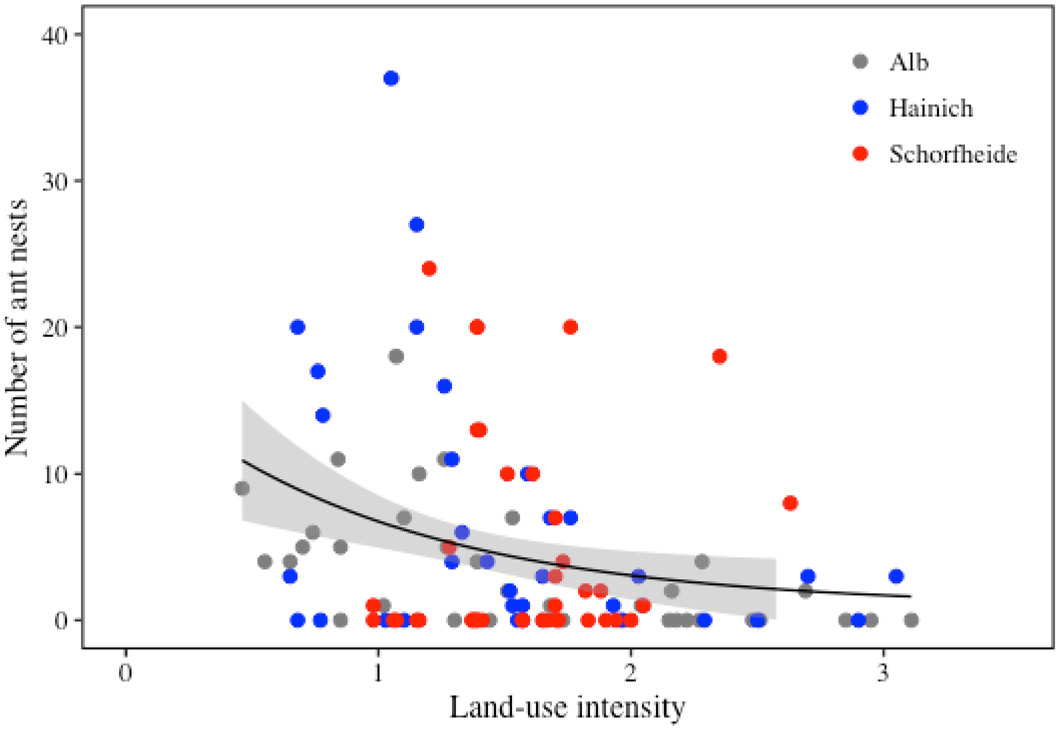

Fig. S3. The number of ant nests (in total 503 nests on 62 plots) in dependence of land-use intensity between the different regions over all plots (n= 110), The black line represents the exponential function of a GLM for number of ant nests and increasing land-use intensity. The grey area represents the 95 % confidence interval.

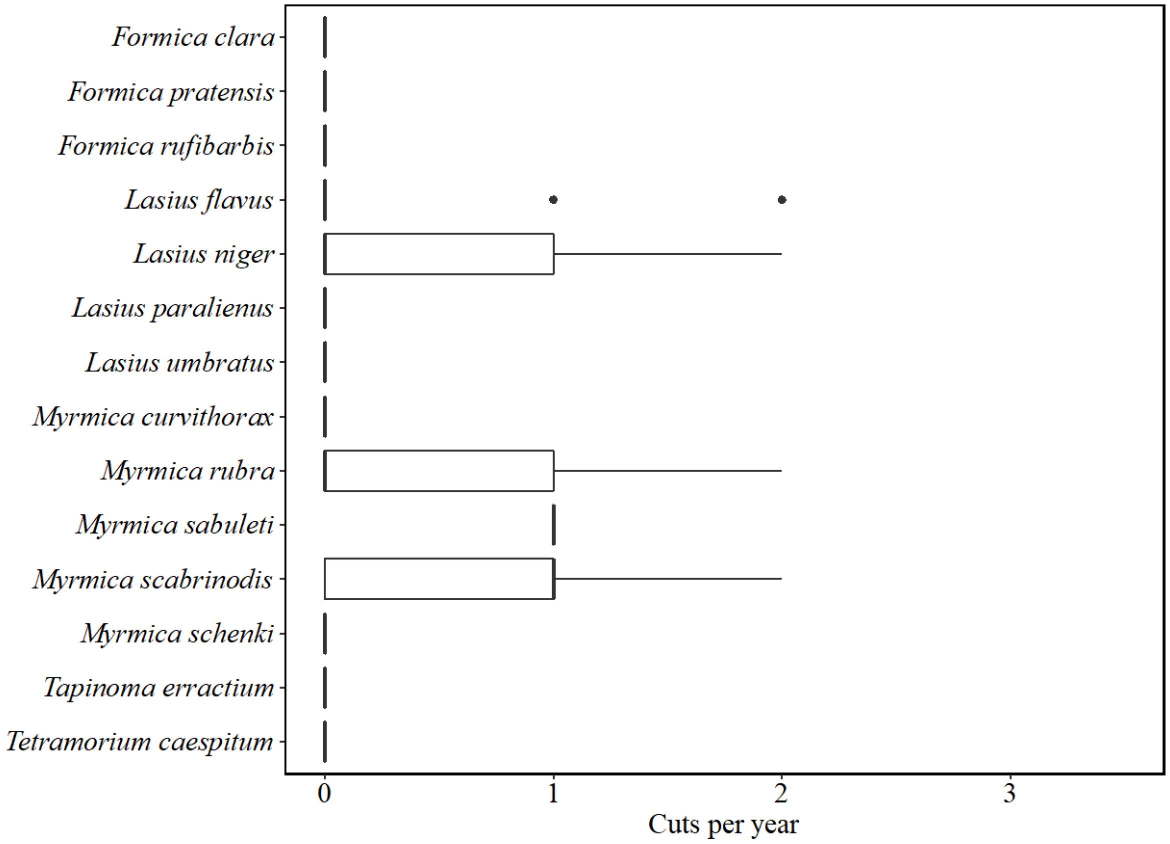

Fig. S4. Boxplot showing the occurrence of visually detected ant nests per species in the three regions along the number of cuts per year, alphabetically ordered. Black dots represent outliers.

**Manuscript 2:**

Authors: Michael E. Grevé, Jörg Hager, Wolfgang W. Weisser, Peter Schall, Martin M. Gossner, Heike Feldhaar

Title: Effect of forest management on temperate ant communities

Journal and status: *Ecosphere*, 9:e02303
DOI: 10.1002/ecs2.2303

Own contribution: concept and study design 10%, data acquisition 50%, analyses of samples 60%, data analyses and figures 60%, discussion of results 60 %, manuscript writing 60%

MMG, HF, MEG and WWW conceived the study. PS provided data, expertise and commented on the manuscript. JH and MEG conducted the morphological measurements and MEG identified the ant species. MEG, MMG and HF analyzed the data and wrote the first version of the manuscript. All authors helped to improve the manuscript. MEG is the corresponding author.

esa ECOSPHERE

# Effect of forest management on temperate ant communities

Michael E. Grevé,[1],† Jörg Hager,[1] Wolfgang W. Weisser,[2] Peter Schall,[3]
Martin M. Gossner,[4] and Heike Feldhaar[1]

[1] *Animal Population Ecology, Animal Ecology I, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Universitätsstrasse 30, 95440 Bayreuth Germany*
[2] *Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, Center for Food and Life Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising-Weihenstephan Germany*
[3] *Silviculture and Forest Ecology of the Temperate Zones, Faculty of Forest Sciences, University of Göttingen, D-37077 Göttingen Germany*
[4] *Forest Entomology, Swiss Federal Research Institute WSL, Birmensdorf CH-8903 Switzerland*

**Citation:** Grevé, M. E., J. Hager, W. W. Weisser, P. Schall, M. M. Gossner, and H. Feldhaar. 2018. Effect of forest management on temperate ant communities. Ecosphere 9(6):e02303. 10.1002/ecs2.2303

**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.

**Key words:** arthropods; canopy cover; functional diversity; land-use intensity; life-history; management strategies; microclimate; species traits.

**Received** 18 January 2018; revised 9 May 2018; accepted 14 May 2018. Corresponding Editor: Robert R. Parmenter.
**Copyright:** © 2018 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
† **E-mail:** Michael.greve@uni-bayreuth.de

## 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, Niemala et al. 1996) and thereby can increase species diversity (Niemala 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. 2018*b*):

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 ($\pi/4 \times$ eye length $\times$ 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 $\Delta\text{AICc} < 2$ 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.

| | Ant species richness | | Number of plots with ants for each management type | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Region | 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 (β = 1.18, standardized coefficient), the overall tree species richness (β = 0.15, standardized coefficient), and ant abundance (β = 1.07, standardized coefficient). Ant abundance was directly and negatively affected by spruce as dominant

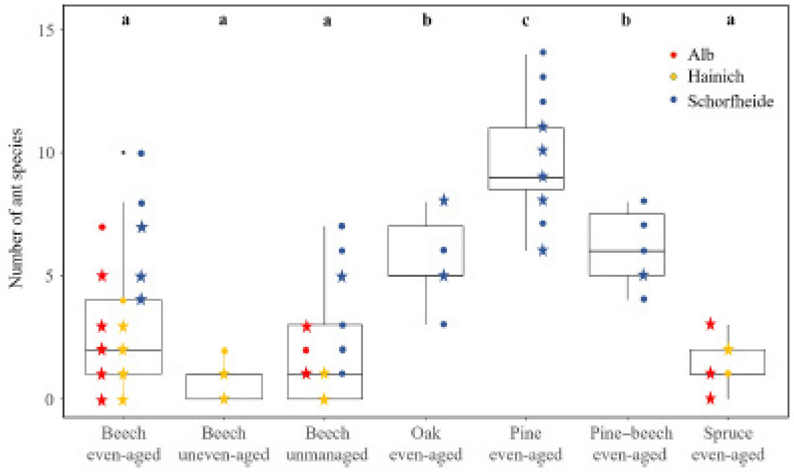

Fig. 1. Number of ant species found in the different management types ($n = 150$ plots). The forest types were defined by the dominant tree species (at least 50% ground cover area) and comprise pure stands as well as partly mixed stands of different broad-leaved and conifer species. Colored dots show 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.

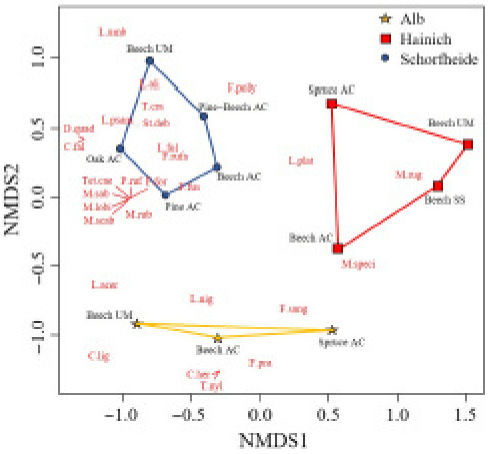

Fig. 2. Ordination plot illustrating the different ant species compositions between the different management types (EA, even-aged; UA, uneven-aged; UM, unmanaged) and the three different regions (different colors and shapes), based on based on species abundances. A non-metric multidimensional scaling (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 sanuguinea*; 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*.

tree species ($\beta = -1.12$, 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 ($\beta = 0.01$, 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 ($\beta = 0.02$, standardized coefficient). The proportion of oak and tree species richness affected arthropod biomass negatively which in turn increase ant abundance ($\beta = -0.05$, standardized coefficient).

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 $\Delta$AICc < 2 over all models in which the variable appears and the number of models which contained the respective variable is stated.

### *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; $\beta = 4.97$, standardized coefficient). In contrast, the proportion of pine reduced stand structural complexity which in turn positively affected $FD_{LH}$ ($\beta = -0.91$, standardized coefficient). Thus, open forests with a low structural complexity have the highest ant $FD_{LH}$. Besides, soil moisture had a positive effect ($\beta = 0.18$, 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

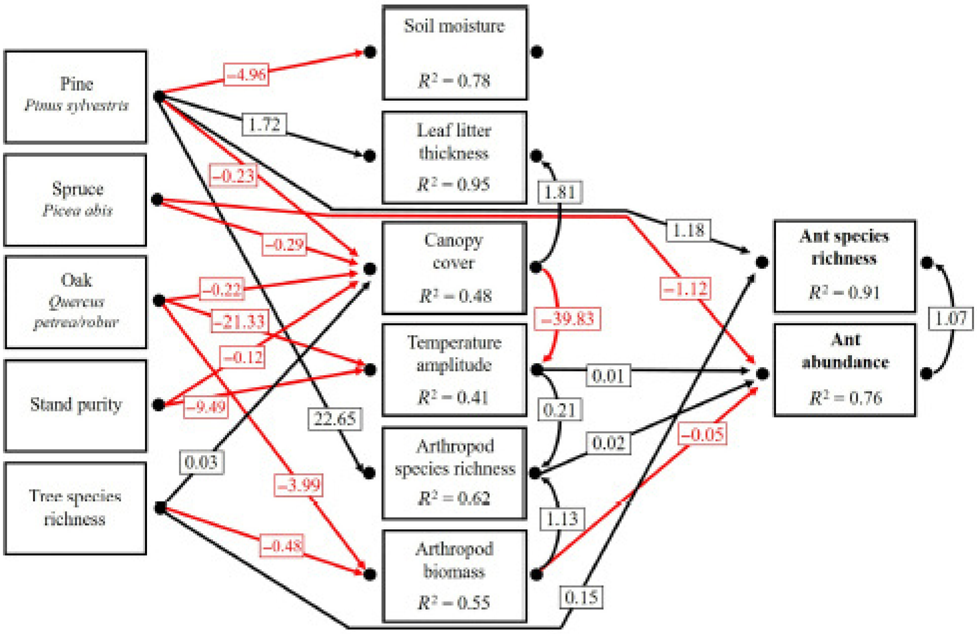

Fig. 3. Final piecewise structural equation model ($n$ = 141 plots) exploring the direct and indirect effects of forest management on ant species richness. Boxes represent measured variables. Arrows represent significant ($P < 0.05$), unidirectional relationships among variables. Black represents positive 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

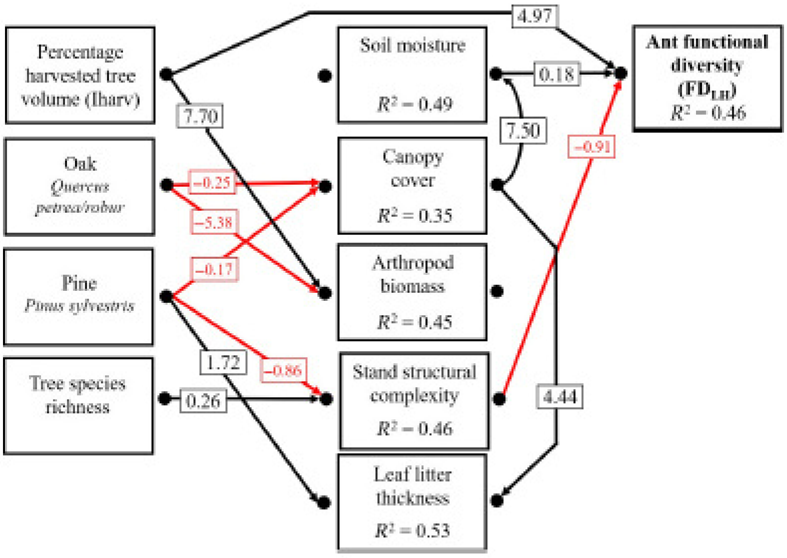

Fig. 4. Final piecewise structural equation model ($n$ = 45 plots) exploring the direct and indirect effects of forest management on the functional diversity based on life-history trait ($FD_{LH}$) at the Schorfheide. Boxes represent measured variables. Arrows represent significant ($P < 0.05$), unidirectional 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.

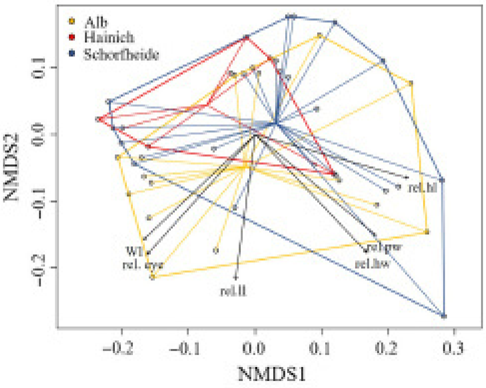

Fig. 5. Ordination plot showing the trait space covered by the ant species sampled the three different regions (different colors), based on morphological species traits. A non-metric multidimensional scaling (NMDS) was conducted based on a Gower distance matrix (stress = 0.05). The morphological traits 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.

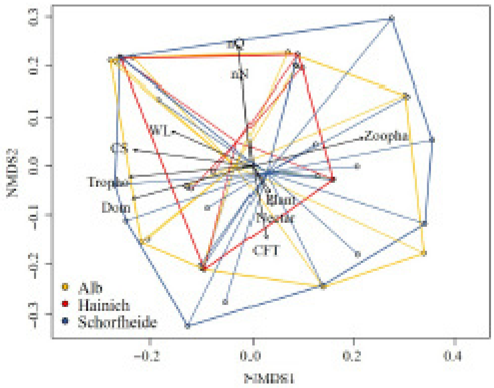

Fig. 6. Ordination plot showing the trait space covered by the ant species sampled the three different regions (different colors), based on life-history species traits. A non-metric multidimensional scaling (NMDS) was conducted based on a Gower distance matrix (Stress = 0.17). The life-history traits 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. 2018*a*), 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. 2018*a*).

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.

## ACKNOWLEDGMENTS

We are grateful to Markus Lange, Esther Pasalic, and Manfred Türke for field sampling; numerous student helpers for sorting the pitfall trap samples in the laboratory; and Boris Büche, Michael-Andreas Fritze, Thomas Wagner (all Coleoptera), Theo Blick (Araneae), Christoph Muster (Pseudoscorpiones, Opiliones), Roland Achtziger (Hemiptera), Günter Köhler (Dermaptera, Dictyoptera, Orthoptera), and Axel Gruppe (Mecoptera, Neuroptera) for species identification. We thank Christian Ammer, Jürgen Bauhus, Tiemo Kahl, Martin Ehbrecht, Ingo Schöning, and Thomas Nauss for providing data which helped to facilitate this study. We thank the managers of the three Exploratories, Konstans Wells, Sonja Gockel, Andreas Hemp, and all former managers for their work in maintaining the plot and project infrastructure; Simone Pfeiffer for giving support through the central office; Jens Nieschulze for managing the central database; and Markus Fischer, Eduard Linsenmair, Dominik Hessenmöller, Daniel Prati, Ingo Schöning, François Buscot, Ernst-Detlef Schulze, and the late Elisabeth Kalko for their role in setting up the Biodiversity Exploratories project. We also would like to thank the two unknown reviewers for their valuable comments. The work has been partly funded by the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories" (DFG-WE 3081/21-1 and FE 631/7-1); MMG obtained funding from SNF 310030E-173542/1); MEG was funded by the BMBF. Fieldwork permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg (according to § 72 BbgNatSchG). This publication was funded by the German Research Foundation (DFG) and the University of Bayreuth in the funding program Open Access Publishing. MMG, HF, MEG, and WWW conceived the study. PS provided data, expertise and commented on the manuscript. JH and MEG conducted the morphological measurements, and MEG identified the ant species. MEG, MMG, and HF analyzed the data and wrote the first version of the manuscript. All authors helped to improve the manuscript.

## Literature Cited

Allan, E., O. Bossdorf, C. F. Dormann, D. Prati, M. M. Gossner, and T. Tscharntke. 2014. Interannual variation in land-use intensity enhances grassland multidiversity. Proceedings of the National Academy of Sciences of the United States of America 111:308–313.

Arnan, X., X. Cerdá, and J. Retana. 2012. Distinctive life traits and distribution along environmental gradients of dominant and subordinate Mediterranean ant species. Oecologia 170:489–500.

Arnan, X., X. Cerdá, and J. Retana. 2017. Relationships among taxonomic, functional, and phylogenetic ant diversity across the biogeographic regions of Europe. Ecography 40:448–457.

Arnan, X., M. Gracia, L. Comas, and J. Retana. 2009. Forest management conditioning ground ant community structure and composition in temperate conifer forests in the Pyrenees Mountains. Forest Ecology and Management 258:51–59.

Bartón, K. 2016. MuMIn: multi-model inference. R package version 1.15.6. https://CRAN.R-project.org/package=MuMIn

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bernadou, A., R. Céréghino, H. Barcet, M. Combe, X. Espadaler, and V. Fourcassié. 2013. Physical and land-cover variables influence ant functional groups and species diversity along elevational gradients. Landscape Ecology 28:1387–1400.

Bihn, J. H., G. Gebauer, and R. Brandl. 2010. Loss of functional diversity of ant assemblages in secondary tropical forests. Ecology 91:782–792.

Bihn, J. H., M. Verhaagh, M. Brändle, and R. Brandl. 2008. Do secondary forests act as refuges for old growth forest animals? Recovery of ant diversity in the Atlantic forest of Brazil. Biological Conservation 141:733–743.

Blatrix, R., C. Lebas, C. Galkowski, P. Wegnez, R. Pimenta, and D. Morichon. 2016. Vegetation cover and elevation drive diversity and composition of ant communities (Hymenoptera: Formicidae) in a Mediterranean ecosystem. Myrmecological News 22:119–127.

Botta-Dukát, Z. 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. Journal of Vegetation Science 16:533–540.

Buse, J. 2012. "Ghosts of the past": Flightless saproxylic weevils (Coleoptera: Curculionidae) are relict species in ancient woodlands. Journal of Insect Conservation 16:93–102.

Cadotte, M. W., K. Carscadden, and N. Mirotchnick. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48:1079–1087.

Cerdá, X., J. Retana, and S. Cros. 1998. Critical thermal limits in Mediterranean ant species: trade-off between mortality risk and foraging performance. Functional Ecology 12:45–55.

Chaudhary, A., Z. Burivalova, L. P. Koh, and S. Hellweg. 2016. Impact of forest management on species richness: global meta-analysis and economic trade-offs. Scientific Reports 6:23954.

Commarmot, B., H. Bachofen, Y. Bundziak, A. Bürgi, Y. Shparyk, D. Sukhariuk, R. Viter, and A. Zingg. 2005. Structures of virgin and managed beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): a comparative study. Forest Snow and Landscape Research 79:45–56.

Commarmot, B., U.-B. Brändli, F. Hamor, and V. Lavnyy. 2013. Inventory of the largest primeval beech forest in Europe. A Swiss-Ukrainian scientific adventure. Swiss Federal Research Institute WSL, Birmensdorf, Switzerland; Ukrainian National

Forestry University, L'viv, Ukrain,; Carpathian Biosphere Reserve, Rakhiv, Ukraine.

Danks, H. V. 2007. The elements of seasonal adaptations in insects. Canadian Entomologist 139:1–44.

Del Toro, I. 2013. Diversity of Eastern North American ant communities along environmental gradients. PLoS ONE 8(7):e67973.

Del Toro, I., R. R. Silva, and A. M. Ellison. 2015. Predicted impacts of climatic change on ant functional diversity and distributions in eastern North American forests. Diversity and Distributions 21:781–791.

Dolek, M., A. Freese-Hager, H. Bussler, A. Floren, A. Liegl, and J. Schmidl. 2009. Ants on oaks: effects of forest structure on species composition. Journal of Insect Conservation 13:367–375.

