

The effect of forest age and habitat structure on the ground-dwelling ant assemblages of lowland poplar plantations

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- Abstract**
- 1 Intensive management causes significant changes to the habitat structure of forest stands and threatens forest specialist insect species. To assess and counteract the effect of periodic intensive forestry interventions, such as clear-cutting and reforestation, it is important to adequately quantify the recovery rate and composition of the native biota. We aimed to characterize the above parameters for ant assemblages in forests with different structure and age.
 - 2 Epigeic ant assemblages were studied using pitfall traps in young (6–10 years old), middle-aged (23–26 years old) and mature (35–37 years old) poplar forest plantations in the Kiskunság region of Hungary.
 - 3 Species richness of ant assemblages and the abundance of nonforest ants did not differ among the age classes. The abundance of forest specialist ants was, however, higher in middle-aged and mature stands compared with young plantations. The assemblage composition of ants significantly correlated with habitat structure and forest age.
 - 4 We conclude that nonforest ant species can persist throughout the entire forestry cycle in poplar plantations with moderate tree density. The present study suggests that forest age and habitat structure together shape the ant assemblages of lowland poplar plantations.

Keywords Clear-cut, forest management, forestry cycle, Kiskunság.

Introduction

During the last century, the intensification of forestry practices has resulted in significant ecological changes in Central European forests (Oxbrough *et al.*, 2014). The species composition of forests has shifted towards non-native tree species and the habitat structure has been homogenized and simplified (Paillet *et al.*, 2010). Intensive forestry management induces changes in the composition of plant and invertebrate species, usually by reducing microhabitat diversity, which in turn reduces the number of species, especially the number of habitat specialists (Okland *et al.*, 2003; Klimes *et al.*, 2012).

The recovery of ground-dwelling forest-specific assemblages in the reforested habitats may depend on the dispersal ability of the species. Previous studies indicate that the number of invertebrate species increases at clear-cut forest sites because of the influx of generalist and open habitat species (Riley & Browne, 2011; Magura *et al.*, 2015). These species have been reported to occur at reforested sites until the forest canopy closes

(Niemelä *et al.*, 1996; Koivula *et al.*, 2002). Active species can colonize young forests easily and establish viable populations (Magura *et al.*, 2015). Proximity to undisturbed mature forests may also increase the recolonization success of forest invertebrates in areas influenced by harvesting or natural disturbance (Baker *et al.*, 2013).

Ants are a diverse and locally very abundant group of omnivorous forest arthropods. Biotic interactions, particularly competition, play an important role in shaping their assemblages (Cerdá *et al.*, 1998; Chong *et al.*, 2011). Abundant and behaviourally dominant species can affect the species richness and the distribution of other ants in the assemblage because they can monopolize concentrated food sources and reduce the number of other ant species within their foraging area (Parr & Gibb, 2010; Baccaro *et al.*, 2012). Dominant ant species can also reduce the abundance of other ground-dwelling invertebrates via direct predation or interference competition (Mestre *et al.*, 2012; Hawes *et al.*, 2013). However, numerous studies emphasize that habitat structure is also important in determining the structure of ant communities (Gallé, 1991, 1999; Alvarado, 2000; Arnan *et al.*, 2009; Gibb, 2011).

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The present study analyses the effects of habitat parameters and forest age on the diversity and composition of ground dwelling ant assemblages in a forest-rich landscape in Southern Hungary. We hypothesized that forest age and habitat structure have an effect on the species richness and species composition of ant assemblages. We expected a higher abundance of good-colonizer and generalist species in the younger forests, whereas forest specialists (i.e. behaviourally dominant red-wood ants) are expected to occur mainly in the middle-aged and older forests.

Materials and methods

Study sites and sampling

The present study was carried out in the southern part of the Hungarian Great Plain. As result of the intensive management, the forests of the region consist of stands with various age, structure and composition. The most widespread tree species include the non-native black locust (*Robinia pseudoacacia*), pines (*Pinus spp.*) and the native silver poplar (*Populus alba*). We established 15 study sites near Bugacpusztaháza village (approximately 46°42'N, 19°36'; see Supporting information, Appendix S1). The study sites were poplar forest plantations where less than 25% of the trees were black locusts. We used a space-for-time substitution procedure to represent the consecutive stages of the forestry cycle. After clear-cuttings, mechanical soil treatment is applied in the region, resulting in bare soil surfaces. Newly established plantations (i.e. less than 6 years old) were excluded from the study because airborne sand precluded the pitfall trap sampling of ground-dwelling fauna. Three stages were sampled. (i) Young plantations, aged between 6 and 10 years. The canopy closure was almost complete, and the shrub and herb layers were sparse with a very low cover of native dicots (mean \pm SD: 2.65 \pm 2.07%). By contrast, the cover of the invasive plant *Asclepias syriaca* was high at young plantations (mean \pm SD: 15.5 \pm 9.25%). (ii) Middle-aged stands 23–26-year-old stands. The closure of the canopy was complete, and the shrub layer was denser compared with other age classes. (iii) Mature forests before clear-cut harvesting; aged 35–37 years. The highest amount of woody debris was found in this stage; therefore, the conditions for nest building was presumably the best in this age group.

The size of the plantations did not differ between age classes (young plantations: 7.08 \pm 5.55 ha, middle-aged stands: 7.70 \pm 5.77 ha, old forests: 11.52 \pm 5.82 ha; one-way analysis of variance, $F = 0.881$, $P = 0.449$).