Ehbrecht, M., P. Schall, C. Ammer, and D. Seidel. 2017. Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate. Agricultural and Forest Meteorology 242:1–9.

Ellison, A. 2015. Out of Oz: opportunities and challenges for using ants (Hymenoptera: Formicidae) as biological indicators in north-temperate cold biomes. Myrmecological News 17:105–119.

Ewers, R. M., et al. 2015. Logging cuts the functional importance of invertebrates in tropical rainforest. Nature Communications 6:6836.

Farji-Brener, A. G., G. Barrantes, and A. Ruggiero. 2004. Environmental rugosity, body size and access to food: a test of the size-grain hypothesis in tropical litter ants. Oikos 104:165–171.

Feener, D. H. J., J. R. B. Lighton, and G. Bartholomew. 1988. Curvilinear allometry, energetics and foraging ecology: a comparison of leaf-cutting ants and army ants. Functional Ecology 2:509–520.

Finch, O. D., and A. Szumelda. 2007. Introduction of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) into Western Europe: epigaeic arthropods in intermediate-aged pure stands in northwestern Germany. Forest Ecology and Management 242: 260–272.

Fischer, M., et al. 2010. Implementing large-scale and long-term functional biodiversity research: the Biodiversity Exploratories. Basic and Applied Ecology 11:473–485.

Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity and Conservation 7:1221–1244.

Fonseca, C. R., and G. Ganade. 2001. Species functional redundancy, random extinctions and the stability of ecosystems. Journal of Ecology 89:118–125.

Gibb, H., and C. L. Parr. 2013. Does structural complexity determine the morphology of assemblages? An experimental test on three continents. PLoS ONE 8:1–7.

Gibb, H., et al. 2017. Habitat disturbance selects against both small and large species across varying climates. Ecography https://doi.org/10.1111/ecog.03244

Gossner, M. M. 2009. Light intensity affects spatial distribution of Heteroptera in deciduous forests. European Journal of Entomology 106:241–252.

Goßner, M., K. Engel, and U. Ammer. 2006. Effects of selection felling and gap felling on forest arthropod communities: a case study in a spruce-beech stand of southern Bavaria. European Journal of Forest Research 125:345–360.

Gossner, M. M., T. Lachat, J. Brunet, G. Isacsson, C. Bouget, H. Brustel, R. Brandl, W. W. Weisser, and J. Müller. 2013. Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. Conservation Biology 27:605–614.

Gossner, M. M., et al. 2016. Land-use intensification causes multitrophic homogenization of grassland communities. Nature 540:266–269.

Gotelli, N. J., and A. M. Ellison. 2002. Biogeography at a regional scale: determinants of ant species density in New England bogs and forests. Ecology 83:1604–1609.

Gower, J. C. 1971. A general coefficient of similarity and some of its properties. Biometrics 27:857.

Graham, J. H., et al. 2009. Species richness, equitability, and abundance of ants in disturbed landscapes. Ecological Indicators 9:866–877.

Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24:699–711.

Hessenmöller, D., J. Nieschulze, N. Von Lüpke, and E. D. Schulze. 2011. Identification of forest management types from ground-based and remotely sensed variables and the effects of forest management on forest structure and composition. Forstarchiv 82:171–183.

Jäkel, A., and M. Roth. 2004. Conversion of single-layered Scots pine monocultures into close-to-nature mixed hardwood forests: effects on parasitoid wasps as pest antagonists. European Journal of Forest Research 123:203–212.

Johnson, R. A. 2002. Semi-claustral colony founding in the seed-harvester ant *Pogonomyrmex californicus*: a comparative analysis of colony founding strategies. Oecologia 132:60–67.

Juchheim, J., C. Ammer, P. Schall, and D. Seidel. 2017. Canopy space filling rather than conventional measures of structural diversity explains productivity of beech stands. Forest Ecology and Management 395:19–26.

Kahl, T., and J. Bauhus. 2014. An index of forest management intensity based on assessment of harvested tree volume, tree species composition and dead wood origin. Nature Conservation 7:15–27.

Kaspari, M. 1996. Testing resource-based models of patchiness in four Neotropical litter ant assemblages. Oikos 76:443–454.

Kipyatkov, V. E., and E. B. Lopatina. 2015. Comparative study of thermal reaction norms for development in ants. Entomological Science 18:174–192.

Klimes, P., C. Idigel, M. Rimandai, T. M. Fayle, M. Janda, G. D. Weiblen, and V. Novotny. 2012. Why are there more arboreal ant species in primary than in secondary tropical forests? Journal of Animal Ecology 81:1103–1112.

Laliberté, E., and P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305.

Laliberté, A. E., P. Legendre, B. Shipley, and M. E. Laliberté. 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package:0–12. https://cran.r-project.org/web/packages/FD/FD.pdf

Lange, M., et al. 2014. Effects of forest management on ground-dwelling beetles (Coleoptera; Carabidae, Staphylinidae) in Central Europe are mainly mediated by changes in forest structure. Forest Ecology and Management 329:166–176.

Lefcheck, J. S. 2016. piecewiseSEM: piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods in Ecology and Evolution 7:573–579.

Lessard, J. P., R. R. Dunn, and N. J. Sanders. 2009. Temperature-mediated coexistence in temperate forest ant communities. Insectes Sociaux 56:149–156.

Maeto, K., and S. Sato. 2004. Impacts of forestry on ant species richness and composition in warm-temperate forests of Japan. Forest Ecology and Management 187:213–223.

Müller, J., et al. 2015. Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. Ecography 38:499–509.

Newbold, T., et al. 2015. Global effects of land use on local terrestrial biodiversity. Nature 520:45–50.

Niemala, J., Y. Haila, P. Punttila, and J. Niemela. 1996. The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. Ecography 19:352–368.

Oksanen, J., F. Blanchet, R. Kindt, P. Legendre, and R. O'Hara. 2016. Vegan: community ecology package. https://github.com/vegandevs/vegan

Paillet, Y., et al. 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conservation Biology 24:101–112.

Palladini, J. D., M. G. Jones, N. J. Sanders, and E. S. Jules. 2007. The recovery of ant communities in regenerating temperate conifer forests. Forest Ecology and Management 242:619–624.

Parui, A. K., S. Chatterjee, and P. Basu. 2015. Habitat characteristics shaping ant species assemblages in a mixed deciduous forest in Eastern India. Journal of Tropical Ecology 31:267–280.

Petchey, O. L., and K. J. Gaston. 2006. Functional diversity: back to basics and looking forward. Ecology Letters 9:741–758.

Podani, J. 1999. Extending Gower's general coefficient of similarity to ordinal characters. Taxon 48:331–340.

Pohl, G. R., D. W. Langor, and J. R. Spence. 2007. Rove beetles and ground beetles (Coleoptera: Staphylinidae, Carabidae) as indicators of harvest and regeneration practices in western Canadian foothills forests. Biological Conservation 137:294–307.

Punttila, P., Y. Haila, J. Niemela, and T. Pajunen. 1994. Ant communities in fragments of old-growth taiga and managed surroundings. Annales Zoologici Fennici 31:131–144.

Punttila, P., Y. Haila, T. Pajunen, and H. Tukia. 1991. Colonisation of clearcut forests by ants in the southern Finnish taiga: a Quantitative Survey. Oikos 61:250–262.

R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Radchenko, A. G., and G. W. Elmes. 2010. *Myrmica* ants (Hymenoptera: Formicidae) of the Old World. Natura optima dux Foundation, Warszawa, Poland.

Retana, J., and X. Cerda. 2000. Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. Oecologia 123:436–444.

Rogers, L. E., W. T. Hinds, and R. L. Buschbom. 1976. A general weight vs. length relationship for insects. Annals of the Entomological Society of America 69:387–389.

Rüther, C., and H. Walentowski. 2008. Tree species composition and historic changes of the Central European oak/beech region. Pages 61–88 *in* A. Floren and J. Schmidl, editors. Canopy arthropod research in Europe. Bioform Entomology, Nuremberg, Germany.

Sanders, N. J., J. P. Lessard, M. C. Fitzpatrick, and R. R. Dunn. 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. Global Ecology and Biogeography 16:640–649.

Sarty, M., K. L. Abbott, and P. J. Lester. 2006. Habitat complexity facilitates coexistence in a tropical ant community. Oecologia 149:465–473.

Schall, P., and C. Ammer. 2013. How to quantify forest management intensity in Central European forests. European Journal of Forest Research 132:379–396.

Schall, P., et al. 2018*a*. The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of Applied Ecology 55:267–278.

Schall, P., E.-D. Schulze, M. Fischer, M. Ayasse, and C. Ammer. 2018*b*. Relations between forest management, stand structure and productivity across different types of Central European forests. Basic and Applied Ecology. *In press*. https://doi.org/10.1016/j.baae.2018.02.007

Seibold, S., C. Bässler, R. Brandl, B. Büche, A. Szallies, S. Thorn, M. D. Ulyshen, and J. Müller. 2016. Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. Journal of Applied Ecology 53:934–943.

Seifert, B. 2007. Die Ameisen Mittel- und Nordeuropas. Lutra Verlag-u. Vertriebsgesellschaft, Boxberg OT Klitten/Tauer, Germany.

Seifert, B. 2017. The ecology of Central European non-arboreal ants – 37 years of a broad-spectrum analysis under permanent taxonomic control. Soil Organisms 89:1–67.

Sformo, T., K. Walters, K. Jeannet, B. Wowk, G. M. Fahy, B. M. Barnes, and J. G. Duman. 2010. Deep supercooling, vitrification and limited survival to −100 C in the Alaskan beetle *Cucujus clavipes puniceus* (Coleoptera: Cucujidae) larvae. Journal of Experimental Biology 213:502–509.

Silva, R. R., and C. R. F. Brandão. 2014. Ecosystem-wide morphological structure of leaf-litter ant communities along a tropical latitudinal gradient. PLoS ONE 9:e93049.

Simons, N. K., W. W. Weisser, and M. M. Gossner. 2016. Multi-taxa approach shows consistent shifts in arthropod functional traits along grassland land-use intensity gradient. Ecology 97:754–764.

Solar, R. R. de. C., J. Barlow, A. N. Andersen, J. H. Schoereder, E. Berenguer, J. N. Ferreira, and T. A. Gardner. 2016. Biodiversity consequences of land-use change and forest disturbance in the Amazon: a multi-scale assessment using ant communities. Biological Conservation 197: 98–107.

Sorvari, J., and H. Hakkarainen. 2007. Wood ants are wood ants: Deforestation causes population declines in the polydomous wood ant *Formica aquilonia*. Ecological Entomology 32:707–711.

Sorvari, J., and H. Hakkarainen. 2009. Forest clear-cutting causes small workers in the polydomous wood ant *Formica aquilonia*. Annales Zoologici Fennici 46:431–438.

Tausan, I., J. Dauber, M. R. Trica, and B. Marko. 2017. Succession in ant communities (Hymenoptera: Formicidae) in deciduous forest clear-cuts – an Eastern European case study. European Journal of Entomology 114:92–100.

Topp, W. 2003. Phenotypic plasticity and development of cold-season insects (Coleoptera: Leiodidae) and their response to climatic change. European Journal of Entomology 100:233–243.

Underwood, E. C., and B. L. Fisher. 2006. The role of ants in conservation monitoring: if, when, and how. Biological Conservation 132:166–182.

Vasconcelos, H. L. 1999. Effects of forest disturbance on the structure of ground-foraging ant communities in central Amazonia. Biodiversity and Conservation 8:409–420.

Véle, A., J. Holuša, and J. Horák. 2016. Ant abundance increases with clearing size. Journal of Forest Research 21:110–114.

Vera, F. W. M. 2000. Grazing ecology and forest history. CABI Publishing, Wallingford, Oxon, UK.

Weiser, M. D., and M. Kaspari. 2006. Ecological morphospace of New World ants. Ecological Entomology 31:131–142.

Wiescher, P. T., J. M. C. Pearce-Duvet, and D. H. Feener. 2012. Assembling an ant community: Species functional traits reflect environmental filtering. Oecologia 169:1063–1074.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2303/full

# Ecosphere

# Effect of forest management on temperate ant communities

Michael E. Grevé, Jörg Hager, Wolfgang W. Weisser, Peter Schall, Martin M. Gossner and Heike Feldhaar

## Appendix S1

Table S1. List of ant species found in each region including the number of plots where they occurred and their abundance as the number of times (month x trap) a species was caught in pitfalls.

| Region | Species | No plots | Abundance |
|---|---|---|---|
| Alb | *Camponotus herculeanus* | 2 | 3 |
| | *Camponotus ligniperdus* | 1 | 1 |
| | *Formica (Serviformica) fusca* | 5 | 7 |
| | *Formica polyctena* * | 1 | 1 |
| | *Formica pratensis* | 5 | 6 |
| | *Formica rufa* * | 1 | 1 |
| | *Formica (Raptiformica) sanguinea* | 4 | 4 |
| | *Lasius niger* | 3 | 3 |
| | *Lasius platythorax* | 10 | 16 |
| | *Lasius psammophilus* | 1 | 1 |
| | *Leptothorax acervorum* | 2 | 2 |
| | *Myrmica rubra* | 7 | 20 |
| | *Myrmica ruginodis* | 40 | 172 |
| | *Temnothorax nylanderi* | 1 | 1 |
| Hainich | *Formica (Serviformica) fusca* | 1 | 2 |
| | *Formica polyctena* | 1 | 4 |
| | *Formica (Raptiformica) sanguinea* | 1 | 1 |
| | *Lasius platythorax* | 7 | 14 |
| | *Myrmica rubra* | 2 | 2 |
| | *Myrmica ruginodis* | 27 | 86 |
| | *Myrmica specioides* | 1 | 1 |
| Schorfheide | *Camponotus fallax* | 1 | 1 |
| | *Dolichoderus quadripunctatus* | 1 | 1 |
| | *Formica (Coptoformica) foreli* | 1 | 1 |
| | *Formica (Serviformica) fusca* | 21 | 45 |
| | *Formica polyctena* * | 36 | 140 |
| | *Formica rufa* * | 25 | 66 |
| | *Formica (Raptiformica) sanguinea* | 3 | 4 |
| | *Lasius alienus* | 3 | 3 |
| | *Lasius (Dendrolasius) fuliginosus* | 12 | 21 |
| | *Lasius niger* | 1 | 1 |
| | *Lasius platythorax* | 31 | 136 |
| | *Lasius psammophilus* | 10 | 13 |

Table S1. Continuation

| Region | Species | No plots | Abundance |
|---|---|---|---|
| Schorfheide | *Lasius (Chthonolasius) umbratus* | 1 | 1 |
| | *Leptothorax acervorum* | 3 | 4 |
| | *Myrmica lobicornis* | 10 | 20 |
| | *Myrmica rubra* | 31 | 87 |
| | *Myrmica ruginodis* | 48 | 341 |
| | *Myrmica sabuleti* | 5 | 8 |
| | *Myrmica scabrinodis* | 10 | 26 |
| | *Polyergus rufescens* | 1 | 1 |
| | *Stenamma debile* | 37 | 115 |
| | *Temnothorax crassispinus* | 46 | 178 |
| | *Tetramorium caespitum* | 3 | 3 |

* Species can produce fertile hybrids. Percentage of assumed hybrids was < 10 %

Table S2. Ant species found at the Schorfheide with the trait values used for the calculation of $FD_{LH}$. Trait information marked with $^{\#}$ are taken from Seifert (2007, 2017) and marked with $^{+}$ are taken from Arnan et al. (2017). Abbreviations: CS, colony size; WL, Weber´s length; Zoo, assumed percentage animal diet of total food intake; Nectar, assumed percentage of nectar diet of total food intake; Troph, assumed percentage trophobiosis based diet of total food intake; Plant, assumed percentage plant based diet of total food intake; Dom, behavioral dominance, nQ, number of queens per nest, nN, number of nests per colony; CFT, colony foundation type. Data type and additional information on the traits are provided in Table S3.

| Species | $^{\#}$CS | WL | $^{\#}$Zoo | $^{\#}$Nectar | $^{\#}$Troph | $^{\#}$Plant | $^{+\#}$Dom | $^{+\#}$nQ | $^{+\#}$nN | $^{+\#}$CFT |
|---|---|---|---|---|---|---|---|---|---|---|
| *Camponotus fallax* | 5.70 | 2.42 | 0.58 | 0.13 | 0.21 | 0.08 | 0 | 0 | 0 | 1 |
| *Formica (Serviformica) fusca* | 7.31 | 1.96 | 0.5 | 0.1 | 0.35 | 0.05 | 0 | 1 | 1 | 1 |
| *Formica polyctena* | 12.20 | 2.40 | 0.3 | 0.03 | 0.65 | 0.02 | 1 | 1 | 1 | 0 |
| *Formica rufa* | 11.00 | 2.54 | 0.3 | 0.03 | 0.65 | 0.02 | 1 | 1 | 1 | 0 |
| *Formica (Raptiformica) sanguinea ** | 8.52 | 2.57 | 0.48 | 0.02 | 0.48 | 0.02 | 1 | 0.5 | 0 | 0.5 |
| *Formica (Coptoformica) foreli ** | 10.13 | 1.63 | 0.4 | 0.02 | 0.56 | 0.02 | 1 | 1 | 1 | 1 |
| *Lasius (Dendrolasius) fuliginosus* | 10.31 | 1.51 | 0.25 | 0.07 | 0.64 | 0.04 | 1 | 0 | 0 | 0 |
| *Lasius niger* | 8.52 | 1.37 | 0.34 | 0.05 | 0.56 | 0.05 | 1 | 0 | 0 | 1 |
| *Lasius platythorax* | 8.52 | 1.22 | 0.34 | 0.05 | 0.56 | 0.05 | 1 | 0 | 0 | 1 |
| *Lasius (Chthonolasius) umbratus* | 9.21 | 1.33 | 0.2 | 0 | 0.8 | 0 | 1 | 0.5 | 0 | 0 |
| *Lasius alienus* | 8.52 | 1.06 | 0.39 | 0.18 | 0.37 | 0.06 | 1 | 0 | 0 | 1 |
| *Lasius psammophilus* | 8.52 | 1.17 | 0.35 | 0.14 | 0.5 | 0.01 | 0 | 0 | 1 | 1 |
| *Polyergus rufescens ** | 7.31 | 2.41 | 0.5 | 0.1 | 0.35 | 0.05 | 1 | 0 | 0 | 0 |
| *Leptothorax acervorum* | 5.19 | 1.02 | 0.87 | 0.02 | 0.07 | 0.04 | 0 | 1 | 0 | 0 |
| *Myrmica lobicornis* | 5.63 | 1.40 | 0.72 | 0.004 | 0.2 | 0.04 | 0 | 0.5 | 0 | 0.5 |
| *Myrmica rubra* | 7.38 | 1.47 | 0.48 | 0.05 | 0.37 | 0.1 | 0 | 1 | 1 | 0.5 |
| *Myrmica ruginodis* | 6.68 | 1.57 | 0.53 | 0.02 | 0.3 | 0.15 | 0 | 0.5 | 0 | 0.5 |
| *Myrmica sabuleti* | 6.48 | 1.43 | 0.51 | 0.07 | 0.37 | 0.05 | 0 | 1 | 0 | 0.5 |
| *Myrmica scabrinodis* | 6.40 | 1.41 | 0.51 | 0.06 | 0.4 | 0.03 | 0 | 0.5 | 0 | 0.5 |
| *Stenamma debile* | 4.03 | 0.99 | 0.95 | 0 | 0.02 | 0.03 | 0 | 1 | 1 | 0 |
| *Temnothorax crassispinus* | 4.38 | 0.77 | 0.95 | 0.02 | 0.03 | 0 | 0 | 0 | 0 | 0.5 |
| *Tetramorium caespitum* | 9.62 | 1.03 | 0.26 | 0.04 | 0.35 | 0.35 | 1 | 0 | 0 | 1 |
| *Dolichoderus quadripunctatus* | 5.70 | 1.1 | 0.61 | 0.13 | 0.13 | 0.13 | 0 | 0 | 1 | 0 |

Table S3. Description of the different traits for the calculation of the $FD_{LH}$

| Trait | Data type | States |
|---|---|---|
| CS | Continuous | Mean colony size (log transformed) |
| WL | Continuous | Mean Weber´s length of worker (mm) |
| Zoo, Nectar, Troph, and Plant | Continuous | Assumed relative percentage of animal-, nectar-, trophobiosis- or plant-based diet. All summed to 100 %. Values are partly assumed by Seifert (2017), but also based on very detailed food analyses* |
| Dom | Binary | (0) Subordinate; (1) Dominant |
| nQ | Ordinal | (0) Monogyny; (0.5) Monogyny or polygyny; (1) Polygyny |
| nN | Ordinal | (0) Monodomy; (0.5) Monodomy or polydomy; (1) Polydomy |
| CFT | Ordinal | (0) Dependent colony founding; (0.5) Dependent and independent colony founding; (1) Independent colony founding |

* detailed analyses are published in e.g. Wellenstein (1952, Adlung (1966) for *Formica rufa*, Horstmann (1970) for *F. polyctena.*

## LITERATURE CITED

Adlung, K. (1966) A critical evaluation of the European research on use of red wood ants (*Formica rufa* group) for the protection of forests against harmful insects. Zeitschrift für angewandte Entomologie 57:167–189.

Horstmann, K. (1970) Investigation on the food consumption of red wood ants (*Formica polyctena* Foerster) in an oak forest. Oecologia 5:138–157.

Wellenstein, G. (1952) Zur Ernährungsbiologie der Roten Waldameise. (*Formica rufa* L.). Zeitschrift für Pflanzenkrankheiten (Pflanzenpathologie) und Pflanzenschutz 59:430–451.

Seifert, B. (2007) Die Ameisen Mittel- und Nordeuropas. Lutra Verlag-u. Vertriebsgesellschaft, Boxberg OT Klitten/Tauer, Germany

Seifert, B. (2017) The ecology of Central European non-arboreal ants – 37 years of a broad-spectrum analysis under permanent taxonomic control. Soil Organisms, 89:1–67.

Table S4. Number of ant species found in the different management types and the number of plots where the particular number of ant species was found for each management type and region (based on n = 150 plots).

| Management type | Number ant species per plot | Alb | Hainich | Schorfheide |
|---|---|---|---|---|
| Beech even-aged | 0 | 5 | 7 | - |
| | 1 | 13 | 8 | - |
| | 2 | 7 | 2 | - |
| | 3 | 5 | 2 | - |
| | 4 | - | 4 | 2 |
| | 5 | 2 | - | 5 |
| | 7 | 1 | - | 4 |
| | 8 | - | - | 1 |
| | 10 | - | - | 1 |
| Beech uneven-aged | 0 | - | 6 | - |
| | 1 | - | 6 | - |
| | 2 | - | 1 | - |
| Beech unmanaged | 0 | - | 10 | - |
| | 1 | 2 | 3 | 1 |
| | 2 | 1 | - | 1 |
| | 3 | 2 | - | 1 |
| | 5 | - | - | 2 |
| | 6 | - | - | 1 |
| | 7 | - | - | 1 |
| Oak even-aged | 3 | - | - | 1 |
| | 5 | - | - | 3 |
| | 6 | - | - | 1 |
| | 8 | - | - | 2 |
| Pine even-aged | 6 | - | - | 2 |
| | 7 | - | - | 1 |
| | 8 | - | - | 1 |
| | 9 | - | - | 4 |
| | 10 | - | - | 2 |
| | 11 | - | - | 2 |
| | 12 | - | - | 1 |
| | 13 | - | - | 1 |

| | | | | |
|---|---|---|---|---|
| | 14 | - | - | 1 |
| Pine-beech even-aged | 4 | - | - | 1 |
| | 5 | - | - | 2 |
| | 6 | - | - | 1 |
| | 7 | - | - | 1 |
| | 8 | - | - | 2 |
| Spruce even-aged | 0 | 2 | - | - |
| | 1 | 8 | 1 | - |
| | 2 | - | 3 | - |
| | 3 | 2 | - | - |

Table S5. Result of the multi model averaging approach for $FD_M$. The relative importance values of each predictor variable are calculated as the sum of AICc weights over all models with ΔAICc< 2 in which the variable appears and the number of models which contained the precise variable is stated.

| Variable | Importance (%) | N containing models |
|---|---|---|
| *Leaf litter thickness* | 92 | 19 |
| *Deadwood volume* | 75 | 16 |
| *Dominant tree species* | 40 | 8 |
| *Tree species diversity* | 39 | 7 |
| *Arthropod biomass* | 30 | 7 |
| *Arthropod species richness* | 28 | 6 |
| *Tree species richness* | 24 | 5 |
| *Stand purity* | 8 | 2 |
| *Percentage harvested tree volume (Iharv)* | 7 | 2 |
| *Canopy cover* | 3 | 1 |
| *Temperature amplitude* | 3 | 1 |

Table S6. Result of the multi model averaging approach for ant species richness with region as fixed factor. The relative importance values of each predictor variable are calculated as the sum of AICc weights over all models with ΔAICc< 2 in which the variable appears and the number of models which contained the precise variable is stated.

| Variable | Importance (%) | N containing models |
|---|---|---|
| *Canopy cover* | 100 | 12 |
| *Arthropod biomass* | 100 | 12 |
| *Arthropod species richness* | 100 | 12 |
| *Dominant tree species* | 100 | 12 |
| *Region* | 100 | 12 |
| *Temperature amplitude* | 100 | 12 |
| *Tree species richness* | 100 | 12 |
| *Stand age* | 78 | 9 |
| *Stand purity* | 66 | 8 |
| *Percentage harvested tree volume (Iharv)* | 65 | 7 |
| *Stand structural complexity* | 46 | 5 |
| *Soil moisture* | 19 | 3 |
| *Tree species diversity* | 15 | 2 |

Table S7. Path coefficients of the significant unidirectional relationships among variables of Fig. S3. Due to the high complexity of Fig S3, the path coefficients are not included in the figure like it was done in Fig 2, 3 and Fig S5.

| Predictor | Response | Coefficient | SE | P-value |
|---|---|---|---|---|
| *Ant abundance* | *Ant species richness* | 1.05 | 9.36e-02 | >0.001 *** |
| *Pine* | *Ant species richness* | 1.34 | 4.16e-01 | 0.002 ** |
| *Tree species richness* | *Ant species richness* | 0.15 | 5.19e-02 | 0.006 ** |
| *Arthropod species richness* | *Ant abundance* | 0.02 | 4.36e-03 | >0.001 *** |
| *Spruce* | *Ant abundance* | -1.09 | 3.42e-01 | 0.002 ** |
| *Hainich (region)* | *Ant abundance* | -0.94 | 3.13e-01 | 0.003 ** |
| *Temperature amplitude* | *Ant abundance* | 0.01 | 4.39e-03 | 0.013 * |
| *Arthropod biomass* | *Ant abundance* | -0.05 | 2.32e-02 | 0.038 * |
| *Hainich (region)* | *Arthropod species richness* | 22.74 | 6.12e+00 | >0.001 *** |
| *Schorfheide (region)* | *Arthropod species richness* | 49.72 | 1.57e+01 | 0.002 ** |
| *Stand structural complexity* | *Arthropod species richness* | 5.65 | 1.94e+00 | 0.004 ** |
| *Arthropod biomass* | *Arthropod species richness* | 1.31 | 4.62e-01 | 0.005 ** |
| *Pine* | *Arthropod species richness* | 22.03 | 7.99e+00 | 0.007 ** |
| *Temperature amplitude* | *Arthropod species richness* | 0.21 | 8.82e-02 | 0.019 * |
| *Canopy cover* | *Arthropod species richness* | -24.48 | 1.09e+01 | 0.027 * |
| *Tree age* | *Arthropod species richness* | -0.09 | 4.43e-02 | 0.043 * |
| *Hainich (region)* | *Arthropod biomass* | -6.74 | 1.02e+00 | >0.001 *** |
| *Tree species richness* | *Arthropod biomass* | -0.47 | 1.94e-01 | 0.017 * |
| *Oak* | *Arthropod biomass* | -4.20 | 1.76e+00 | 0.019 * |
| *Canopy cover* | *Temperature amplitude* | -46.14 | 1.02e+01 | >0.001 *** |
| *Tree age* | *Temperature amplitude* | -0.11 | 4.34e-02 | 0.009 ** |
| *Leaf litter thickness* | *Temperature amplitude* | 5.17 | 2.02e+00 | 0.012 * |
| *Oak* | *Temperature amplitude* | -20.78 | 9.02e+00 | 0.023 * |
| *Schorfheide (region)* | *Temperature amplitude* | -29.32 | 1.42e+01 | 0.041 * |
| *Hainich (region)* | *Soil moisture* | -7.73 | 1.38e+00 | >0.001 *** |
| *Schorfheide (region)* | *Soil moisture* | -22.95 | 4.46e+00 | >0.001 *** |
| *Pine* | *Soil moisture* | -5.11 | 2.33e+00 | 0.03 * |
| *Spruce* | *Canopy cover* | -0.28 | 5.60e-02 | >0.001 *** |
| *Schorfheide (region)* | *Canopy cover* | -0.17 | 5.49e-02 | 0.002 ** |
| *Pine* | *Canopy cover* | -0.19 | 6.29e-02 | 0.003 ** |
| *Tree species richness* | *Canopy cover* | 0.03 | 9.14e-03 | 0.003 ** |
| *Stand purity* | *Canopy cover* | -0.12 | 4.25e-02 | 0.005 ** |
| *Oak* | *Canopy cover* | -0.20 | 8.26e-02 | 0.019 * |
| *Schorfheide (region)* | *Leaf litter thickness* | 6.28 | 4.01e-01 | >0.001 *** |
| *Pine* | *Leaf litter thickness* | 1.90 | 3.11e-01 | >0.001 *** |
| *Canopy cover* | *Leaf litter thickness* | 1.75 | 4.12e-01 | >0.001 *** |
| *Hainich (region)* | *Leaf litter thickness* | -0.69 | 2.20e-01 | 0.002 ** |
| *Tree age* | *Leaf litter thickness* | 0.00 | 1.83e-03 | 0.031 * |

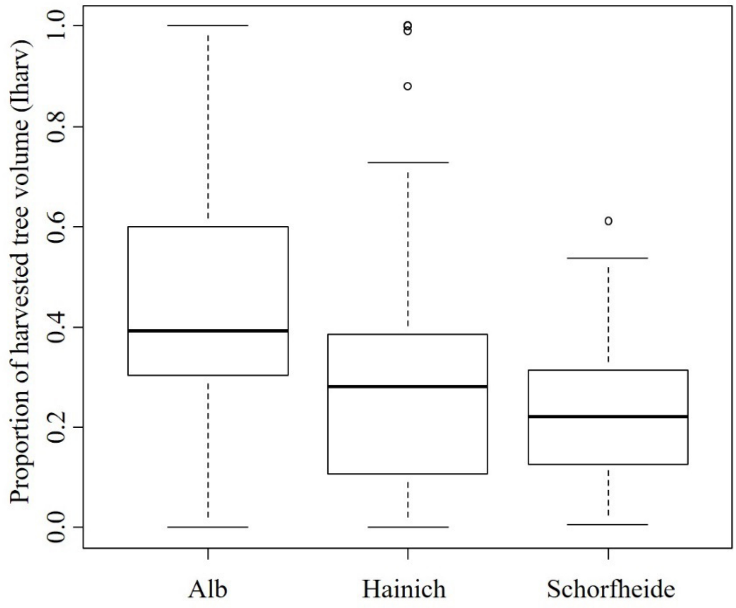

**Fig. S1.** Proportion of harvested tree volume (*Iharv*) between the different regions.

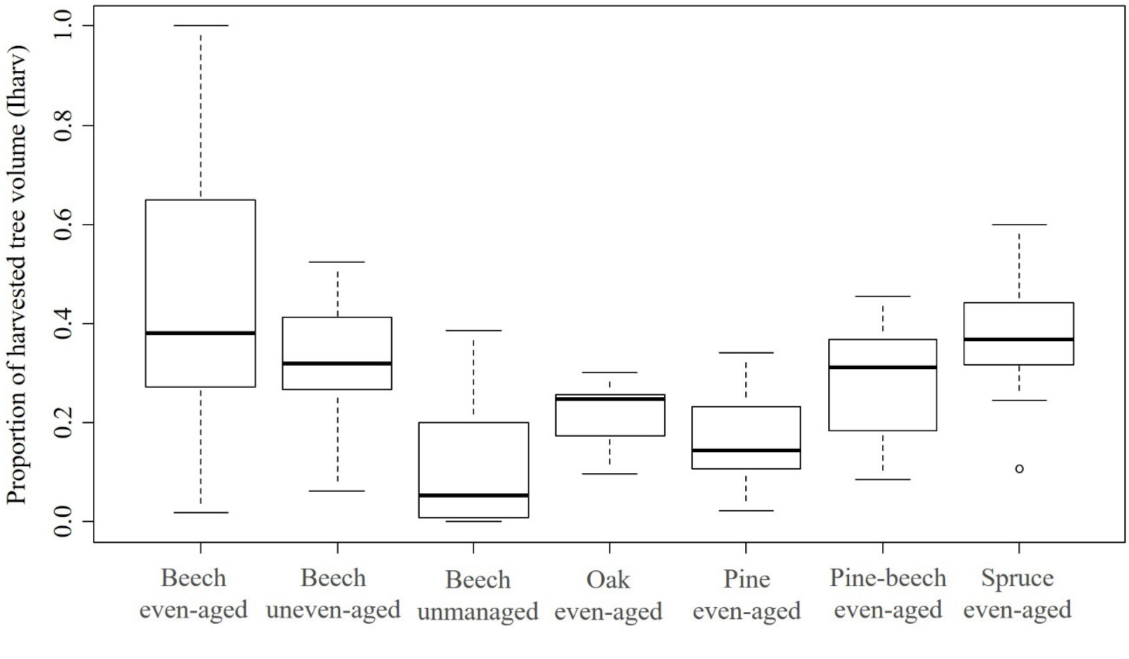

**Fig. S2.** Proportion of harvested tree volume (*Iharv*) between the different management types (based on n = 150 plots)

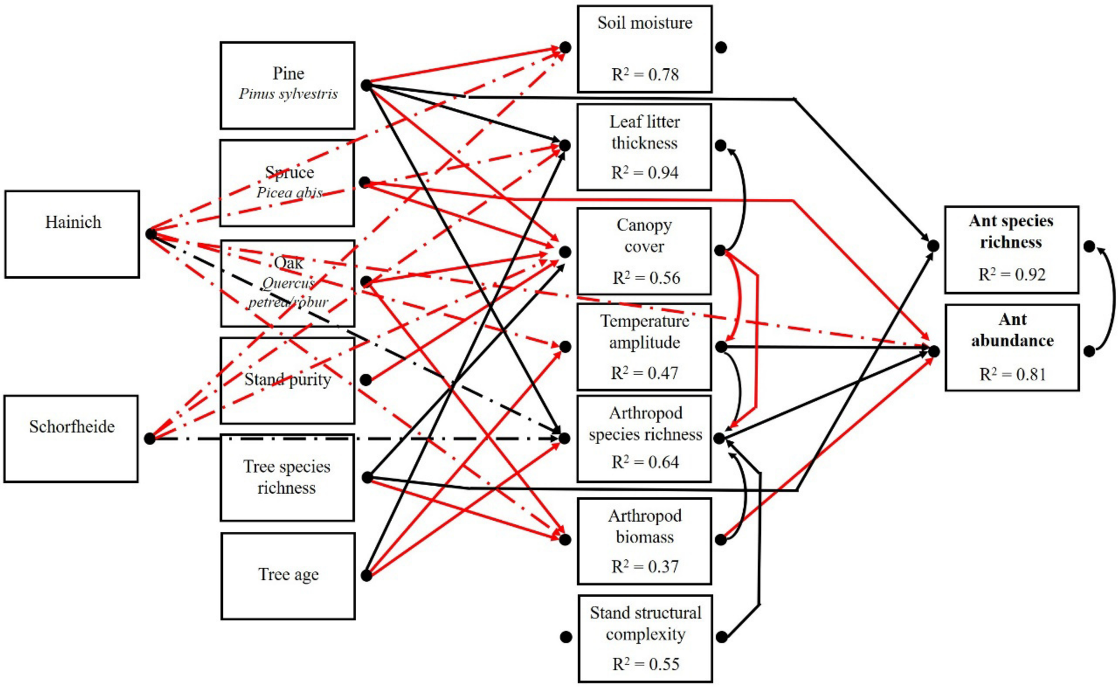

**Fig. S3**. Final piecewise structural equation model (based on n = 141 plots) exploring the direct and indirect effects of forest management on ant species richness with the region as fixed factor in the global model. Boxes represent measured variables. Arrows represent significant ($p < 0.05$), unidirectional relationships among variables. Black are positive and red are negative relationships. Dashed arrows are used to reduce the overlay. We report the path coefficients as standardized effect sizes in Table S7 to enhance the comprehensibility. $R^2$ values for component models are given in the boxes of their response variables.

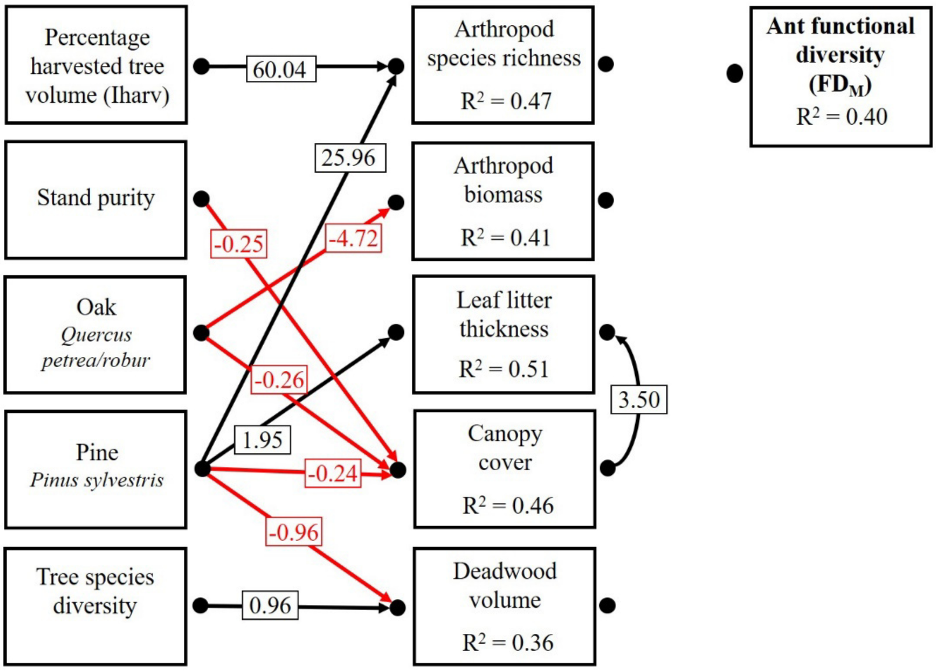

**Fig. S4**. Final piecewise structural equation model (based on n = 44 plots) exploring the direct and indirect effects of forest management on $FD_M$ at the Schorfheide. Boxes represent measured variables. Arrows represent significant ($p < 0.05$), unidirectional relationships among variables. Black are positive and red are negative relationships.

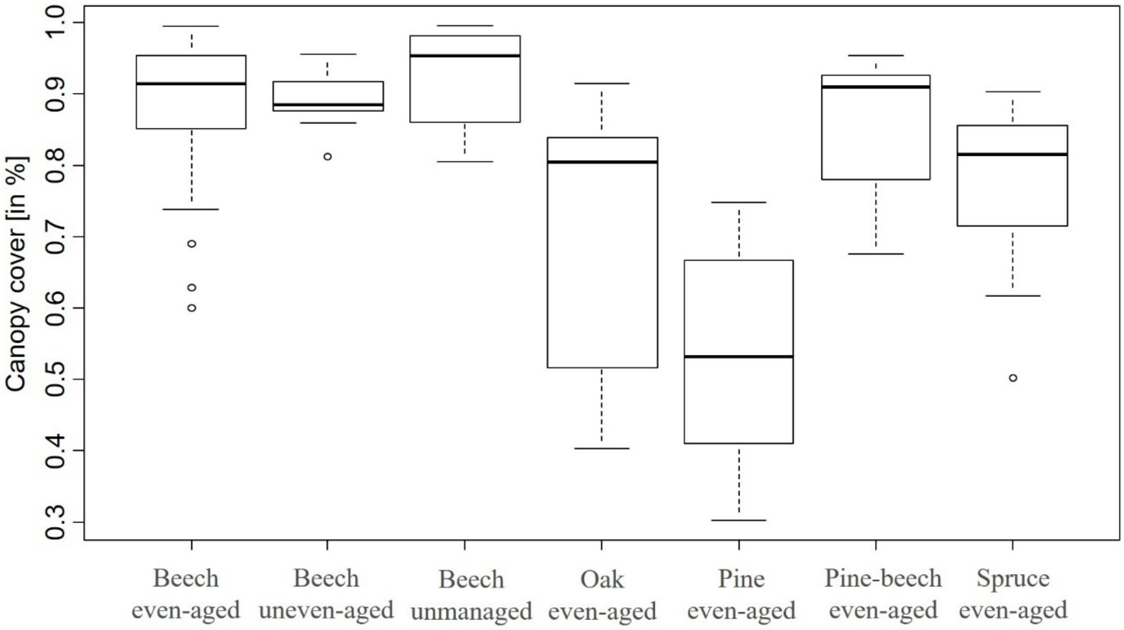

**Fig. S5.** Percentage of canopy cover of the different management types (based on n = 150 plots) assessed by airborne LiDAR in summer 2008 and 2009 during leaf-on condition.

**Manuscript 3:**

Authors: Michael E. Grevé, Sanja Bláha, Joseph Teuber, Melanie Rothmaier, Heike Feldhaar

Title: The effect of ground surface rugosity on ant running speed is species-specific rather than size dependent.

Journal and status: *Insectes Sociaux*. (2019). 66:355–364
https://doi.org/10.1007/s00040-019-00694-z

Own contribution: concept and study design 80%, data acquisition 20%, analyses of samples 20%, data analyses and figures 95%, discussion of results 80 %, manuscript writing 80%

MEG and HF conceived the study. SB; JT and MR performed the experiments. MEG and HF analyzed the data. MEG and HF wrote the manuscript. All authors helped to improve the manuscript. MEG is the corresponding author.

Insectes Sociaux (2019) 66:355–364
https://doi.org/10.1007/s00040-019-00694-z

**Insectes Sociaux**

RESEARCH ARTICLE

# The effect of ground surface rugosity on ant running speed is species-specific rather than size dependent

**M. E. Grevé**[1] · **S. Bláha**[1] · **J. Teuber**[1] · **M. Rothmaier**[1] · **H. Feldhaar**[1]

Received: 12 December 2018 / Revised: 7 February 2019 / Accepted: 1 March 2019 / Published online: 7 March 2019
© International Union for the Study of Social Insects (IUSSI) 2019

## Abstract

Foraging is one of the main reasons for ants to walk. Foraging speed is mainly dependent on morphological traits, but also on the surface structure. The size-grain hypothesis (SGH) suggests that (1) relative leg length should increase allometrically with body size, and (2) smaller, shorter legged species have an advantage with increasing habitat complexity in comparison to larger and longer legged species. In general, it is thought that leg length is a good predictor for running speed. We performed morphological analyses and running experiments with differently sized ant species along an artificial gradient of surface rugosity. We measured running speed, number of steps, body size and leg length to answer the question, if morphological traits can be used to predict the running speed of ants in complex habitats, as predicted by the SGH. We found that (1) leg length increased allometrically with body size, and that (2) the largest species were among the fastest and could sustain their speed with increasing surface rugosity. The smallest species with the relatively shortest legs were the fastest on the flattest surface, but their speed decreased rapidly with increasing rugosity. Leg length was not a good predictor for running speed. Similar-sized species responded idiosyncratically to high surface rugosity, which might be related to species-specific habitat preferences. Species-specific behavior or stride frequency influenced running speed strongly, which hampers precise predictions on their running speed, based on morphological traits exclusively.

**Keywords** Size-grain hypotheses · Formicidae · Locomotion · Body size · Leg length

## Introduction

Today, using life-history and morphological traits is a common approach to investigate ant species community compositions (Bihn et al. 2010; Gibb and Parr 2013; Silva and Brandão 2014; Gibb et al. 2015). Morphological traits of single species and trait compositions of species communities are for example often analyzed along environmental gradients (Arnan et al. 2014), between spatial scales (Yates et al. 2014) or differently structured habitats (Gibb and Parr 2010). For the latter, for instance, different habitat structures and complexities (e.g., desert vs rainforest, shrubland vs forests) can result in differently shaped species communities (Farji-Brener et al. 2004; Lassau and Hochuli 2004; Sarty et al. 2006; Schofield et al. 2016).

Differences in morphological traits among ant communities living in habitats of different complexity have been analyzed in the light of the size-grain hypotheses (SGH) by Kaspari and Weiser (1999). The SGH proposes that, as the size of a terrestrial, walking organism decreases, it perceives the landscape as more rugose. If the leg length and the body size determines an organism's ability to walk within a particular environment, larger species should have advantages in more planar and smaller in more complex environments (Kaspari and Weiser 1999; Farji-Brener et al. 2004). Thereby, large species with long legs can "flatten" their environment and reduce the costs of locomotion/running due to an increased stride length, which enables the ants to walk over interstices and obstacles. In contrast, smaller species can benefit from shorter legs by fitting through interstices between obstacles and reduced allocation costs in the construction of long legs. Hence, the SGH broadly predicts: (1) that across ant

---

**Electronic supplementary material** The online version of this article (https://doi.org/10.1007/s00040-019-00694-z) contains supplementary material, which is available to authorized users.

✉ M. E. Grevé
Michael.greve@uni-bayreuth.de

[1] Animal Population Ecology, Animal Ecology I, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany

species leg length increases allometrically with body size (evolutionary prediction); and (2) that ant species use the same landscape differently according to body size (ecological prediction).

Several studies found support (Kaspari and Weiser 1999; Espadaler and Gómez 2001; Parr et al. 2003; partly Kaspari and Weiser 2007) for the evolutionary prediction, but some did not find the predicted patterns in their studies [for ants: Sarty et al. (2006), for multiple taxa: Teuscher et al. (2009)]. For the ecological prediction, evidence was partly found with larger-bodied species (Gibb and Parr 2010; Arnan et al. 2013; Gibb et al. 2015) or at least with relatively longer legged species being more dominant in open habitats than in more complex ones with assumingly higher surface rugosity (Gibb and Parr 2010, 2013; Wiescher et al. 2012). By comparing ant community structures in the tropical forest canopy and leaf litter, Yanoviak and Kaspari (2000) found large species moving over and smaller species moving through a rugose environment (litter layer), while intermediate sized species were mainly found in more planar environments (tree canopy). Concerning movements over or through their environment, ants were found to be slower in food discovery in highly rugose habitats (Nielsen 2001; Gibb and Parr 2010) with smaller ants having an advantage (Farji-Brener et al. 2004; Radnan et al. 2018).

Based on these findings of the ecological predictions of the SGH, the question arises whether morphological traits can be used to predict how a species is affected by increasing surface rugosity in differently complex habitats. Or in a broader view: how reliable are morphological traits as functional traits? A very simple but fundamental functional trait is the running speed of a species, which is dependent on the morphology (intrinsic factor), the habitat and ambient temperature (extrinsic factors). A high running speed enables ants to cover large distances faster, which enhances the chance of finding food and reduces the duration of exposal to harsh surroundings (Pearce-Duvet et al. 2011; Wahl et al. 2015) and avoid competitors (Ślipiński and Żmihorski 2017). Running speed can be important for, e.g., the community structure, especially when a discovery-dominance trade-off is present (Davidson 1998; Adler et al. 2007).

In ant-functional trait studies (e.g., Parr et al. 20167), the hypothesized trait function of leg length is the predictor for running speed and habitat complexity (Feener et al. 1988) and thermoregulatory strategies (Sommer and Wehner 2012). Hence, species with long legs should be faster than similarly sized species with shorter legs and running speed should increase with body size and leg length [Hurlbert et al. (2008), but see Frizzi (2018)] in simple, but slower in more rugose habitats. Surprisingly, only a few studies have compared running speed on different surfaces intra- and interspecifically with regard to species body size and morphology. Earlier studies on stepping patterns (Zollikofer 1994a, b; Steck et al. 2009) and effects of surface characteristics on ant locomotion (Nielsen 2001; Bernadou and Fourcassié 2008; Weihmann and Blickhan 2009; Yanoviak et al. 2012) found that ants are sensitive towards increasing surface roughness and adapt their movements accordingly. Recently, Yanoviak et al. (2017) found decreasing running speed of arboreal ants with increasing roughness of plant surfaces, with the effect of roughness being highest on medium-sized ants. These results fit with the ecological prediction of the SGH and strongly encourage to pursue and develop this approach with ground-living ants. Here, we measure intra- and interspecific variation in running speed of differently sized non-arboreal ant species along an increasing surface rugosity gradient, to investigate whether we find support for the evolutionary and ecological predictions of the SGH and the suitability of morphological traits as functional traits. We are testing whether in our species: (1) the leg length increases allometrically with body size; (2) running speed increases with body size and leg length; (3) the effect of increasing rugosity differs between small, medium-sized and large species; and (4) similar-sized species will respond similarly to the increasing surface rugosity.

## Materials and methods

### Ant species

To compare interspecific differences in morphology and the effect on running speed, we conducted an experiment with seven formicine species: six temperate species *Formica fuscocinerea*, *F. cunicularia*, *F. rufibarbis* and *F. sanguinea* as well as *Lasius niger* and *L. fuliginosus*, which were all sampled on the campus of the University of Bayreuth and in Southern Germany in Summer 2017. In addition, a tropical *Camponotus* species: *C. spec* (unknown origin) with only minors, no medias and a very low number of majors (not included), was kept in a climate chamber (25 °C, 12-h day–night cycle) for several years. Since colony size influences foraging behavior (Herbers and Choiniere 1996), we used a standardized group size for each species. The groups consisted of 200 workers plus five–ten larvae from the stock colony. As stock colony, we used one colony per species. Groups were kept in plastic boxes with artificial gypsum nest chambers.

To compare intraspecific differences in running speed in dependence of morphological differences we compared the running speed of workers of different sizes in the polymorphic species *Camponotus floridanus* (Florida, USA) and *C. maculatus* (Uganda, Africa), which were kept at the same conditions as *C. spec*. in a climate chamber. Workers of these species were divided into three differently sized morphological castes (small minors, medium-sized medias, and large majors) with 200 workers per caste.

## Experimental design

The experiments were conducted in plastic arenas (7 × 70 × 5 cm, $h \times l \times w$, Fig. S1), with a hole for a tube at ground level at one end as an entrance for the workers from each species or caste. The bottom of each arena was filled with a thin layer of gypsum and the walls were coated with paraffin oil to prevent ants from escaping.

Interspecific comparison: as treatments and to generate a gradient of increasing surface rugosity, the arena was prepared with bare gypsum (smooth) or the gypsum was covered with a loose layer of sand (Ø 0.9–1.2 mm) or gravel (Ø 2–3 mm). We use surface rugosity as a proxy for habitat complexity since it is the actual surface rugosity with which ants have to deal when they walk. The 'smooth' surface shows how fast a species can move over a surface without any obstacles. The 'sand' surface represents a low complexity open habitat with bare sand or soil. The 'gravel' surface represents a more complex, rough habitat. For the intraspecific comparison in running speed of the differently sized castes of *C. floridanus* and *C. maculatus*, we elaborated the gradient by adding treatments with 'very fine sand' (Ø 0.1–0.3 mm), 'fine sand' (Ø 0.4–0.8 mm), and 'coarse sand' (Ø 1–2 mm), thus resulting in six different treatments (Fig. S1).

To record a run, a video camera [Panasonic DMC-TZ40 with 50 frames per second (fps)] was positioned in the center above the arena, recording 5 cm of the pathway/arena (Fig. S2). Each species and caste was tested on each surface (interspecific: three surfaces per species; intraspecific: six surfaces per caste and species). Before the experiments, all worker groups were acclimatized for at least 48 h at a temperature of 22.0 ± 1.0 °C. The experiments were conducted within the same temperature range to prevent speed changes due to temperature variation. Before each trial, each worker group was starved for 48 h. 50 ants per worker group were marked on the thorax with one or two small color dots of acrylic paint to enable the identification of individual ants after the trials. At the far end of the arena, we placed a carbohydrate (honey-water) and a protein source (dead cockroach) (Fig. S2) to stimulate foraging and recruiting behavior. To start the trials, we connected the box containing the worker group with the arena. The trials were stopped after 60–90 min when the running activity decreased distinctly. After each trial, the arenas were cleaned with water and placed into a drying chamber overnight at a temperature of 55 °C to remove chemical trails laid by foraging workers (van Oudenhove et al. 2012).

The video recording was analyzed with the program 'DaVinci Resolve' (Version 14.0.0.078, © 2017 Blackmagic Design). The video recordings were started 20 min after the box containing the worker group was connected with the arena with a tube to allow the ants to accustom themselves to their surroundings and start foraging. During the exploration of new areas, ants move in a complex form with low speed and move faster and more rectilinear after finding the food (Johnson 1991; Herbers and Choiniere 1996). The speed of all straight runs (without change of direction, deceleration or abrupt stops) was measured over a distance of 5 cm irrespective of the direction (towards the food source or the nest). We measured the speed by counting the number of frames. The counting was started when an ant completely crossed a defined mark with its gaster and stopped when its gaster completely crossed the next 5-cm mark. With a frame rate of 50 fps, each frame had a length of 20 ms. For further analysis, we only used the 25 fastest runs of unmarked ants and the fastest runs of five marked ants which were later retrieved from the worker groups and stored in ethanol for subsequent morphometric measurements. For all measured runs ($n$ = 30 measured runs per species, caste, and treatment) we counted the number of strides an ant needed to cover the 5 cm. A stride was defined as the setting down of a foot to the setting down of the same foot and should not be confused with a step [which would be from the footfall of a leg pairs' right leg to the footfall of the left leg or vice versa (Alexander 2003; Wahl et al. 2015)]. Stride frequency was measured to examine how the frequency changes with surface structure, running speed and species since mean stride frequency is known to be highly variable among species (Zollikofer 1994b). We measured the strides for one of the middle pair of legs.

Since both *Lasius* species and *F. fuscocinerea* were too small for the markings, the trials were, in addition to being recorded by camera, observed in person and five ants were retrieved after running a straight line during the experiment. The retrieval of the respective ants did not seem to change the behavior of the other workers left in the arena. However, to ensure that ants did not change running speed due to a potential disturbance at least 1 min were given between the retrievals. After the trial, all ants removed from the worker group were replaced with ants from the stock colony to keep the number of ants per worker group stable for the trail on a different surface.

## Morphometric measurements and allometric analyses

The marked ants (interspecific: $n = 3$ surfaces × 5 workers per species; intraspecific: $n = 6$ surfaces × 5 workers per caste and species) were measured to examine the correlation of body size, leg length, and running speed. Morphological traits were measured using a Leica M165 C binocular system and the software 'Leica Application Suite'. The following four traits were measured: thorax length (Weber's length—WL) and pronotum width (PW) as measures for body size (Kaspari and Weiser 1999; Espadaler and Gómez 2001), and femur length (FL) and tibia length (TL) of one of the hindleg combined to leg length (LL). In addition, we measured dry body mass (M) using an analytical balance with 0.01 mg accuracy after the ants were dried for 48 h in a drying oven. For the allometric analyses, we used the R-package 'SMATR 3.4-3' [(Standardized) Major Axis Estimation and Testing Routines] (Warton et al. 2006, 2012). We analyzed our trait data with and without the major caste of *C. floridanus* and *C. maculatus* separately since *Camponotus* majors would affect overall species comparisons distinctly due to their enlarged heads and overall different morphological proportions compared to minor and media workers. For the SGH, Kaspari and Weiser (1999) excluded individuals of the major caste from their analyses.

Using ordinary least square (OLS) regression, we calculated $a$ and $b$ in the scaling equation $Y = aX^b$, with $Y$ and $X$ being $\log_{10}$-transformed trait data over all species, once with the *C. floridanus* and *C. maculatus* majors excluded and once including them. In addition, we analyzed these two *Camponotus* species separately over all three castes. For a positive allometric relationship of leg length and body size, the SGH predicts $b > 1$ for linear vs linear measures (e.g., LL = $aWL^{b>1}$) and $b > 0.333$ for linear measures vs mass LL = $aM^{b>0.333}$. We tested the null hypothesis of isometry ($H_{0(\text{body size})}$: $b = 1$; $H_{0(\text{body mass})}$: $b = 0.333$) using a $t$ test ('slope.test'-function).

### Analyses of running speed

All data were tested for normality before analysis (with Shapiro–Wilk tests). We used linear models to compare the slope among species and on the different surfaces. A linear regression over the whole surface gradient would have led to misleading results, due to the idiosyncratic walking speed of some species. We used linear models with running speed as the response variable and the predictor variables species and surface, which were allowed to interact. For each model, we used subsets with only two species and either the smooth-sand or the sand-gravel gradient, resulting in pairwise species comparisons. We tested the homogeneity of variance of the running speed between species using a Levene's test [R package "car", John and Weisberg (2011)] and analyzed the LMs using ANOVA. A non-significant interaction of species and surface indicated a similar slope of two species.

## Results

### Morphometric measurements and allometric analyses

The workers of the different species we measured covered a range from a mean of 1.31–3.98 mm in Weber´s length and a body mass range from 0.89 up to 8.72 mg (Table 1; Fig. 1). The allometric analyses corroborated the evolutionary prediction of the SGH (Kaspari and Weiser 1999) as leg length of the species increased allometrically with Weber's length and pronotum width, with the scaling exponent $b > 1$ and body mass with $b > 0.333$ (Table 2). However, when we included the major workers of *C. floridanus* and *C. maculatus* in the analyses, the slope for all analyses (grey line Fig. 1b) was reduced, resulting in an isometric relationship ($b = 1$) of Weber's length and leg length (Table 2). Thus, within these two polymorphic *Camponotus* species, leg length did not increase allometrically with Weber's length. In both species, larger specimens did not have proportionally longer legs than smaller specimens: (*C.*

**Table 1** Overview over the trait measurements [Weber's length (WL), pronotum width (PW) and leg length (LL)] of all measured ant species and castes as well as the relative leg length (LL/WL) and body mass

| Species | WL (mm) | PW (mm) | LL (mm) | LL/WL (mm) | Body mass (mg) |
|---|---|---|---|---|---|
| *C. maculatus—major* | 3.98 | 1.82 | 7.19 | 1.81 | 8.72 |
| *C. maculatus—media* | 3.79 | 1.54 | 7.07 | 1.88 | 5.62 |
| *C. maculatus—minor* | 3.35 | 1.22 | 6.2 | 1.85 | 2.63 |
| *C. floridanus—major* | 3.25 | 1.65 | 5.37 | 1.65 | 5.82 |
| *C. floridanus—media* | 2.71 | 1.27 | 4.68 | 1.73 | 2.77 |
| *C. floridanus—minor* | 2.38 | 1.03 | 4.18 | 1.75 | 1.43 |
| *F. sanguinea* | 2.56 | 1.22 | 4.19 | 1.63 | 2.77 |
| *F. rufibarbis* | 2.33 | 1.09 | 3.9 | 1.67 | 2.01 |
| *F. cunicularia* | 2.19 | 0.99 | 3.65 | 1.66 | 1.95 |
| *C. spec.* | 2.15 | 0.89 | 4.16 | 1.93 | 1.34 |
| *F. fuscocinerea* | 1.92 | 0.87 | 3.12 | 1.62 | 1.3 |
| *L. fuliginosus* | 1.52 | 0.87 | 3.22 | 2.12 | 1.69 |
| *L. niger* | 1.31 | 0.7 | 2.19 | 1.67 | 0.89 |

Values state the mean trait value for each species and caste

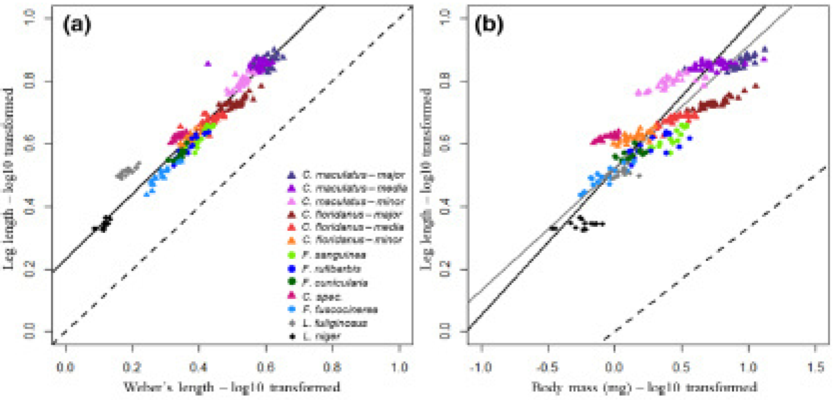

**Fig. 1** Relationship between body size (Weber's length and body weight) and leg length of all measured ants ($n=286$) using log10-transformed trait values. **a** The solid line represents the slope of ordinary least square (OLS) regression (only worker ants); the dashed line indicates isometry (scaling exponent $b=1$). **b** The solid line represents the slope of the OLS regressions with *C. floridanus* and *C. maculatus* majors included (grey) and excluded (black). The dashed line represents the scaling exponent $b=0.333$. For regression statistics, see Table 2

*floridanus*: $\mathrm{LL} = 0.34\ \mathrm{WL}^{0.75 < 1}$ and $\mathrm{LL} = 0.59\ M^{0.17 < 0.33}$; *C. maculatus* $\mathrm{LL} = 0.47\ \mathrm{WL}^{0.64}$ and $\mathrm{LL} = 0.75\ M^{0.12}$).

## Analyses of running speed

An increasing surface rugosity led to a decrease of running speed in all tested species and both experiments. However, the response to increasing surface rugosity was highly species-specific (Fig. 2). In the interspecific comparison among the seven species, the majority of species showed a nearly linear decreased speed while *F. sanguinea* and *F. cunicularia* showed an increased running speed from 'sand' to 'gravel' (Fig. 2a). Comparing the running speed of the different castes of both polymorphic *Camponotus* species, we found that *C. floridanus* maintained a rather high running speed over the whole surface rugosity gradient, while *C. maculatus* was overall faster but lost considerable amounts of speed with increased surface rugosity (Fig. 2b).

Comparing the number of strides on the different surfaces between the species, it stands out that all species were rather consistent in their number of strides, except for *L. niger* and *F. fuscocinerea* which increased their number of strides along the surface gradient (Fig. S3). The comparison of both polymorphic *Camponotus* species showed a consistent number of strides within species as well, with a slight increase of *C. maculatus* medias and majors on 'very fine sand' (Fig. S4).

## Running speed and body size

Running speed did not consistently increase with increasing body size and leg length. In all species running speed was highest on the smooth surface. Especially on this surface speed did not distinctly increase with body size. While *F. sanguinea* was the largest and fastest *Formica* species, the second fastest species, *F. fuscocinerea*, was the smallest (Figs. 1, 2a). In spite of being intermediate in body size and having relatively long legs *Camponotus* spec. was the slowest on nearly all surfaces (Table 1).

In intraspecific comparisons, media workers were fastest in *C. maculatus*. They were similar in WL and LL to their majors (Fig. 1a), but distinctly lighter (Fig. 1b; Table 1). In *C. floridanus*, the minor caste was the fastest.

## The response of similarly sized species to increasing surface rugosity

*F. cunicularia* and *F. rufibarbis* were relatively similar-sized in WL, PW, and LL (Table 1). According to theory, both species should have a similar running speed and similar speed reduction on more rugose surfaces. However, *F. cunicularia* was 1.36× faster than *F. rufibarbis* on the 'smooth' surface but lost 48% of its speed on 'sand', while *F. cunicularia* lost only 17%.

The effect sizes (*F* values) in Table 3 state how different the slopes of two species between two surfaces were, with increasing *F* values indicating larger differences. Most species had significantly different slopes compared to the next smaller species (except *F. fuscocinerea*, and *L. fuliginosus* with *L. niger* on smooth-sand), indicating that they slowed down less or stronger than the smaller species.

**Table 2** Comparison of the leg length and body length measurements for calculations of *a* and *b* in the scaling equation $Y = aX^b$ of log10 transformed data

| *Y* (log 10) | *X* (log 10) | OLS-regression without *Camponotus* major | | | | | | | | With *Camponotus* major | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *df* | $R^2$ | *a* | *b* | 95% CI | | *r* | *p* | *df* | $R^2$ | *a* | *b* | 95% CI | | *r* | *p* |
| Leg length | Weber's length | 223 | 0.93 | 0.23 | 1.048 | 1.013 | 1.085 | 0.179 | 0.007 | 283 | 0.938 | 0.235 | 1.028 | 0.998 | 1.058 | 0.1108 | 0.062 |
| Leg length | Pronotum width | 223 | 0.85 | 0.59 | 1.43 | 1.35 | 1.52 | 0.65 | <0.001 | 283 | 0.787 | 0.579 | 1.17 | 1.11 | 1.24 | 0.33 | <0.001 |
| Leg length | Body mass (mg) | 223 | 0.74 | 0.518 | 0.466 | 0.436 | 0.499 | − 0.85 | <0.001 | 283 | 0.75 | 0.522 | 0.391 | 0.369 | 0.415 | − 0.91 | <0.001 |
| For Weber's length and pronotum width: $H_0$: $b$=1 | | | | | | | | For body mass: $H_0$: $b$=0.333 | | | | | | | | | |

OLS analyses were done over all measured species with *C. floridanus* and *C. maculatus* majors excluded and included separately

## Discussion

Since the SGH was published in 1999 (Kaspari and Weiser 1999), multiple studies found support for its evolutionary and ecological prediction. In accordance with the evolutionary prediction, we found that leg length of the species increased allometrically with body size, measured as Weber's length or body mass. These results corroborate the results of (Kaspari and Weiser 1999; Espadaler and Gómez 2001; Parr et al. 2003; partly Kaspari and Weiser 2007). Interestingly, this pattern was not found in intraspecific comparisons within the two size-polymorphic *Camponotus* species we tested. In *C. floridanus*, the relative leg length decreased with increasing body length and body mass. In *C. maculatus* specimens of the major caste had distinctly shorter legs, relative to their large body size, which is in line with the findings of Willott et al. (2000) and Frizzi (2018) in polymorphic harvester ants.

The running speed shapes the way of life of terrestrial, flightless organisms. For ants, running speed defines factors such as home range size, foraging mode or predator avoidance. Simultaneously, the running speed is influenced by the species' morphology and behavior (intrinsic factors), the habitat structure and the ambient temperature (extrinsic factors). As many ants have overlapping trophic niches they often compete aggressively for resources. A high running speed allows ants to reduce exploitation competition since they are able to discover food resources first (e.g., Fellers 1987; Gibb and Parr 2010; Radnan et al. 2018). Here, we studied the running speed of differently sized ant species and investigated how different species, but also differently sized workers within polymorphic species responded to increasing surface roughness.

In the interspecific comparison of running speed among seven ant species measured on three different surfaces did not increase with body size and leg length. *F. fuscocinerea* is smaller than *F. cunicularia* and *F. rufibarbis*, but was significantly faster on the smooth surface and sand. Likewise, *L. niger*, the smallest species, had a running speed similar to the distinctly larger *F. rufibarbis*. Thus, small species have the potential to have a higher running speed than larger species, if not limited by obstacles. On a more rugose surface, like sand or gravel, the smaller species lost speed with *F. fuscocinerea* and *L. niger* being among the slowest on gravel. These idiosyncratic patterns suggest a very species-specific response on increasing surface roughness and that running speed is not only determined by leg length, but also other factors.

Yanoviak et al. (2017) measured the running speed of four common tropical arboreal ant species on different plant surface rugosities and found that the largest species (*Cephalotes atratus*) and the smallest (*Crematogaster*

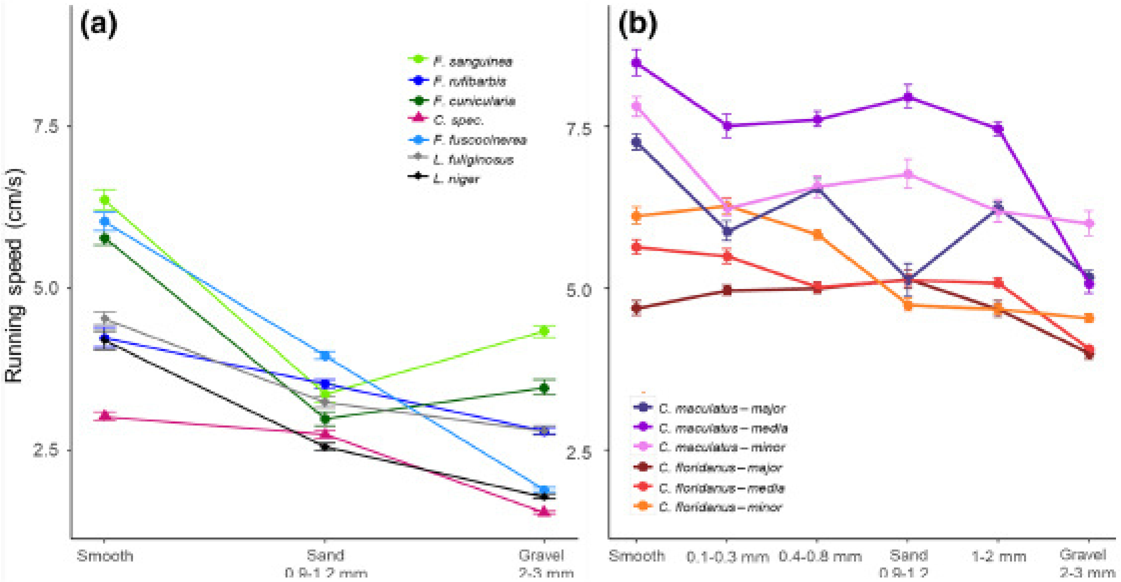

**Fig. 2** Running speed of ant species on different surfaces. **a** Among species comparison of experiment one over the three different surfaces. **b** Comparison of the different *Camponotus* castes of both species over the six different surfaces. Points are means, whiskers are standard errors of the 30 speed measurements per species and surface. In the legend, species are named in declining body size (Weber's length)

**Table 3** Statistical, interspecific comparisons

| | *F. sanguinea* | | *F. rufibarbis* | | *F. cunicularia* | | *C. spec.* | | *F. fuscocinerea* | | *L. fuliginosus* | | *L. niger* | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* |
| *F. sanguinea* | | | *70.83* | *** | *0.57* | *0.45* | *134.79* | *** | *13.31* | *** | *48.06* | *** | *26.18* | *** |
| *F. rufibarbis* | 82.98 | *** | | | *80.62* | *** | *4.66* | *0.03* | *35.68* | *** | *7.66* | ** | *16.47* | *** |
| *F. cunicularia* | 4.32 | * | 45.03 | *** | | | *181.65* | *** | *10.98* | ** | *55.74* | *** | *26.57* | *** |
| *C. spec* | 148.96 | *** | 20.43 | *** | 95.95 | *** | | | *89.13* | *** | *40.33* | *** | *54.28* | *** |
| *F. fuscocinerea* | 339.54 | *** | 178.20 | *** | 255.33 | *** | 99.04 | *** | | | *14.81* | *** | *3.66* | *0.06* |
| *L. fuliginosus* | 49.16 | *** | 4.39 | * | 22.34 | *** | 36.30 | *** | 185.93 | *** | | | *3.15* | *0.08* |
| *L. niger* | 94.84 | *** | 0.15 | 0.70 | 52.68 | *** | 23.08 | *** | 218.36 | *** | 6.72 | * | | |

Result of linear models with the running speed as the response variable and the predictor variables species and surface which were allowed to interact. Shown are the results of the interaction. A non-significant interaction indicates similar slopes of the two species, while a significant interaction indicates that the change in running speed over the different surfaces differs between the respective species. Values with italics show the comparison between the surface 'smooth' and 'sand', underlined values show the comparison from 'sand' to 'gravel'. Species are arranged in declining body-size order from left to right and top to bottom

*brasiliensis*) lost less speed than the two medium-sized species (*Azteca trigona* and *Dolichoderus bispinosus*) with increasing rugosities. The spectrum of sizes of the species tested in our study was comparable to that of the respective species studied by Yanoviak et al. (2017). Their medium-sized species are similar in body size range to the *Formica* species tested here, and their smallest matches approximately with *Lasius niger*. The large *Cephalotes* had even longer legs than our *Camponotus* species. Here, we also found that the medium-sized *Formica* species are more affected than the large *Camponotus* species.

Within the two polymorphic *Camponotus* species, the smaller *C. floridanus* was less affected by increasing rugosity than the larger *C. maculatus*, since the speed reduction from smooth to the most rugose 'gravel' surface was lower for all castes. The differences in running speed between the size groups within and between both species suggest that the running speed is influenced by the body weight as well as the species-specific abilities to walk on loose surfaces. While *C. maculatus* minors and medias were able to maintain their speed on the other sand surfaces, the speed of the heavier major workers dropped again on the 'sand'-surface. The 'sand' grains appear to be looser than the smaller, but more condensed 'fine sand' grains. This lack of surface stability might have led to the observed slower speed of the heavier ants. We assume that the weight is the crucial factor, since the lighter castes and the other, lighter species were not affected. Although the light *F. sanguinea* and *F. cunicularia* slowed down on the 'sand' surface as well, both species increased their number of steps (Fig. S3), which *C. maculatus* majors did not. Thus, in contrast du C. maculatus majors the two Formica species seem to be able to behaviourally adjust their locomotion to deal with the surface structure. Yanoviak et al. (2017) found, e.g., that a species can run stably on solid surfaces of different rugosity, but slows down on softer surfaces such as moss or lose sand like in the present study.

Ants walk using a tripod gait with not more than three legs in the air at any time (Zollikofer 1994a; Reinhardt and Blickhan 2014). The front and the rear leg of one side and the middle leg of the other side move simultaneously during a stride. The mean stride length and tripod size are limited by the leg length and constant across species when measured on smooth surfaces [except for fast running desert ants (Zollikofer 1994b; Collett et al. 2006)] while stride frequency varies interspecifically (Zollikofer 1994b). Thus, ants increase their running speed by increasing their stride frequency and ants likely adjust their stride frequency to different surface structures. When measured on a smooth surface, Zollikofer (1994b) found a much higher stride frequency in *L. niger* and *F. fuscocinerea* than in other tested species, including species of similar body size. Here, these two species showed the highest number of strides per 5 cm as well (Fig S3). This high stride frequency could explain their high running speed on the smoothest surface. Both species also showed the largest increase in stride number on 'sand' and 'gravel' compared to the other species, but still had a slower running speed. These relatively small species must deal with the vertical distance of large obstacles (sand/gravel grains) which they have to climb over. This increased total running distance is highly dependent on the species size and unfortunately could not be measured here.

These findings fit with the predictions of the SGH where larger species can walk over obstacles while smaller species have to walk around them. Beside the stride frequency, ants might reduce their stride length as well to keep their stability on very rugose surfaces, which would reduce running speed tremendously though. Another possibility would be that species reduce stride length but increase their locomotory rate. Therewith, the decrease in running speed would be mainly driven by the increased walking distance.

Since the absolute leg length determines the stride length, ants with longer legs, relative to their body length, should show higher running speeds than ants of species with relatively shorter legs. In addition, the longer legs should be less sensitive to increasing surface rugosity because they can step over obstacles. Indeed, the rather small, but relatively long-legged *L. fuliginosus* is less affected by increasing rugosity than *L. niger* or *F. fuscocinerea* and showed a similar running speed as the distinctly larger *F. rufibarbis*. But these effects are not generalizable and rather species-specific as can be seen at *C. spec*. This species had the second highest relative leg length of all species but was distinctly slower than smaller, shorter legged species.

Making simple predictions on a species' running speed based on morphology only is difficult. In spite of being of similar size and body shape the running speed of *F. cunicularia* and *F. rufibarbis* differs significantly. Seifert (2007) noted that both species preferred open, sandy habitats, but *F. cunicularia* could be found more often in tall grass meadows while *F. rufibarbis* avoids areas with dense vegetation. Both species also have similar food preferences (Seifert 2017) which would make them competitors when sharing a habitat. Since *F. rufibarbis* is more aggressive and competitive, the running patterns of *F. cunicularia*, which enables higher speed on the most rugose surface 'gravel', might bring advantages in highly complex habitats such as tall grass meadows. Oster and Wilson (1978) discussed the idea that different ant species, often of similar size or occurring in similar climates, appear to vary in the tempo of foraging activity, and that this variation may reflect different selective foraging strategies. Yanoviak et al. (2017), e.g., found that opportunistic species were faster runners and discovered baits earlier than similar-sized more aggressive species. Hence, the running speed is of crucial importance in communities where the discovery-dominance trade-off is present (Fellers 1987) and less dominant species depend on a rapid discovery of available resources.

Comparing the running speed of *F. cunicularia* and *F. fuscocinerea*, it stands out that the latter has the strongest loss of speed of all species with increasing surface rugosity. While faster on 'smooth' and 'sand' than *F. cunicularia*, it is distinctly slower on 'gravel'. This pattern might explain the distribution of these species in their natural habitat in which *F. fuscocinerea* excludes *F. cunicularia* on open surfaces within a habitat; but when co-occurring in meadows, *F. cunicularia* frequently replaces *F. fuscocinerea* (personal observation by the first author). Hence, while the SGH assumes that, based on the rather similar morphology, both species should respond similarly to increasing rugosity, our findings show that a species' behavior influences the movement patterns strongly (Ślipiński and Żmihorski 2017).

Thus, in general, we found support for the evolutionary prediction of the SGH since leg length increased with body size. However, results were ambiguous for its ecological prediction. While large species were able to sustain their speed on increasing surface rugosity, small species slowed down distinctly. This suggests that these species use the same landscape differently. The effect of surface rugosity was the strongest for medium-sized ants, but responses were idiosyncratic and species-specific. Within species, different morphological castes reacted differently which may suggest caste-specific task allocations. Our results indicate that it is overall difficult to make precise predictions of the running speed by a species' morphological traits as leg length (in absolute and relative values) appears not to be a strong predictor for running speed on different surfaces. Other, species-specific factors such as stride frequency or the species' behavior can influence the running speed tremendously. The detected differences in running speed on different surfaces obtained in our lab experiments can contribute to the understanding of competitive interactions between ant species in the field.

**Acknowledgements** We would like to thank Oliver Otti and Simon Tragust for fruitful discussions on the experimental design. MEG has been funded by the Federal Ministry of Education and Research (BMBF), "Qualitätsoffensive Lehrerbildung", support code 01JA160.

## References

Adler FR, LeBrun EG, Feener DH Jr (2007) Maintaining diversity in an ant community: modeling, extending, and testing the dominance-discovery trade-off. Am Nat 169:323–333

Alexander RM (2003) Principles of animal locomotion. Princeton University Press, Princeton

Arnan X, Cerdá X, Retana J (2014) Ant functional responses along environmental gradients. J Anim Ecol 83:1398–1408. https://doi.org/10.1111/1365-2656.12227

Arnan X, Cerdá X, Rodrigo A, Retana J (2013) Response of ant functional composition to fire. Ecography 36:1182–1192. https://doi.org/10.1111/j.1600-0587.2013.00155.x

Bernadou A, Fourcassié V (2008) Does substrate coarseness matter for foraging ants? An experiment with *Lasius niger* (Hymenoptera; Formicidae). J Insect Physiol 54:534–542. https://doi.org/10.1016/j.jinsphys.2007.12.001

Bihn JH, Gebauer G, Brandl R (2010) Loss of functional diversity of ant assemblages in secondary tropical forests. Ecology 91:782–792

Collett M, Collett TS, Srinivasan MV (2006) Insect navigation: measuring travel distance across ground and through air. Curr Biol 16:R887–R890. https://doi.org/10.1016/J.CUB.2006.09.027

Davidson DW (1998) Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. Ecol Entomol 23:484–490

Espadaler X, Gómez C (2001) Formicine ants comply with the size-grain hypothesis. Funct Ecol 15:136–138. https://doi.org/10.1046/j.1365-2435.2001.00490.x

Farji-Brener AG, Barrantes G, Ruggiero A (2004) Environmental rugosity, body size and access to food: a test of the size-grain hypothesis in tropical litter ants. Oikos 104:165–171

Feener DHJ, Lighton JRB, Bartholomew G (1988) Curvilinear allometry, energetics and foraging ecology: a comparison of leaf-cutting ants and army ants. Funct Ecol 2:509–520

Fellers JH (1987) Interference and exploitation in a guild of woodland ants. Ecol Soc Am 68:1466–1478

Frizzi F (2018) Complexity of searching movement in the European harvester ant *Messor wasmanni*: effect of temperature and body size. Insect Soc 65:263–273. https://doi.org/10.1007/s00040-018-0609-8

Gibb H, Parr CL (2010) How does habitat complexity affect ant foraging success? A test using functional measures on three continents. Oecologia 164:1061–1073. https://doi.org/10.1007/s00442-010-1703-4

Gibb H, Parr CL (2013) Does structural complexity determine the morphology of assemblages? An experimental test on three continents. PLoS One 8:1–7

Gibb H, Stoklosa J, Warton DI et al (2015) Does morphology predict trophic position and habitat use of ant species and assemblages? Oecologia 177:519–531. https://doi.org/10.1007/s00442-014-3101-9

Herbers JM, Choiniere E (1996) Foraging behaviour and colony structure in ants. Anim Behav 51:141–153. https://doi.org/10.1006/anbe.1996.0012

Hurlbert AH, Ballantyne IVF, Powell S (2008) Shaking a leg and hot to trot: the effects of body size and temperature on running speed in ants. Ecol Entomol 33:144–154

John Fox and Sanford Weisberg (2011) An R Companion to Applied Regression, 2nd edn. Sage, Thousand Oaks CA

Johnson RA (1991) Learning, memory, and foraging efficiency in two species of desert seed-harvester ants. Ecology 72:1408–1419

Kaspari M, Weiser M (2007) The size-grain hypothesis: do macroarthropods see a fractal world? Ecol Entomol 32:279–282. https://doi.org/10.1111/j.1365-2311.2007.00870.x

Kaspari M, Weiser MD (1999) The size-grain hypothesis and interspecific scaling in ants. Funct Ecol 13:530–538. https://doi.org/10.1046/j.1365-2435.1999.00343.x

Lassau SA, Hochuli DF (2004) Effects of habitat complexity on ant assemblages. Ecography 27:157–164. https://doi.org/10.1111/j.0906-7590.2004.03675.x

Nielsen MG (2001) Energetic cost of foraging in the ant *Rhytidoponera aurata* in tropical Australia. Physiol Entomol 26:248–253. https://doi.org/10.1046/j.0307-6962.2001.00242.x

Oster GF, Wilson EO (1978) Caste and ecology in the social insects. Princeton University Press, Princeton UK

Parr CL, Dunn RR, Sanders NJ et al (2017) GlobalAnts: a new database on the geography of ant traits (Hymenoptera: Formicidae). Insect Conserv Divers 10:5–20. https://doi.org/10.1111/icad.12211

Parr ZJE, Parr CL, Chown SL (2003) The size-grain hypothesis: a phylogenetic and field test. Ecol Entomol 28:475–481. https://doi.org/10.1046/j.1365-2311.2003.00529.x

Pearce-Duvet JMC, Elemans CPH, Feener DH (2011) Walking the line: search behavior and foraging success in ant species. Behav Ecol 22:501–509. https://doi.org/10.1093/beheco/arr001

Radnan GN, Gibb H, Eldridge DJ (2018) Soil surface complexity has a larger effect on food exploitation by ants than a change from grassland to shrubland. Ecol Entomol 43:379–388. https://doi.org/10.1111/een.12510

Reinhardt L, Blickhan R (2014) Level locomotion in wood ants: evidence for grounded running. J Exp Biol 217:2358–2370. https://doi.org/10.1242/jeb.098426

Sarty M, Abbott KL, Lester PJ (2006) Habitat complexity facilitates coexistence in a tropical ant community. Oecologia 149:465–473

Schofield SF, Bishop TR, Parr CL (2016) Morphological characteristics of ant assemblages (Hymenoptera: Formicidae) differ among contrasting biomes. Myrmecol News 23:129–137

Seifert B (2007) Die Ameisen Mittel-und Nordeuropas. lutra Verlags- und Vertriebsgesellschaft 368

Seifert B (2017) The ecology of Central European non-arboreal ants—37 years of a broad-spectrum analysis under permanent taxonomic control. Soil Org 89:1–67

Silva RR, Brandão CRF (2014) Ecosystem-wide morphological structure of leaf-litter ant communities along a tropical latitudinal gradient. PLoS One 9:e93049

Ślipiński P, Żmihorski M (2017) Changes in the speed of ants as a result of aggressive interactions. Insect Sci 24:842–852. https://doi.org/10.1111/1744-7917.12354

Sommer S, Wehner R (2012) Leg allometry in ants: extreme long-leggedness in thermophilic species. Arthropod Struct Dev 41:71–77

Steck K, Wittlinger M, Wolf H (2009) Estimation of homing distance in desert ants, *Cataglyphis fortis*, remains unaffected by disturbance of walking behaviour. J Exp Biol 2012:2893–2901. https://doi.org/10.1242/jeb.030403

Teuscher M, Brändle M, Traxel V, Brandl R (2009) Allometry between leg and body length of insects: lack of support for the size-grain hypothesis. Ecol Entomol 34:718–724. https://doi.org/10.1111/j.1365-2311.2009.01124.x

van Oudenhove L, Boulay R, Lenoir A et al (2012) Substrate temperature constrains recruitment and trail following behavior in ants. J Chem Ecol 38:802–809. https://doi.org/10.1007/s10886-012-0130-x

Wahl V, Pfeffer SE, Wittlinger M (2015) Walking and running in the desert ant *Cataglyphis fortis*. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 201:645–656. https://doi.org/10.1007/s00359-015-0999-2

Warton DI, Duursma RA, Falster DS, Taskinen S (2012) smatr 3—an R package for estimation and inference about allometric lines. Methods Ecol Evol 3:257–259. https://doi.org/10.1111/j.2041-210X.2011.00153.x

Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. Biol Rev Camb Philos Soc 81:259–291. https://doi.org/10.1017/S1464793106007007

Weihmann T, Blickhan R (2009) Comparing inclined locomotion in a ground-living and a climbing ant species: sagittal plane kinematics. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 195:1011–1020. https://doi.org/10.1007/s00359-009-0475-y

Wiescher PT, Pearce-Duvet JMC, Feener DH (2012) Assembling an ant community: species functional traits reflect environmental filtering. Oecologia 169:1063–1074

Willott J, Compton G, Incoll D (2000) Foraging, food selection and worker size in the seed harvesting ant *Messor bouvieri*. Oecologia 125:35–44

Yanoviak S, Kaspari M (2000) Community structure and the habitat templet: ants in the tropical forest canopy and litter. Oikos 89:259–266

Yanoviak SP, Silveri C, Hamm CA, Solis M (2012) Stem characteristics and ant body size in a Costa Rican rain forest. J Trop Ecol 28:199–204. https://doi.org/10.1017/S026646741100071X

Yanoviak SP, Silveri C, Stark AY et al (2017) Surface roughness affects the running speed of tropical canopy ants. Biotropica 49:92–100. https://doi.org/10.1111/btp.12349

Yates M, Andrew N, Binns M, Gibb H (2014) Morphological traits: predictable responses to macrohabitats across a 300 km scale. PeerJ 2:e271

Zollikofer CPE (1994a) Stepping patterns in ants—Part I—influence of speed and curvature. J Exp Biol 192:119–127

Zollikofer CPE (1994b) Stepping patterns in ants—Part II—influence of body morphology. J Exp Biol 192:107–118

# The effect of ground surface rugosity on ant running speed is species-specific rather than size dependent.

Michael E. Grevé, Sanja Bláha, Joseph Teuber, Melanie Rothmaier and Heike Feldhaar

## Appendix

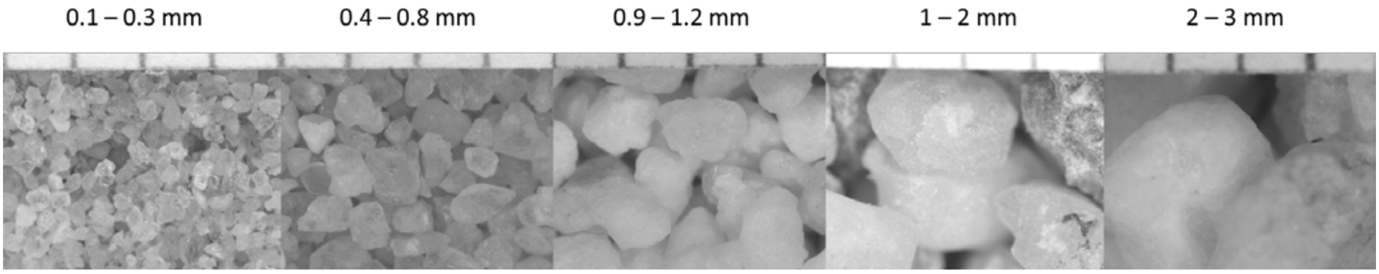

**Fig. S1** The different surfaces used in this study under 20x magnification. The grain sizes are stated above each picture.

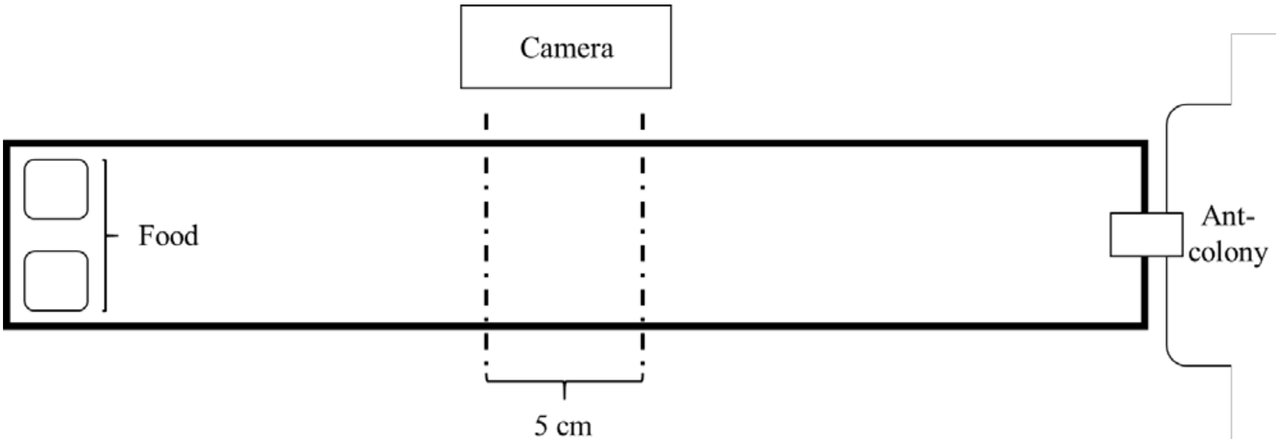

**Fig. S2** Design of the arenas used in the experiments

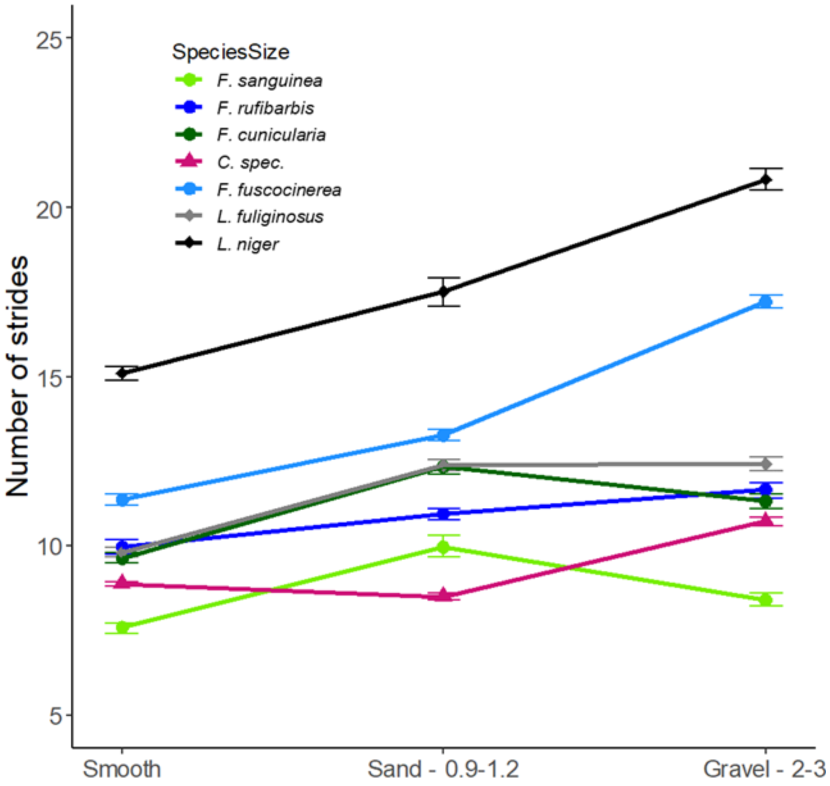

**Fig. S3** The number of strides per species made to walk the measured five centimeters over the different surfaces. A stride was defined as the setting down of a foot to the setting down of the same foot.

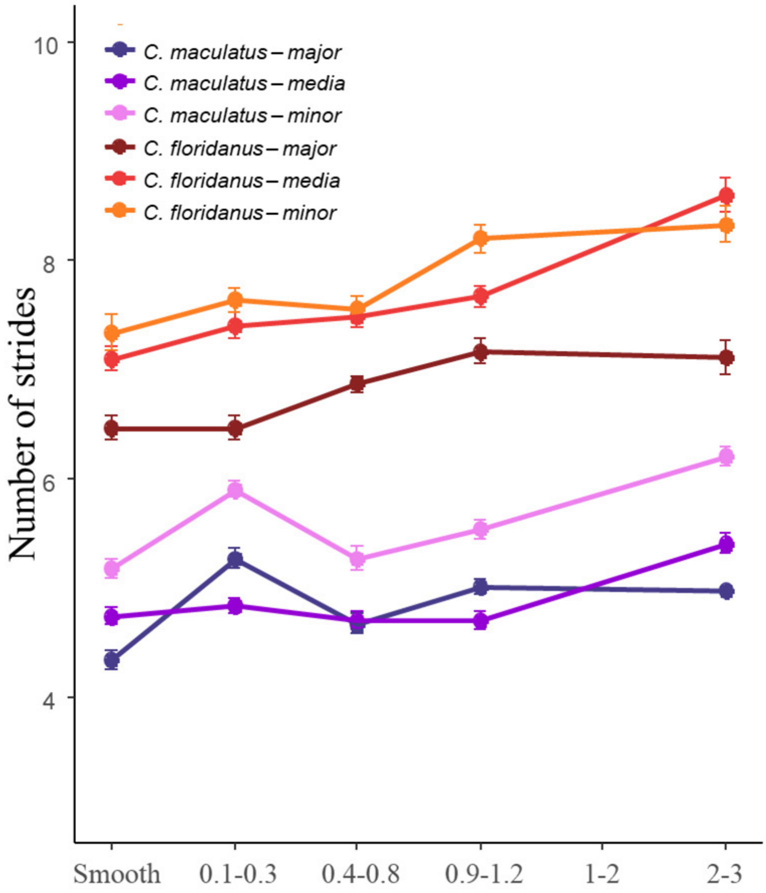

**Fig. S4** Comparison of the number of strides of the different *Camponotus* castes of both species made to walk the measured five centimetres over the six different surfaces. A stride was defined as the setting down of a foot to the setting down of the same foot. Due to color variation of the `1-2 mm´ sand, it was not possible to count the exact number of strides, as the contours of the legs became fuzzy.

## Funding

This project was funded by the Federal Ministry of Education and Research – BMBF within the „Qualitätsoffensive Lehrerbildung“, support code 01JA160.
(„Das diesem Bericht zugrundeliegende Vorhaben wurde im Rahmen der gemeinsamen „Qualitätsoffensive Lehrerbildung“ von Bund und Ländern mit Mitteln des Bundesministeriums für Bildung und Forschung unter dem Förderkennzeichen 01JA160 gefördert. Die Verantwortung für den Inhalt dieser Veröffentlichung liegt beim Autor.“)

## Acknowledgements

I had a great time working on this project and would like to thank everyone, I had the pleasure or honor to work with. This thesis is long enough, so let’s make it short:
First of all, I would like to thank Heike for her enormous support, for letting me work on this fascinating project and the always fruitful discussions.
Also “wart schnell”-Otti, Basti, Sara, Anja, Lionel, Fritzi, Nadine, Christina, Simon, and Lisa: thank you for the wonderful times in our office. Thank you for your help, friendship and for all the sarcasm and all the nonsense you had to listen to.
I am very grateful for all my co-authors, technical support by Jörg, and students helping me in the lab or field, contributing greatly to the success of this thesis.
I would like to thank my parents for their support and always keeping theirs hopes up on me.
But my deepest thanks go to Stephanie, for her moral support and motivation. Without her, this thesis would not have been possible.

# References

AbenspergTraun, M., G. T. Smith, G. W. Arnold, and D. E. Steven. 1996. The effects of habitat fragmentation and livestock-grazing on animal communities in remnants of gimlet Eucalyptus salubris woodland in the Western Australian wheatbelt .1. Arthropods. Journal of Applied Ecology 33:1281-130.

Allan, E., O. Bossdorf, C. F. Dormann, D. Prati, M. M. Gossner, T. Tscharntke, N. Bluthgen, M. Bellach, K. Birkhofer, S. Boch, S. Bohm, C. Borschig, A. Chatzinotas, S. Christ, R. Daniel, T. Diekotter, C. Fischer, T. Friedl, K. Glaser, C. Hallmann, L. Hodac, N. Holzel, K. Jung, A. M. Klein, V. H. Klaus, T. Kleinebecker, J. Krauss, M. Lange, E. K. Morris, J. Muller, H. Nacke, E. Pašalić, M. C. Rillig, C. Rothenwohrer, P. Schall, C. Scherber, W. Schulze, S. A. Socher, J. Steckel, I. Steffan-Dewenter, M. Türke, C. N. Weiner, M. Werner, C. Westphal, V. Wolters, T. Wubet, S. Gockel, M. Gorke, A. Hemp, S. C. Renner, I. Schöning, S. Pfeiffer, B. König-Ries, F. Buscot, K. E. Linsenmair, E.-D. Schulze, W. W. Weisser, and M. Fischer. 2014. Interannual variation in land-use intensity enhances grassland multidiversity. Proceedings of the National Academy of Sciences of the United States of America 111:308–313.

Allegro, G., and R. Sciaky. 2003. Assessing the potential role of ground beetles (Coleoptera, Carabidae) as bioindicators in poplar stands, with a newly proposed ecological index (FAI). Forest Ecology and Management 175:275–284.

Andersen, A. 1997. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. Journal of Biogeography 24:433–460.

Andersen, A. N. 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. Journal of Biogeography 22:15-29.

Andersen, A. N. 2008. Not enough niches: Non-equilibrial processes promoting species coexistence in diverse ant communities. Austral Ecology 33:211–220.

Andersen, A. N. 2019. Responses of ant communities to disturbance: Five principles for understanding the disturbance dynamics of a globally dominant faunal group. Journal of Animal Ecology 88:350–362.

Andersen, A. N., B. D. Hoffmann, W. J. Müller, and A. D. Griffiths. 2002. Using ants as bioindicators in land managment: simplififyings assessment of ant community responses. Journal of Applied Ecology 39:8–17.

Andersen, A. N., and J. D. Majer. 2004. Ants show the way Down Under: invertebrates as bioindicators in land management. Frontiers in Ecology and the Environment 2:291–298.

Andersen, A. N., and G. P. Sparling. 1997. Ants as indicators of restoration success: Relationship with soil microbial biomass in the Australian seasonal tropics. Restoration Ecology 5:109–114.

Andersson, J., J. Hjältén, and M. Dynesius. 2012. Long-term effects of stump harvesting and landscape composition on beetle assemblages in the hemiboreal forest of Sweden. Forest Ecology and Management 271:75–80.

Arcoverde, G. B., A. N. Andersen, and S. A. Setterfield. 2017. Is livestock grazing compatible with biodiversity conservation? Impacts on savanna ant communities in the Australian seasonal tropics. Biodiversity and Conservation 26:883–897.

Arnan, X., X. Cerdá, and J. Retana. 2012. Distinctive life traits and distribution along environmental gradients of dominant and subordinate Mediterranean ant species. Oecologia 170:489–500.

Arnan, X., X. Cerdá, and J. Retana. 2014. Ant functional responses along environmental gradients. Journal of Animal Ecology 83:1398–1408.

Arnan, X., X. Cerdá, and J. Retana. 2017. Relationships among taxonomic, functional, and phylogenetic ant diversity across the biogeographic regions of Europe. Ecography 40:448–457.

Arnan, X., M. Gracia, L. Comas, and J. Retana. 2009. Forest management conditioning ground ant community structure and composition in temperate conifer forests in the Pyrenees Mountains. Forest Ecology and Management 258:51–59.

Arnan, X., A. Rodrigo, and J. Retana. 2007. Uncoupling the effects of shade and food resources of vegetation on Mediterranean ants: An experimental approach at the community level. Ecography 30:161–172.

Attwood, S. J., M. Maron, A. P. N. House, and C. Zammit. 2008. Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? Global Ecology and Biogeography 17:585–599.

Azcárate, F. M., and B. Peco. 2012. Abandonment of grazing in a mediterranean grassland area: Consequences for ant assemblages. Insect Conservation and Diversity 5:279–288.

Azcárate, F. M., J. Seoane, S. Castro, and B. Peco. 2013. Drove roads: Keystone structures that promote ant diversity in Mediterranean forest landscapes. Acta Oecologica 49:107–115.

Babik, H., T. Włodarczyk, and M. Sterzyńska. 2013. How does a strip of clearing affect the forest community of ants (Hymenoptera: Formicidae)? Fragmenta Faunistica 53:125–141.

Bauhus, J., K. Puettmann, and C. Messier. 2009. Silviculture for old-growth attributes. Forest Ecology and Management 258:525–537.

Bauhus, J., and J. Schmerbeck. 2010. Silvicultural options to enhance and use forest plantation biodiversity. Pages 96–139 *in* Bauhus J, van der Meer P, Kanninen M, editors. Ecosystem goods and services from plantation forests. Earthscan, London.

Beever, E. A., and J. E. Herrick. 2006. Effects of feral horses in Great Basin landscapes on soils and ants: Direct and indirect mechanisms. Journal of Arid Environments 66:96–112.

Bernadou, A., R. Céréghino, H. Barcet, M. Combe, X. Espadaler, and V. Fourcassié. 2013. Physical and land-cover variables influence ant functional groups and species diversity along elevational gradients. Landscape Ecology 28:1387–1400.

Bernes, C. 1994. Biological diversity in Sweden: a country study. Swedish Environmental Protection Agency Monitor. 14th edition. Ingvar Bingman.Trosa, Sweden

Bestelmeyer, B. T., and J. A. Wiens. 1996. The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. Ecological Applications 6:1225–1240.

Bestelmeyer, B. T., and J. A. Wiens. 2001a. Local and regional-scale responses of ant diversity to a semiarid biome transition. Ecography 24:381–392.

Bestelmeyer, B. T., and J. A. Wiens. 2001b. Ant biodiversity in semiarid landscape mosaics: The consequences of grazing vs. natural heterogeneity. Ecological Applications 11:1123–1140.

Bihn, J. H., G. Gebauer, and R. Brandl. 2010. Loss of functional diversity of ant assemblages in secondary tropical forests. Ecology 91:782–92.

Birkhofer, K., T. Diekötter, C. Meub, K. Stötzel, and V. Wolters. 2015a. Optimizing arthropod predator conservation in permanent grasslands by considering diversity components beyond species richness. Agriculture, Ecosystems and Environment 211:65–72.

Birkhofer, K., M. M. Gossner, T. Diekötter, C. Drees, O. Ferlian, M. Maraun, S. Scheu, W. W. Weisser, V. Wolters, S. Wurst, A. S. Zaitsev, and H. G. Smith. 2017. Land-use type and intensity differentially filter traits in above- and below-ground arthropod communities. Journal of Animal Ecology 86:511–520.

Birkhofer, K., H. G. Smith, W. W. Weisser, V. Wolters, and M. M. Gossner. 2015b. Land-use effects on the functional distinctness of arthropod communities. Ecography 38:889–900.

Blatrix, R., C. Lebas, C. Galkowski, P. Wegnez, R. Pimenta, and D. Morichon. 2016. Vegetation cover and elevation drive diversity and composition of ant communities (Hymenoptera: Formicidae) in a Mediterranean ecosystem. Myrmecological News 22:119–127.

Blüthgen, N., C. F. Dormann, D. Prati, V. H. Klaus, T. Kleinebecker, N. Hölzel, F. Alt, S. Boch, S. Gockel, A. Hemp, J. Müller, J. Nieschulze, S. C. Renner, I. Schöning, U. Schumacher, S. A. Socher, K. Wells, K. Birkhofer, F. Buscot, Y. Oelmann, C. Rothenwöhrer, C. Scherber, T. Tscharntke, C. N. Weiner, M. Fischer, E. K. V Kalko, K. E. Linsenmair, E. D. Schulze, and W. W. Weisser. 2012. A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. Basic and Applied Ecology 13:207–220.

Blüthgen, N., and H. Feldhaar. 2010. Food and shelter: How resources influence ant ecology. Pages 115–136 *in* L. Lach, C. L. Parr, and K. L. Abbott, editors. Ant Ecology. Oxford University Press, New York.

Blüthgen, N., N. K. Simons, K. Jung, D. Prati, S. C. Renner, S. Boch, M. Fischer, N. Hölzel, V. H. Klaus, T. Kleinebecker, M. Tschapka, W. W. Weisser, and M. M. Gossner. 2016. Land use imperils plant and animal community stability through changes in asynchrony rather than diversity. Nature Communications 7:10697.

Boch, S., D. Prati, J. Müller, S. Socher, H. Baumbach, F. Buscot, S. Gockel, A. Hemp, D. Hessenmöller, E. K. V Kalko, K. E. Linsenmair, S. Pfeiffer, U. Pommer, I. Schöning, E. D. Schulze, C. Seilwinder, W. W. Weisser, K. Wells, and M. Fischer. 2013. High plant species richness indicates management-related disturbances rather than the conservation status of forests. Basic and Applied Ecology 14:496–505.

Bolton, B., G. Alpert, P. S. Ward, and P. Naskrecki. 2007. Bolton's catalogue of ants of the world, 1758-2005. Harvard University Press, Cambridge, USA.

Boots, B., A. M. Keith, R. Niechoj, J. Breen, O. Schmidt, and N. Clipson. 2012. Unique soil microbial assemblages associated with grassland ant species with different nesting and foraging strategies. Pedobiologia 55:33–40.

Boulay, R., J. Coll-Toledano, A. J. Manzaneda, and X. Cerdá. 2007. Geographic variations in seed dispersal by ants: Are plant and seed traits decisive? Naturwissenschaften 94:242–246.

Boulton, A. M., and K. D. Amberman. 2006. How ant nests increase soil biota richness and abundance: A field experiment. Biodiversity and Conservation 15:69–82.

Boulton, A. M., K. F. Davies, and P. S. Ward. 2005. Species richness, abundance, and composition of ground-dwelling ants in Northern California grasslands: Role of plants, soil, and grazing. Environmental Entomology 34:96–104.

Brang, P., P. Spathelf, J. B. Larsen, J. Bauhus, A. Bončína, C. Chauvin, L. Drössler, C. García-Güemes, C. Heiri, G. Kerr, M. J. Lexer, B. Mason, F. Mohren, U. Mühlethaler, S. Nocentini, and M. Svoboda. 2014. Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. Forestry 87:492–503.

Bromham, L., M. Cardillo, A. F. Bennett, and M. A. Elgar. 1999. Effects of stock grazing on the ground invertebrate fauna of woodland remnants. Austral Ecology 24:199–207.

Brukas, V., and N. Weber. 2009. Forest management after the economic transition—at the crossroads between German and Scandinavian traditions. Forest Policy and Economics 11:586–592.

Buckley, R. C. 1987. Interactions involving plants, Homoptera, and ants. Annual Review of Ecology and Systematics 18:111–135.

Bundeswaldinventur 3 (2012). https://bwi.info/start.aspx

Calcaterra, L. A., S. M. Cabrera, F. Cuezzo, I. J. Peréz, and J. A. Briano. 2010. Habitat and grazing influence on terrestrial ants in subtropical grasslands and savannas of Argentina. Annals of the Entomological Society of America 103:635–646.

Campbell, K. U., and T. O. Crist. 2017. Ant species assembly in constructed grasslands is structured at patch and landscape levels. Insect Conservation and Diversity 10:180–191.

Chisté, M. N., K. Mody, M. M. Gossner, N. K. Simons, G. Köhler, W. W. Weisser, and N. Blüthgen. 2016. Losers, winners, and opportunists: How grassland land-use intensity affects orthopteran communities. Ecosphere 7:e01545.

Chytrý, M., T. Dražil, M. Hájek, V. Kalníková, Z. Preislerová, J. Šibík, K. Ujházy, I. Axmanová, D. Bernátová, D. Blanár, M. Dančák, P. Dřevojan, K. Fajmon, D. Galvánek, P. Hájková, T. Herben, R. Hrivnák, Š. Janeček, M. Janišová, Š. Jiráská, J. Kliment, J. Kochjarová, J. Lepš, A. Leskovjanská, K. Merunková, J. Mládek, M. Slezák, J. Šeffer, V. Šefferová, I. Škodová, J. Uhlířová, M. Ujházyová, and M. Vymazalová. 2015. The most species-rich plant communities in the Czech Republic and Slovakia (with new world records). Preslia 87:217–278.

Cizek, O., J. Zamecnik, R. Tropek, P. Kocarek, and M. Konvicka. 2012. Diversification of mowing regime increases arthropods diversity in species-poor cultural hay meadows. Journal of Insect Conservation 16:215–226.

Conrad, K. F., M. S. Warren, R. Fox, M. S. Parsons, and I. P. Woiwod. 2006. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. Biological Conservation 132:279–291.

Crist, T. O. 2009. Biodiversity, species interactions, and functional roles of ants (Hymenoptera : Formicidae) in fragmented landscapes: a review. Myrmecological News 12:3–13.

Dahms, H., L. Lenoir, R. Lindborg, V. Wolters, and J. Dauber. 2010. Restoration of seminatural grasslands: What is the impact on ants? Restoration Ecology 18:330-337.

Dahms, H., C. Wellstein, V. Wolters, and J. Dauber. 2005. Effects of management practices on ant species richness and community composition in grasslands (Hymenoptera: Formicidae). Myrmecologische Nachrichten 7:9–16.

Dáttilo, W., and L. Dyer. 2014. Canopy openness enhances diversity of ant-plant interactions in the Brazilian Amazon rain forest. Biotropica 46:712–719.

Dauber, J., J. Bengtsson, and L. Lenoir. 2006a. Evaluating effects of habitat loss and land-use continuity on ant species richness in seminatural grassland remnants. Conservation Biology 20:1150–1160.

Dauber, J., R. Niechoj, H. Baltruschat, and V. Wolters. 2008. Soil engineering ants increase grass root arbuscular mycorrhizal colonization. Biology and Fertility of Soils 44:791–796.

Dauber, J., A. Rommeler, and V. Wolters. 2006b. The ant *Lasius flavus* alters the viable seed bank in pastures. European Journal of Soil Biology 42:157–163.

Dauber, J., and V. Wolters. 2004. Edge effects on ant community structure and species richness in an agricultural landscape. Biodiversity & Conservation 13:901–915.

Dauber, J., and V. Wolters. 2005. Colonization of temperate grassland by ants. Basic and Applied Ecology 6:83–91.

Dean, W. R. J., S. J. Milton, and S. Klotz. 1997. The role of ant nest-mounds in maintaining small-scale patchiness in dry grasslands in Central Germany. Biodiversity and Conservation 6:1293–1307.

Dejean, A., B. Corbara, J. Orivel, and M. Leponce. 2007. Rainforest canopy ants: The implications of territoriality and predatory behavior. Functional Ecosystems and Communities 1:105–120.

Dekoninck, W., H. De Koninck, J. Y. Baugnée, and J. P. Maelfait. 2007. Ant biodiversity conservation in Belgian calcareous grasslands: Active management is vital. Belgian Journal of Zoology 137:137–146.

Demarais, S., J. P. Verschuyl, G. J. Roloff, D. A. Miller, and T. B. Wigley. 2017. Tamm review: Terrestrial vertebrate biodiversity and intensive forest management in the U.S. Forest Ecology and Management 385:308–330.

Dengler, J., T. Becker, E. Ruprecht, A. Szabó, U. Becker, M. Beldean, C. Bita-Nicolae, C. Dolnik, I. Goia, J. Peyrat, L. M. E. Sutcliffe, P. D. Turtureanu, and E. Uğurlu. 2012. *Festuco-Brometea* communities of the Transylvanian Plateau (Romania) - A preliminary overview on syntaxonomy, ecology, and biodiversity. Tuexenia 32:319–359.

Deslippe, R. J., and R. Savolainen. 1995. Sex investment in a social insect: The proximate role of food. Ecology 76:375–382.

Diaz, S., and M. Cabido. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution 16:646–655.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. Science 345:401–406.

Dolek, M., A. Freese-Hager, H. Bussler, A. Floren, A. Liegl, and J. Schmidl. 2009. Ants on oaks: Effects of forest structure on species composition. Journal of Insect Conservation 13:367–375.

Domisch, T., M. Ohashi, L. Finér, A. C. Risch, L. Sundström, J. Kilpeläinen, and P. Niemelä. 2008. Decomposition of organic matter and nutrient mineralisation in wood ant (*Formica rufa* group) mounds in boreal coniferous forests of different age. Biology and Fertility of Soils 44:539–545.

Dröse, W., L. R. Podgaiski, C. F. Dias, and M. De Souza Mendonça. 2019. Local and regional drivers of ant communities in forest-grassland ecotones in South Brazil: A taxonomic and phylogenetic approach. PLoS ONE 14:e0215310.

Ehbrecht, M., P. Schall, C. Ammer, and D. Seidel. 2017. Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate. Agricultural and Forest Meteorology 242:1–9.

Ehrle, A., A. N. Andersen, S. R. Levick, J. Schumacher, S. E. Trumbore, and B. Michalzik. 2017. Yellow-meadow ant (*Lasius flavus*) mound development determines soil properties and growth responses of different plant functional types. European Journal of Soil Biology 81:83–93.

Ellenberg, H. 1996. Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. Fifth edition. Ulmer, Stuttgart, Germany.

Ellison, A. 2012. Out of Oz: Opportunities and challenges for using ants (Hymenoptera: Formicidae) as biological indicators in north-temperate cold biomes. Myrmecological News 17:105–119.

Ewers, R. M., M. J. W. Boyle, R. A. Gleave, N. S. Plowman, S. Benedick, H. Bernard, T. R. Bishop, E. Y. Bakhtiar, V. K. Chey, A. Y. C. Chung, R. G. Davies, D. P. Edwards, P. Eggleton, T. M. Fayle, S. R. Hardwick, R. Homathevi, R. L. Kitching, M. S. Khoo, S. H. Luke, J. J. March, R. Nilus, M. Pfeifer, S. V. Rao, A. C. Sharp, J. L. Snaddon, N. E. Stork, M. J. Struebig, O. R. Wearn, K. M. Yusah, and E. C. Turner. 2015. Logging cuts the functional importance of invertebrates in tropical rainforest. Nature Communications 6:6836.

Farji-Brener, A. G., G. Barrantes, and A. Ruggiero. 2004. Environmental rugosity, body size and access to food: A test of the size-grain hypothesis in tropical litter ants. Oikos 104:165–171.

Fauteux, D., L. Imbeau, P. Drapeau, and M. J. Mazerolle. 2012. Small mammal responses to coarse woody debris distribution at different spatial scales in managed and unmanaged boreal forests. Forest Ecology and Management 266:194–205.

Fedrowitz, K., J. Koricheva, S. C. Baker, D. B. Lindenmayer, B. Palik, R. Rosenvald, W. Beese, J. F. Franklin, J. Kouki, E. Macdonald, C. Messier, A. Sverdrup-Thygeson, and L. Gustafsson. 2014. Can retention forestry help conserve biodiversity? A meta-analysis. Journal of Applied Ecology 51:1669–1679.

Feldhaar, H., G. Gebauer, and N. Blüthgen. 2010. Stable isotopes: past and future in exposing secrets of ant nutrition (Hymenoptera: Formicidae). Myrmecological News 13:3–13.

Fischer, M., O. Bossdorf, S. Gockel, F. Hänsel, A. Hemp, D. Hessenmöller, G. Korte, J. Nieschulze, S. Pfeiffer, D. Prati, S. Renner, I. Schöning, U. Schumacher, K. Wells, F. Buscot, E. K. V Kalko, K. E. Linsenmair, E. D. Schulze, and W. W. Weisser. 2010. Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. Basic and Applied Ecology 11:473–485.

Floren, A., A. Biun, and K. E. Linsenmair. 2002. Arboreal ants as key predators in tropical lowland rainforest trees. Oecologia 131:137–144.

Flynn, D. F. B., M. Gogol-Prokurat, T. Nogeire, N. Molinari, B. T. Richers, B. B. Lin, N. Simpson, M. M. Mayfield, and F. DeClerck. 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters 12:22–33.

Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: A review. Biodiversity & Conservation 7:1221-1244.

Frouz, J., and V. Jilková. 2008. The effect of ants on soil properties and processes ( Hymenoptera : Formicidae ). Myrmecological News 11:191–199.

Frouz, J., H. Santruckova, and J. Kalcik. 1997. The effect of wood ants (*Formica polyctena* Foerst.) on the transformation of phosphorus in a spruce plantation. Pedobiologia 41:437–447.

Fuller, R. J., T. H. Oliver, and S. R. Leather. 2008. Forest management effects on carabid beetle communities in coniferous and broadleaved forests: Implications for conservation. Insect Conservation and Diversity 1:242–252.

Gámez-Virués, S., D. J. Perović, M. M. Gossner, C. Börschig, N. Blüthgen, H. de Jong, N. K. Simons, A.-M. Klein, J. Krauss, G. Maier, C. Scherber, J. Steckel, C. Rothenwöhrer, I. Steffan-Dewenter, C. N. Weiner, W. Weisser, M. Werner, T. Tscharntke, and C. Westphal. 2015. Landscape simplification filters species traits and drives biotic homogenization. Nature Communications 6:8568.

Gao, T., M. Hedblom, T. Emilsson, and A. B. Nielsen. 2014. The role of forest stand structure as biodiversity indicator. Forest Ecology and Management 330:82–93.

Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405:220–227.

Gastreich, K. R. 1999. Trait-mediated indirect effects of a theridiid spider on an ant-plant mutualism. Ecology 80:1066–1070.

Gibb, H., and C. L. Parr. 2010. How does habitat complexity affect ant foraging success? A test using functional measures on three continents. Oecologia 164:1061–1073.

Gibb, H., and C. L. Parr. 2013. Does structural complexity determine the morphology of assemblages? An experimental test on three continents. PLoS ONE 8:1–7.

Gibb, H., J. Stoklosa, D. I. Warton, A. M. Brown, N. R. Andrew, and S. A. Cunningham. 2015. Does morphology predict trophic position and habitat use of ant species and assemblages? Oecologia 177:519–531.

Di Giulio, M., P. J. Edwards, and E. Meister. 2001. Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. Journal of Applied Ecology 38:310–319.

Gossner, M. M. 2009. Light intensity affects spatial distribution of Heteroptera in deciduous forests. European Journal of Entomology 106:241–252.

Gossner, M. M., T. Lachat, J. Brunet, G. Isacsson, C. Bouget, H. Brustel, R. Brandl, W. W. Weisser, and J. Müller. 2013. Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. Conservation Biology 27:605–614.

Gossner, M. M., T. M. Lewinsohn, T. Kahl, F. Grassein, S. Boch, D. Prati, K. Birkhofer, S. C. Renner, J. Sikorski, T. Wubet, H. Arndt, V. Baumgartner, S. Blaser, N. Blüthgen, C. Börschig, F. Buscot, T. Diekötter, L. R. Jorge, K. Jung, A. C. Keyel, A.-M. Klein, S. Klemmer, J. Krauss, M. Lange, J. Müller, J. Overmann, E. Pašalić, C. Penone, D. J. Perović, O. Purschke, P. Schall, S. A. Socher, I. Sonnemann, M. Tschapka, T. Tscharntke, M. Türke, P. C. Venter, C. N. Weiner, M. Werner, V. Wolters, S. Wurst, C. Westphal, M. Fischer, W. W. Weisser, and E. Allan. 2016. Land-use intensification causes multitrophic homogenization of grassland communities. Nature 540:266–269.

Gossner, M. M., W. W. Weisser, and S. T. Meyer. 2014. Invertebrate herbivory decreases along a gradient of increasing land-use intensity in German grasslands. Basic and Applied Ecology 15:347–352.

Gotelli, N. J. 1996. Ant community structure: Effects of predatory ant lions. Ecology 77:630–638.

Graham, J. H., A. J. Krzysik, D. A. Kovacic, J. J. Duda, D. C. Freeman, J. M. Emlen, J. C. Zak, W. R. Long, M. P. Wallace, C. Chamberlin-Graham, J. P. Nutter, and H. E. Balbach. 2009. Species richness, equitability, and abundance of ants in disturbed landscapes. Ecological Indicators 9:866–877.

Greenslade, P. J. M., and P. Greenslade. 1977. Some effects of vegetation cover and disturbance on a tropical ant fauna. Insectes Sociaux 24:163–182.

Grevé, M. E., S. Bláha, J. Teuber, M. Rothmaier, and H. Feldhaar. 2019. The effect of ground surface rugosity on ant running speed is species-specific rather than size dependent. Insectes Sociaux (online early).

Grevé, M. E., J. Hager, W. W. Weisser, P. Schall, M. M. Gossner, and H. Feldhaar. 2018. Effect of forest management on temperate ant communities. Ecosphere 9:e02303.

Grill, A., D. F. R. Cleary, C. Stettmer, M. Bräu, and J. Settele. 2008. A mowing experiment to evaluate the influence of management on the activity of host ants of *Maculinea* butterflies. Journal of Insect Conservation 12:617–627.

Guzmán-Mendoza, R., and G. Castaño Meneses. 2016. The diversity of ant communities and its connections with other arthropod communities from three temperate forest of Central Mexico. Revista de Biología Tropical 64:571.

Habel, J. C., J. Dengler, M. Janišová, P. Török, C. Wellstein, and M. Wiezik. 2013. European grassland ecosystems: Threatened hotspots of biodiversity. Biodiversity and Conservation 22:2131–2138.

Habel, J. C., M. J. Samways, and T. Schmitt. 2019. Mitigating the precipitous decline of terrestrial European insects: Requirements for a new strategy. Biodiversity and Conservation 28:1343–1360.

Habel, J. C., A. Segerer, W. Ulrich, O. Torchyk, W. W. Weisser, and T. Schmitt. 2016. Butterfly community shifts over two centuries. Conservation Biology 30:754–762.

Haddad, N. M., J. Haarstad, and D. Tilman. 2000. The effects of long-term nitrogen loading on grassland insect communities. Oecologia 124:73–84.

Halaj, J., D. W. Ross, and A. R. Moldenke. 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. Oikos 90:139–152.

Hallanaro, E.-L., M. Pylvänäinen, and F. Weaver. 2002. Nature in northern Europe: biodiversity in a changing environment. Nordisk Ministerråd, Copenhagen, Denmark

Hallmann, C. A., M. Sorg, E. Jongejans, H. Siepel, N. Hofland, H. Schwan, W. Stenmans, A. Müller, H. Sumser, T. Hörren, D. Goulson, and H. De Kroon. 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS ONE 12.

Hannah, L., J. L. Carr, and A. Lankerani. 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. Biodiversity and Conservation 4:128–155.

Harpole, W. S., and D. Tilman. 2007. Grassland species loss resulting from reduced niche dimension. Nature 446:791–793.

Hawes, C., A. J. A. Stewart, and H. F. Evans. 2002. The impact of wood ants (*Formica rufa*) on the distribution and abundance of ground beetles (Coleoptera: Carabidae) in a Scots pine plantation. Oecologia 131:612–619.

Hector, A., and R. Bagchi. 2007. Biodiversity and ecosystem multifunctionality. Nature 448:188.

Heil, M., and D. McKey. 2003. Protective ant-plant interactions as model systems in ecological and evolutionary research. Annual Review of Ecology, Evolution, and Systematics 34:425–553.

Hejcman, M., P. Hejcmanová, V. Pavlů, and J. Beneš. 2013. Origin and history of grasslands in central europe - A review. Grass and Forage Science 68:345–363.

Helden, A. J., A. Anderson, H. Sheridan, and G. Purvis. 2010. The role of grassland sward islets in the distribution of arthropods in cattle pastures. Insect Conservation and Diversity 3:291–301.

Hendrickx, F., J. P. Maelfait, W. Van Wingerden, O. Schweiger, M. Speelmans, S. Aviron, I. Augenstein, R. Billeter, D. Bailey, R. Bukacek, F. Burel, T. Diekötter, J. Dirksen, F. Herzog, J. Liira, M. Roubalova, V. Vandomme, and R. Bugter. 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. Journal of Applied Ecology 44:340–351.

Herbers, J. M. 1980. On caste ratios in ant colonies: population responses to changing environments. Evolution 34:575–585.

Heuss, L., M. E. Grevé, D. Schäfer, V. Busch, and H. Feldhaar. 2019. Direct and indirect effects of land-use intensification on ant communities in temperate grasslands. Ecology and Evolution 9:4013–4024.

Heywood, V. H., and R. T. Watson. 1995. Global biodiversity assessment. Cambridge University Press, Cambridge, United Kingdom.

Hiroaki T. Ishii, Shin-ichi Tanabe, and Tsutom Hiura. 2004. Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. Forest Science 50:342–355.

Hoffmann, B. D. 2010. Using ants for rangeland monitoring: Global patterns in the responses of ant communities to grazing. Ecological Indicators 10:105-111.

Hölldobler, B., and E. O. Wilson. 1990. The Ants. Harvard University Press. Harvard University Press.

Horak, J., S. Vodka, J. Kout, J. P. Halda, P. Bogusch, and P. Pech. 2014. Biodiversity of most dead wood-dependent organisms in thermophilic temperate oak woodlands thrives on diversity of open landscape structures. Forest Ecology and Management 315:80–85.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201–228.

Humbert, J.-Y., J. Ghazoul, N. Richner, and T. Walter. 2010. Hay harvesting causes high orthopteran mortality. Agriculture, Ecosystems & Environment 139:522–527.

Humphrey, J. W., C. Hawes, A. J. Peace, R. Ferris-Kaan, and M. R. Jukes. 1999. Relationships between insect diversity and habitat characteristics in plantation forests. Forest Ecology and Management 113:11–21.

Hutchinson, K. J., and K. L. King. 1980. The effects of sheep stocking level on invertebrate abundance, biomass and energy utilization in a temperate, sown grassland. The Journal of Applied Ecology 17:369.

Isbell, F., V. Calcagno, A. Hector, J. Connolly, W. S. Harpole, P. B. Reich, M. Scherer-Lorenzen, B. Schmid, D. Tilman, J. van Ruijven, A. Weigelt, B. J. Wilsey, E. S. Zavaleta, and M. Loreau. 2011. High plant diversity is needed to maintain ecosystem services. Nature 477:199–202.

Isselstein, J., B. Jeangros, and V. Pavlu. 2005. Agronomic aspects of biodiversity targeted management of temperate grasslands in Europe – A review. Agronomy Research 3:139–151.

Jacobson, M. K. 2001. History and principles of close to nature forest management : A Central European perspective. Tools for preserving biodiversity in the nemoral and boreonemoral biomes of Europe:56–60.

Jäkel, A., and M. Roth. 2004. Conversion of single-layered Scots pine monocultures into close-to-nature mixed hardwood forests: Effects on parasitoid wasps as pest antagonists. European Journal of Forest Research 123:203–212.

Joern, A., and A. N. Laws. 2013. Ecological mechanisms underlying arthropod species diversity in grasslands. Annual Review of Entomology 58:19–36.

Kaila, L., P. Martikainen, and P. Punttila. 1997. Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. Biodiversity and Conservation 6:1–18.

Kalif, K. A. B., C. Azevedo-Ramos, P. Moutinho, and S. A. O. Malcher. 2001. The effect of logging on the ground-foraging ant community in Eastern Amazonia. Studies on Neotropical Fauna and Environment 36:215–219.

Kaspari, M., and M. D. Weiser. 1999. The size-grain hypothesis and interspecific scaling in ants. Functional Ecology 13:530–538.

Kiehl, K., A. Kirmer, T. W. Donath, L. Rasran, and N. Hölzel. 2010. Species introduction in restoration projects - Evaluation of different techniques for the establishment of semi-natural grasslands in Central and Northwestern Europe. Basic and Applied Ecology 11:285–299.

King, T. J. 1977. The plant ecology of ant hills in calcareous grasslands. I. Patterns of species in relation to ant hills in southern England. The Journal of Ecology 65:235–256.

Kipyatkov, V. E., and E. B. Lopatina. 2015. Comparative study of thermal reaction norms for development in ants. Entomological Science 18:174–192.

Kleijn, D., F. Kohler, A. Baldi, P. Batary, E. . Concepcion, Y. Clough, M. Diaz, D. Gabriel, A. Holzschuh, E. Knop, A. Kovacs, E. J. . Marshall, T. Tscharntke, and J. Verhulst. 2009. On the relationship between farmland biodiversity and land-use intensity in Europe. Proceedings of the Royal Society B: Biological Sciences 276:903–909.

Klimes, P., C. Idigel, M. Rimandai, T. M. Fayle, M. Janda, G. D. Weiblen, and V. Novotny. 2012. Why are there more arboreal ant species in primary than in secondary tropical forests? Journal of Animal Ecology 81:1103–1112.

van Klink, R., F. van der Plas, C. G. E. T. van Noordwijk, M. F. WallisDeVries, and H. Olff. 2015. Effects of large herbivores on grassland arthropod diversity. Biological Reviews 90:347–366.

Knoke, T. 2003. Predicting red heartwood formation in beech trees (*Fagus sylvatica* L.). Ecological Modelling 169:295–312.

Köhler F (2000) Saproxylic beetles in nature forests of the northern Rhineland. Comparative studies on the saproxylic beetles of Germany and contributions to German nature forest research. Schrr LÖBF/LAfAO NRW 18:1–351.

Korösi, Á., I. Szentirmai, P. Batáry, S. Kövér, N. Örvössy, and L. Peregovits. 2014. Effects of timing and frequency of mowing on the threatened scarce large blue butterfly - A fine-scale experiment. Agriculture, Ecosystems and Environment 196:24–33.

Kruess, A., and T. Tscharntke. 2002. Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. Conservation Biology 16:1570–1580.

Küster, H. 1996. Auswirkungen von Klimaschwankungen und menschlicher Landschaftsnutzung auf die Arealverschiebung von Pflanzen und die Ausbildung mitteleuropäischer Wälder. Forstwissenschaftliches Centralblatt 115:301–320.

Laakso, J., and H. Setälä. 2000. Impacts of wood ants (*Formica aquilonia* Yarr.) on the invertebrate food web of the boreal forest floor. Annales Zoologici Fennici 37:93–100.

Lachat, T., B. Wermelinger, M. M. Gossner, H. Bussler, G. Isacsson, and J. Müller. 2012. Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. Ecological Indicators 23:323–331.

Larrieu, L., Y. Paillet, S. Winter, R. Bütler, D. Kraus, F. Krumm, T. Lachat, A. K. Michel, B. Regnery, and K. Vandekerkhove. 2018. Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization. Ecological Indicators 84:194–207.

Lassau, S. A., and D. F. Hochuli. 2004. Effects of habitat complexity on ant assemblages. Ecography 27:157–164.

Lassauce, A., Y. Paillet, H. Jactel, and C. Bouget. 2011, September 1. Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecological Indicators 11:1027-1039.

Lawes, M. J., A. M. Moore, A. N. Andersen, N. D. Preece, and D. C. Franklin. 2017. Ants as ecological indicators of rainforest restoration: Community convergence and the development of an ant forest indicator index in the Australian wet tropics. Ecology and Evolution 7:8442–8455.

Lawton, J. H., D. E. Bignell, B. Bolton, G. F. Bloemers, P. Eggleton, P. M. Hammond, M. Hodda, R. D. Holt, T. B. Larsen, N. A. Mawdsley, N. E. Stork, D. S. Srivastava, and A. D. Watt. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391:72–76.

Leal, I. R., B. K. C. Filgueiras, J. P. Gomes, L. Iannuzzi, and A. N. Andersen. 2012. Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest. Biodiversity and Conservation 21:1687–1701.

Leather, S. R. 2018. "Ecological Armageddon" – more evidence for the drastic decline in insect numbers. Annals of Applied Biology 172:1–3.

Lefcheck, J. S., V. A. G. Bastazini, and J. N. Griffin. 2015. Choosing and using multiple traits in functional diversity research. Environmental Conservation 42:104–107.

Leidinger, J., S. Seibold, W. W. Weisser, M. Lange, P. Schall, M. Türke, and M. M. Gossner. 2019. Effects of forest management on herbivorous insects in temperate Europe. Forest Ecology and Management 437:232–245.

Lengyel, S., A. D. Gove, A. M. Latimer, J. D. Majer, and R. R. Dunn. 2009. Ants sow the seeds of global diversification in flowering plants. PLoS ONE 4:e5480.

Lessard, J. P., R. R. Dunn, and N. J. Sanders. 2009. Temperature-mediated coexistence in temperate forest ant communities. Insectes Sociaux 56:149–156.

Leuschner, C., and H. Ellenberg. 2017. Ecology of Central European forests: Vegetation ecology of Central Europe. Springer, Berlin, Germany.

Lonsdale, D., M. Pautasso, and O. Holdenrieder. 2008. Wood-decaying fungi in the forest: conservation needs and management options. European Journal of Forest Research 127:1–22.

Luke, S. H., T. M. Fayle, P. Eggleton, E. C. Turner, and R. G. Davies. 2014. Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. Biodiversity and Conservation 23:2817–2832.

Luoto, M., S. Rekolainen, J. Aakkula, and J. Pykälä. 2009. Loss of plant species richness and habitat connectivity in grasslands associated with agricultural change in finland. AMBIO: A Journal of the Human Environment 32:447–452.

Maeto, K., and S. Sato. 2004. Impacts of forestry on ant species richness and composition in warm-temperate forests of Japan. Forest Ecology and Management 187:213–223.

MacKay, W. P., A. Rebeles, H. C. Arrendondo, A. D. Gonzalez, and S. B. Vinson. 1991. Impact of the slashing and burning of a tropical rain forest on the native ant fauna (Hymenoptera: Formicidae). Sociobiology 18: 257-268

Majer, J. D. 1983. Ants: Bio-indicators of minesite rehabilitation, land-use, and land conservation. Environmental Management 7:375–383.

Majer, J. D., and G. Beeston. 1996. The biodiversity integrity index: An illustration using ants in Western Australia. Conservation Biology 10:65–73.

Maleque, M. A, K. Maeto, H. T. Ishii, M. A. M. Aleque, K. M. Aeto, and H. T. I. Shii. 2009. Arthropods as bioindicators of sustainable forest management, with a focus on plantation forests. Applied Entomology and Zoology 44:1–11.

Mangels, J., K. Fiedler, F. D. Schneider, and N. Blüthgen. 2017. Diversity and trait composition of moths respond to land-use intensification in grasslands: generalists replace specialists. Biodiversity and Conservation 26:3385–3405.

Manolis, J. C., D. E. Andersen, and F. J. Cuthbert. 2008. Edge effect studies in fragmentation northern analysis and in Minnesota results landscapes: Retrospective power analyses abd Minnesota results. Wildlife Society Bulletin 28:1088–1101.

Marini, L., P. Fontana, M. Scotton, and S. Klimek. 2007. Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. Journal of Applied Ecology 45:361–370.

Maxwell, S. L., R. A. Fuller, T. M. Brooks, and J. E. M. Watson. 2016. Biodiversity: The ravages of guns, nets and bulldozers. Nature 536:143-145.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21:178–185.

McGlynn, T. P., T. Dunn, E. Wayman, and A. Romero. 2010. A thermophile in the shade: light-directed nest relocation in the Costa Rican ant *Ectatomma ruidum*. Journal of Tropical Ecology 26:559–562.

MCPFE. 2003. State of Europe's Forests 2003.The MCPFE Report on sustainable forest management in Europe. Vienna, Austria: MCPFE Liaison Unit.

Messier, C., K. Puettmann, R. Chazdon, K. P. Andersson, V. A. Angers, L. Brotons, E. Filotas, R. Tittler, L. Parrott, and S. A. Levin. 2015. From Management to stewardship: Viewing forests as complex adaptive systems in an uncertain world. Conservation Letters 8:368–377.

Meyer, P., and M. Schmidt. 2011. Accumulation of dead wood in abandoned beech (*Fagus sylvatica* L.) forests in northwestern Germany. Forest Ecology and Management 261:342–352.

Mezger, D., and M. Pfeiffer. 2010. Is nest temperature an important factor for niche partitioning by leaf-litter ants (Hymenoptera: Formicidae) in Bornean rain forests? Journal of Tropical Ecology 26:445–455.

Moning, C., and J. Müller. 2009. Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (*Fagus sylvatica* L.) dominated forests. Ecological Indicators 9:922–932.

Morris, M. G. 2000. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. Biological Conservation 95:129–142.

Müller, J., H. Brustel, A. Brin, H. Bussler, C. Bouget, E. Obermaier, I. M. M. Heidinger, T. Lachat, B. Förster, J. Horak, J. Procházka, F. Köhler, L. Larrieu, U. Bense, G. Isacsson, L. Zapponi, and M. M. Gossner. 2015. Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. Ecography 38:499–509.

Müller, J., R. F. Noss, H. Bussler, and R. Brandl. 2010. Learning from a "benign neglect strategy" in a national park: Response of saproxylic beetles to dead wood accumulation. Biological Conservation 143:2559–2569.

Munyai, T. C., and S. H. Foord. 2012. Ants on a mountain: Spatial, environmental and habitat associations along an altitudinal transect in a centre of endemism. Journal of Insect Conservation 16:677–695.

Murdoch, W. W., F. C. Evans, and C. H. Peterson. 1972. Diversity and pattern in plants and insects. Ecological Society of America 53:819–829.

Nemec, K. T. 2014. Tallgrass prairie ants: Their species composition, ecological roles, and response to management. Journal of Insect Conservation 18:509-521.

Neuvonen, S., and P. Niemelä. 1981. Species richness of Macrolepidoptera on Finnish deciduous trees and shrubs. Oecologia 51:364–370.

New, T. R. 2000. How useful are ant assemblages for monitoring habitat disturbance on grasslands in south eastern Australia? Journal of Insect Conservation 4:153–159.

Nickel, H., and J. Hildebrandt. 2003. Auchenorrhyncha communities as indicators of disturbance in grasslands (Insecta, Hemiptera) - A case study from the Elbe flood plains (northern Germany). Agriculture, Ecosystems and Environment 98:183–199.

Niemela, J. 1997. Invertebrates and boreal forest management. Conservation Biology 11:601-610.

Noordijk, J., A. P. Schaffers, T. Heijerman, P. Boer, M. Gleichman, and K. V. Sýkora. 2010. Effects of vegetation management by mowing on ground-dwelling arthropods. Ecological Engineering 36:740–750.

Öckinger, E., A. K. Eriksson, and H. G. Smith. 2006. Effects of grassland abandonment, restoration and management on butterflies and vascular plants. Biological Conservation 133:291–300.

Økland, T., K. Rydgren, R. H. Økland, K. O. Storaunet, and J. Rolstad. 2003. Variation in environmental conditions, understorey species number, abundance and composition among natural and managed *Picea abies* forest stands. Forest Ecology and Management 177:17–37.

Oliver, I., R. Mac Nally, and A. York. 2000. Identifying performance indicators of the effects of forest management on ground-active arthropod biodiversity using hierarchical partitioning and partial canonical correspondence analysis. Forest Ecology and Management 139:21–40.

Paillet, Y., L. Bergès, J. Hjältén, P. Ódor, C. Avon, M. Bernhardt-Römermann, R. J. Bijlsma, L. De Bruyn, M. Fuhr, U. Grandin, R. Kanka, L. Lundin, S. Luque, T. Magura, S. Matesanz, I. Mészáros, M. T. Sebastià, W. Schmidt, T. Standovár, B. Tóthmérész, A. Uotila, F. Valladares, K. Vellak, and R. Virtanen. 2010. Biodiversity differences between managed and unmanaged forests: Meta-analysis of species richness in Europe. Conservation Biology 24:101–112.

Paine, C. E. T., C. Baraloto, and S. Díaz. 2015. Optimal strategies for sampling functional traits in species-rich forests. Functional Ecology 29:1325–1331.

Palladini, J. D., M. G. Jones, N. J. Sanders, and E. S. Jules. 2007. The recovery of ant communities in regenerating temperate conifer forests. Forest Ecology and Management 242:619–624.

Parr, C. L., and H. Gibb. 2010. Competition and the role of dominant ants. Pages 77–96 *in* L. Lach, C. L. Parr, and K. L. Abbott, editors. Ant Ecology. Oxford University Press, New York.

Parr, Z. J. E., C. L. Parr, and S. L. Chown. 2003. The size-grain hypothesis: A phylogenetic and field test. Ecological Entomology 28:475–481.

Pärtel, M., H. H. Bruun, and M. Sammul. 2005. Biodiversity in temperate European grasslands: origin and conservation. Grassland Science in Europe 10:1-14.

Parviainen, J., W. Bücking, K. Vandekerkhove, A. Schuck and Päivinen R. 2000. Strict forest reserves in Europe: efforts to enhance biodiversity and research on forests left for free development in Europe (EU-COST-Action E4) Forestry 73:107-118.

Pech, P., J. Dolanský, R. Hrdlička, and J. Lepš. 2015. Differential response of communities of plants, snails, ants and spiders to long-term mowing in a small-scale experiment. Community Ecology 16:115–124.

Penick, C. A., and W. R. Tschinkel. 2008. Thermoregulatory brood transport in the fire ant, *Solenopsis invicta*. Insectes Sociaux 55:176–182.

Perfecto, I., and R. Snelling. 1995. Biodiversity and the transformation of a tropical agroecosystem: Ants in coffee plantations. Ecological Applications 5:1084–1097.

Perfecto, I., J. Vandermeer, P. Hanson, and V. Cartín. 1997. Arthropod biodiversity loss and the transformation of a tropical agro-ecosystem. Biodiversity and Conservation 6:935–945.

Pfeiffer, M., D. Mezger, and J. Dyckmans. 2014. Trophic ecology of tropical leaf litter ants (Hymenoptera: Formicidae)– a stable isotope study in four types of Bornean rain forest. Myrmecological News 19:31–41.

Philpott, S. M., I. Perfecto, I. Armbrecht, and C. L. Parr. 2010. Ant diversity and function in disturbed and changing habitats. Pages 137–156 *in* L. Lach, C. L. Parr, and K. L. Abbott, editors. Ant Ecology. Oxford University Press, New York.

Pihlgren, A., L. Lenoir, and H. Dahms. 2010. Ant and plant species richness in relation to grazing, fertilisation and topography. Journal for Nature Conservation 18:118–125.

Piper, S. D., C. P. Catterall, J. J. Kanowski, and H. C. Proctor. 2009. Biodiversity recovery during rainforest reforestation as indicated by rapid assessment of epigaeic ants in tropical and subtropical Australia. Austral Ecology 34:422–434.

Pohl, G. R., D. W. Langor, and J. R. Spence. 2007. Rove beetles and ground beetles (Coleoptera: Staphylinidae, Carabidae) as indicators of harvest and regeneration practices in western Canadian foothills forests. Biological Conservation 137:294–307.

Poschlod, P., and M. F. WallisDeVries. 2002. The historical and socioeconomic perspective of calcareous grasslands - Lessons from the distant and recent past. Biological Conservation 104:361-376.

Pro Silva (2012) Pro Silva and biodiversity. https://prosilvaeurope.wordpress.com/prosilva-forestry-principles- 2012/.

Puettmann, K. J., S. M. G. Wilson, S. C. Baker, P. J. Donoso, L. Drössler, G. Amente, B. D. Harvey, T. Knoke, Y. Lu, S. Nocentini, F. E. Putz, T. Yoshida, and J. Bauhus. 2015. Silvicultural alternatives to conventional even-aged forest management - What limits global adoption? Forest Ecosystems 2.

Punttila, P. 1996. Succession, forest fragmentation and the distribution of wood ants. Oikos 75:291–298.

Punttila, P., Y. Haila, J. Niemela, and T. Pajunen. 1994. Ant communities in fragments of old-growth Taiga and managed surroundings. Annales Zoologici Fennici 31:131–144.

Punttila, P., Y. Haila, T. Pajunen, and H. Tukia. 1991. Colonisation of clearcut forests by ants in the Southern Finnish Taiga: A quantitative survey. Oikos 61:250–262.

Putz, F. E., P. A. Zuidema, T. Synnott, M. Peña-Claros, M. A. Pinard, D. Sheil, J. K. Vanclay, P. Sist, S. Gourlet-Fleury, B. Griscom, J. Palmer, and R. Zagt. 2012. Sustaining conservation values in selectively logged tropical forests: The attained and the attainable. Conservation Letters 5:296–303.

Rackham, O. 2008. Ancient woodlands: Modern threats. New Phytologist 180:571–586.

Radchenko, A. G., and G. W. Elmes. 2010. Myrmica ants (Hymenoptera: Formicidae) of the Old World. Page Fauna Mundi. Natura Optima Dux Foundation, Warsaw, Poland.

Radnan, G. N., H. Gibb, and D. J. Eldridge. 2018. Soil surface complexity has a larger effect on food exploitation by ants than a change from grassland to shrubland. Ecological Entomology 43:379–388.

Ratajczak, Z., J. B. Nippert, and S. L. Collins. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. Ecology 93:697–703.

Reiss, K. Z. 2001. Using phylogenies to study convergence: the case of the ant-eating mammals'. American Zoologist 41:507–525.

Reyes-López, J., N. Ruiz, and J. Fernández-Haeger. 2003. Community structure of ground-ants: The role of single trees in a Mediterranean pastureland. Acta Oecologica 24:195–202.

Rondeux, J., and C. Sanchez. 2010. Review of indicators and field methods for monitoring biodiversity within national forest inventories. Core variable: Deadwood. Environmental Monitoring and Assessment 164:617–630.

Rosumek, F. B., F. A. O. Silveira, F. De S. Neves, N. P. Newton, L. Diniz, Y. Oki, F. Pezzini, G. W. Fernandes, and T. Cornelissen. 2009. Ants on plants: a meta-analysis of the role of ants as plant biotic defenses. Oecologia 160:537–549.

Roth, D. S., I. Perfecto, and B. Rathcke. 1994. The effects of management systems on ground-foraging ant diversity in Costa Rica. Ecological Applications 4:423–436.

Rüther, C., and H. Walentowski. 2008. Tree species composition and historic changes of the Central European oak / beech region. Pages 61–88 *in* Floren, A. and Schmidl, J. (eds): Canopy arthropod research in Europe. bioform entomology, Nuremberg, Germany.

Ryder Wilkie, K. T., A. L. Mertl, and J. F. A. Traniello. 2009. Diversity of ground-dwelling ants ( Hymenoptera : Formicidae ) in primary and secondary forests in Amazonian Ecuador. Myrmecological News 12:139–147.

Sala, O. E. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770–1774.

Sammul, M., K. Kull, A. Tamm, S. F. Geobotanica, and N. Mar. 2003. Clonal growth in a species-rich grassland : Results of a 20-year fertilization experiment. Folia Geobotanica 38:1–20.

Samways, M. J. 2005. Insect diversity conservation. Page Insect Diversity Conservation.

Sanders, N. J., J. P. Lessard, M. C. Fitzpatrick, and R. R. Dunn. 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. Global Ecology and Biogeography 16:640–649.

Sarty, M., K. L. Abbott, and P. J. Lester. 2006. Habitat complexity facilitates coexistence in a tropical ant community. Oecologia 149:465–473.

Schall, P., M. M. Gossner, S. Heinrichs, M. Fischer, S. Boch, D. Prati, K. Jung, V. Baumgartner, S. Blaser, S. Böhm, F. Buscot, R. Daniel, K. Goldmann, K. Kaiser, T. Kahl, M. Lange, J. Müller, J. Overmann, S. C. Renner, E.-D. Schulze, J. Sikorski, M. Tschapka, M. Türke, W. W. Weisser, B. Wemheuer, T. Wubet, and C. Ammer. 2018. The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of Applied Ecology 55:267–278.

Schelhaas, M. J., G. J. Nabuurs, and A. Schuck. 2003. Natural disturbances in the European forests in the 19th and 20th centuries. Global Change Biology 9:1620–1633.

Schofield, S. F., T. R. Bishop, and C. L. Parr. 2016. Morphological characteristics of ant assemblages (Hymenoptera: Formicidae) differ among contrasting biomes. Myrmecological News 23:129–137.

Seibold, S., C. Bässler, P. Baldrian, L. Reinhard, S. Thorn, M. D. Ulyshen, I. Weiß, and J. Müller. 2016a. Dead-wood addition promotes non-saproxylic epigeal arthropods but effects are mediated by canopy openness. Biological Conservation 204:181–188.

Seibold, S., C. Bässler, R. Brandl, B. Büche, A. Szallies, S. Thorn, M. D. Ulyshen, and J. Müller. 2016b. Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. Journal of Applied Ecology 53:934–943.

Seifert, B. 2007. Die Ameisen Mittel- und Nordeuropas. lutra Verlags- und Vertriebsgesellschaft, Tauer, Germany.

Seifert, B. 2017. The ecology of Central European non-arboreal ants – 37 years of a broad-spectrum analysis under permanent taxonomic control. Soil Organisms 89:1–67.

Seifert, B. 2018. The Ants of Central and North Europe. lutra Verlags- und Vertriebsgesellschaft, Tauer, Germany.

Shortall, R. C., A. Moore, E. Smith, J. M. Hall, P. I. Woiwod, and R. Harrington. 2009. Long-term changes in the abundance of flying insects. Insect Conservation and Diversity 2:251–260.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Oikos:11–41.

Silva, R. R., and C. R. F. Brandão. 2014. Ecosystem-wide morphological structure of leaf-litter ant communities along a tropical latitudinal gradient. PloS ONE 9:e93049.

Simons, N. K., M. M. Gossner, T. M. Lewinsohn, S. Boch, M. Lange, J. Müller, E. Pašalić, S. A. Socher, M. Türke, M. Fischer, and W. W. Weisser. 2014. Resource-mediated indirect effects of grassland management on arthropod diversity. PLoS ONE 9:e107033.

Simons, N. K., M. M. Gossner, T. M. Lewinsohn, M. Lange, M. Türke, and W. W. Weisser. 2015. Effects of land-use intensity on arthropod species abundance distributions in grasslands. Journal of Animal Ecology 84:143–154.

Simons, N. K., T. Lewinsohn, N. Blüthgen, F. Buscot, S. Boch, R. Daniel, M. M. Gossner, K. Jung, K. Kaiser, J. Müller, D. Prati, S. C. Renner, S. A. Socher, I. Sonnemann, C. N. Weiner, M. Werner, T. Wubet, S. Wurst, and W. W. Weisser. 2017. Contrasting effects of grassland management modes on species-abundance distributions of multiple groups. Agriculture, Ecosystems and Environment 237:143–153.

Simons, N. K., and W. W. Weisser. 2017. Agricultural intensification without biodiversity loss is possible in grassland landscapes. Nature Ecology and Evolution 1:1136–1145.

Simons, N. K., W. W. Weisser, and M. M. Gossner. 2016. Multi-taxa approach shows consistent shifts in arthropod functional traits along grassland land-use intensity gradient. Ecology 97:754–764.

Sjödin, N. E., J. Bengtsson, and B. Ekbom. 2008. The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. Journal of Applied Ecology 45:763–772.

Socher, S. A., D. Prati, S. Boch, J. Müller, H. Baumbach, S. Gockel, A. Hemp, I. Schöning, K. Wells, F. Buscot, E. K. V. Kalko, K. E. Linsenmair, E. D. Schulze, W. W. Weisser, and

M. Fischer. 2013. Interacting effects of fertilization, mowing and grazing on plant species diversity of 1500 grasslands in Germany differ between regions. Basic and Applied Ecology 14:126–136.

Socher, S. A., D. Prati, S. Boch, J. Müller, V. H. Klaus, N. Hölzel, and M. Fischer. 2012. Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. Journal of Ecology 100:1391–1399.

Soliveres, S., P. Manning, D. Prati, M. M. Gossner, F. Alt, H. Arndt, V. Baumgartner, J. Binkenstein, K. Birkhofer, S. Blaser, N. Blüthgen, S. Boch, S. Böhm, C. Börschig, F. Buscot, T. Diekötter, J. Heinze, N. Hölzel, K. Jung, V. H. Klaus, A.-M. Klein, T. Kleinebecker, S. Klemmer, J. Krauss, M. Lange, E. K. Morris, J. Müller, Y. Oelmann, J. Overmann, E. Pašalić, S. C. Renner, M. C. Rillig, H. M. Schaefer, M. Schloter, B. Schmitt, I. Schöning, M. Schrumpf, J. Sikorski, S. A. Socher, E. F. Solly, I. Sonnemann, E. Sorkau, J. Steckel, I. Steffan-Dewenter, B. Stempfhuber, M. Tschapka, M. Türke, P. Venter, C. N. Weiner, W. W. Weisser, M. Werner, C. Westphal, W. Wilcke, V. Wolters, T. Wubet, S. Wurst, M. Fischer, and E. Allan. 2016. Locally rare species influence grassland ecosystem multifunctionality. Philosophical Transactions of the Royal Society B: Biological Sciences 371:20150269.

Sorvari, J., and H. Hakkarainen. 2004. Habitat-related aggressive behaviour between neighbouring colonies of the polydomous wood ant *Formica aquilonia*. Animal Behaviour 67:151–153.

Sorvari, J., and H. Hakkarainen. 2005. Deforestation reduces nest mound size and decreases the production of sexual offspring in the wood ant *Formica aquilonia*. Annales Zoologici Fennici 42:259–267.

Sorvari, J., and H. Hakkarainen. 2007. Wood ants are wood ants: Deforestation causes population declines in the polydomous wood ant *Formica aquilonia*. Ecological Entomology 32:707–711.

Sorvari, J., and H. Hakkarainen. 2009. Forest clear-cutting causes small workers in the polydomous wood ant *Formica aquilonia*. Annales Zoologici Fennici 46:431–438.

Stewart, G. B., and A. S. Pullin. 2008. The relative importance of grazing stock type and grazing intensity for conservation of mesotrophic “old meadow” pasture. Journal for Nature Conservation 16:175–185.

Stuart-Smith, R. D., A. E. Bates, J. S. Lefcheck, J. E. Duffy, S. C. Baker, R. J. Thomson, J. F. Stuart-smith, N. A. Hill, S. J. Kininmonth, L. Airoldi, M. A. Becerro, S. J. Campbell, T. P. Dawson, S. A. Navarrete, G. A. Soler, E. M. A. Strain, T. J. Willis, and G. J. Edgar. 2013. Integrating abundance and functional traits revealsnew global hotspots of fish diversity. Nature 501:539–542.

Styrsky, J. D., and M. D. Eubanks. 2007. Ecological consequences of interactions between ants and honeydew-producing insects. Proceedings of the Royal Society B: Biological Sciences 274:151–164.

Tausan, I., J. Dauber, M. R. Trica, and B. Marko. 2017. Succession in ant communities (Hymenoptera: Formicidae) in deciduous forest clear-cuts - an Eastern European case study. European Journal of Entomology 114:92–100.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. Journal of Biogeography 31:79-92.

Thomas, J. A., D. J. Simcox, and R. T. Clarke. 2009. Successful conservation of a threatened *Maculinea* butterfly. Science 325:80–83.

Thomas, J. A., M. G. Telfer, D. B. Roy, C. D. Preston, J. J. D. Greenwood, J. Asher, R. Fox, R. T. Clarke, and J. H. Lawton. 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science 303:1879–1881.

Thorbek, P., and T. Bilde. 2004. Reduced numbers of generalist arthropod predators after crop management. Journal of Applied Ecology 41:526–538.

Tilman, D. 1986. A consumer-resource approach to community structure. Integrative and Comparative Biology 26:5–22.

Tilman, D. 2001. Functional Diversity. Pages 109–121 *in* Levin, S.A. (editors) Encyclopedia of Biodiversity, Volume 3. Academic Press, London, United Kingdom

Topp, W. 2003. Phenotypic plasticity and development of cold-season insects (Coleoptera: Leiodidae) and their response to climatic change. European Journal of Entomology 100:233–243.

Del Toro, I. 2013. Diversity of Eastern North American Ant Communities along Environmental Gradients. PLoS ONE 8: e67973.

Del Toro, I., R. R. Ribbons, and S. L. Pelini. 2012. The little things that run the world revisited: A review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). Myrmecological News 17:133–146.

Del Toro, I., R. R. Silva, and A. M. Ellison. 2015. Predicted impacts of climatic change on ant functional diversity and distributions in eastern North American forests. Diversity and Distributions 21:781–791.

Del Toro, I., K. Towle, D. N. Morrison, and S. L. Pelini. 2013. Community structure and ecological and behavioral traits of ants (Hymenoptera: Formicidae) in Massachusetts open and forested habitats. Northeastern Naturalist 20:103–114.

Underwood, E. C., and B. L. Fisher. 2006. The role of ants in conservation monitoring: If, when, and how. Biological Conservation 132:166–182.

Vasconcelos, H. L. 1999. Effects of forest disturbance on the structure of ground-foraging ant communities in central Amazonia. Biodiversity & Conservation 8:409–420.

Vasconcelos, H. L., M. F. Leite, J. M. S. Vilhena, A. P. Lima, and W. E. Magnusson. 2008. Ant diversity in an Amazonian savanna: Relationship with vegetation structure, disturbance by fire, and dominant ants. Austral Ecology 33:221–231.

Vasconcelos, H. L., J. M. S. Vilhena, and G. J. A. Caliri. 2000. Responses of ants to selective logging of a central Amazonian forest. Journal of Applied Ecology 37:508–514.

Véle, A., J. Holuša, and J. Horák. 2016. Ant abundance increases with clearing size. Journal of Forest Research 21:110–114.

Watt, A. D., N. E. Stork, and B. Bolton. 2002. The diversity and abundance of ants in relation to forest disturbance and plantation establishment in southern Cameroon. Journal of Applied Ecology 39:18–30.

Way, M. J., and K. C. Khoo. 1992. Role of ants in pest management. Annual Review of

Entomology 37:479–503.

Whitford, W. G., J. Van Zee, M. S. Nash, W. E. Smith, and J. E. Herrick. 1999. Ants as indicators of exposure to environmental stressors in North American desert grasslands. Environmental Monitoring and Assessment 54:143–171.

Wiescher, P. T., J. M. C. Pearce-Duvet, and D. H. Feener. 2012. Assembling an ant community: Species functional traits reflect environmental filtering. Oecologia 169:1063–1074.

Wiezik, M., M. Svitok, A. Wieziková, and M. Dovčiak. 2013. Shrub encroachment alters composition and diversity of ant communities in abandoned grasslands of western Carpathians. Biodiversity and Conservation 22:2305–2320.

Wilson, E. O., and B. Hölldobler. 2005. The rise of the ants: a phylogenetic and ecological explanation. Proceedings of the National Academy of Sciences of the United States of America 102:7411–7414.

Wilson, J. B., R. K. Peet, J. Dengler, and M. Pärtel. 2012. Plant species richness: The world records. Journal of Vegetation Science 23:796–802.

Winfree, R., I. Bartomeus, and D. P. Cariveau. 2011. Native pollinators in anthropogenic habitats. Annual Review of Ecology, Evolution, and Systematics 42:1–22.

Woinarski, J. C. Z., A. N. Andersen, T. B. Churchill, and A. J. Ash. 2002. Response of ant and terrestrial spider assemblages to pastoral and military land use, and to landscape position, in a tropical savanna woodland in northern Australia. Austral Ecology 27:324–333.

Yanoviak, S. P., C. Silveri, A. Y. Stark, J. T. Van Stan, and D. F. Levia. 2017. Surface roughness affects the running speed of tropical canopy ants. Biotropica 49:92–100.

Yates, M., N. Andrew, M. Binns, and H. Gibb. 2014. Morphological traits: predictable responses to macrohabitats across a 300 km scale. PeerJ 2:e271.

Yoshimura, M. 2009. Impact of secondary forest management on ant assemblage composition in the temperate region in Japan. Journal of Insect Conservation 13:563–568.

Zechmeister, H. G., I. Schmitzberger, B. Steurer, J. Peterseil, and T. Wrbka. 2003. The influence of land-use practices and economics on plant species richness in meadows. Biological Conservation 114:165–177.

## (Eidesstattliche) Versicherungen und Erklärungen

(§ 9 Satz 2 Nr. 3 PromO BayNAT)

*Hiermit versichere ich eidesstattlich, dass ich die Arbeit selbstständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe (vgl. Art. 64 Abs. 1 Satz 6 BayHSchG).*

(§ 9 Satz 2 Nr. 3 PromO BayNAT)

*Hiermit erkläre ich, dass ich die Dissertation nicht bereits zur Erlangung eines akademischen Grades eingereicht habe und dass ich nicht bereits diese oder eine gleichartige Doktorprüfung endgültig nicht bestanden habe.*

(§ 9 Satz 2 Nr. 4 PromO BayNAT)

*Hiermit erkläre ich, dass ich Hilfe von gewerblichen Promotionsberatern bzw. -vermittlern oder ähnlichen Dienstleistern weder bisher in Anspruch genommen habe noch künftig in Anspruch nehmen werde.*

(§ 9 Satz 2 Nr. 7 PromO BayNAT)

*Hiermit erkläre ich mein Einverständnis, dass die elektronische Fassung meiner Dissertation unter Wahrung meiner Urheberrechte und des Datenschutzes einer gesonderten Überprüfung unterzogen werden kann.*

(§ 9 Satz 2 Nr. 8 PromO BayNAT)

*Hiermit erkläre ich mein Einverständnis, dass bei Verdacht wissenschaftlichen Fehlverhaltens Ermittlungen durch universitätsinterne Organe der wissenschaftlichen Selbstkontrolle stattfinden können.*

…………………………………………………………………………………….

Ort, Datum, Unterschrift