The surrounding landscape mainly consisted of different aged forests (66.7 \pm 20.6%) closed canopy forests in a 500-m buffer around the sampling sites, agricultural fields and pastures (Gallé *et al.*, 2014a). To sample the forest floor ant fauna, pitfall traps were used. Ten traps were installed at each site and were placed 5 m apart. The pitfall trap method does not give an exact density estimate; rather, it assesses the activity density of ants. However, several studies have demonstrated that the pitfall trap method is a relatively good tool for comparing the assemblage structure of ants because the cruising radius of workers can reach 150 m around their usually fixed nests (Andersen, 1991; Schlick-Steiner *et al.*, 2006; Underwood & Fisher, 2006; Gotelli *et al.*, 2011). Hand-sampling is more efficient than pitfall traps

because it usually yields more species and direct estimates of nest densities; however, hand-sampling can be affected by the expertise of the collector and vegetation structure of the sampled habitat. In the case of the present study, the structure of the understory vegetation and the amount of woody debris were different; thus, we used the pitfall trap method exclusively. The data of the pitfall traps were pooled prior to data analyses. To minimize the confounding effect of edges, traps were placed at least 50 m from the edge of the studied forest stand because Larrivée *et al.* (2008) found that ground-dwelling invertebrates of adjacent habitats do not penetrate this far into the forest interior. We used plastic jars as traps (6.5 cm in diameter), filled them up to one-third with a 70% ethylene glycol dissolved in water and added a few drops of an odourless detergent (Koivula *et al.*, 2003; Schmidt *et al.*, 2006). A plastic roof was placed above each trap to prevent dilution of the preservative solution by rain. Trapping was conducted continuously between 19 May and 20 June 2012 (32 days).

To characterize habitat structure, the percentage cover of leaf litter, understory vegetation and the average height of the herbaceous vegetation were recorded within four 1 \times 1 m quadrats at each site. The photographs were analyzed in the laboratory by visually assessing the proportion of leaves. The decaying woody material was collected and measured after the invertebrate sampling. We measured the cumulative length of fine (diameter <8 cm) and coarse (diameter 8–15 cm) woody debris and recorded the presence of bigger trunks (diameter >15 cm) in four 2 \times 2 m quadrats at each site. We did not find significant correlations between the habitat parameters (see Supporting information, Appendix S2).

We identified ants using the keys of Seifert (2007) and Czechowski *et al.* (2012). Nomenclature follows Czechowski *et al.* (2012).

Statistical analysis

Characteristic ant species of the forestry cycle stages were identified by the IndVal (Indicator Value) calculation on the basis of the relative frequency and relative average abundance of the species in the samples (Dufrene & Legendre, 1997). The statistical significance of the species indicator values was evaluated by a Monte Carlo procedure.

The effect of forest stage and habitat parameters on ant species richness were tested with general linear models (GLM) with poisson error term and log-link function, followed by stepwise model selection procedure on the basis of Akaike's information criterion. We allocated habitat requirements to ant species on the basis of Czechowski *et al.* (2012); the categories that we used were the forest specialists and nonforest species (species with no prevalence in forests). The effects of forest stage and habitat structure on the amount of ants belonging to the above categories were tested with GLMs with a negative binomial error term because of the overdispersion of the data.

The multivariate response of assemblages to forest stage and habitat structure was studied with constrained ordination. A preliminary detrended correspondence analysis was conducted to gain insight into how the species respond to the environmental gradient. The gradient length was 2.17 and did not exceed 4.0, indicating a linear response of the species variance to

the environmental gradient. We performed a linear redundancy analysis. To identify the parameters that explain a significant proportion of the variation, we performed a stepwise model selection procedure (ordisstep function in the Vegan package in R; R Foundation for Statistical Computing, Austria). The marginal effects of the variables were calculated and tested by Monte Carlo permutation tests with 5000 permutations.

Similarity patterns in species composition and assemblage structure between the sampling sites were explored using non-metric multidimensional scaling (NMDS) based on Bray–Curtis distance matrix. To visualize their effect, the significant environmental variables of the redundancy analysis were fitted passively onto the NMDS ordination plot.

Results

We collected 13 147 ant individuals from 22 species (see Supporting information, Appendix S3). This included 2006 individuals of 17 species in the young plantations, 5933 individuals of 18 species in the middle-aged stands and 5208 individuals of 18 species in the mature plantations. The most common ant species was *Formica (Serviformica) fusca* Linnaeus 1758, representing 6258 individuals. This very common opportunistic ant species is at the lowest level of the interspecific competition hierarchy (Czechowski *et al.*, 2012). Two *Lasius* species, *Lasius paralienus* (Seifert, 1992) and *Lasius niger* (Linnaeus, 1758), were also abundant. These widespread species are not forest species but were found in most of the sampling sites. Members of the *Formica rufa* group are the top dominant species in the interspecific competition hierarchy of forest assemblages (Pisarski & Vepsäläinen, 1989). Five species, but only 197 specimens, of these territorial mound-building ants were collected.

Three significant indicator species were identified with the indicator value procedure: *Tetramorium caespitum* (Linnaeus, 1758) for young stands (IndVal = 0.792, $P = 0.015$), and *Temnothorax crassispinus* (Karavaiev, 1926) (IndVal = 0.718, $P = 0.031$) and *Temnothorax unifasciatus* (Latreille, 1798) (IndVal = 0.607, $P = 0.010$) for mature plantations.

We found no significant model for the species richness of ant assemblages; however, in accordance with our hypothesis, the abundance of forest specialist species was lower in the young plantation than in the middle-aged plantations ($Z = 5.114$, $P < 0.001$, $n = 15$) and the old forest stands ($Z = 7.799$, $P < 0.001$, $n = 15$). The presence of tree trunks ($Z = -2.190$, $P = 0.028$, $n = 15$) and the vegetation cover ($Z = -3.492$, $P < 0.001$, $n = 15$) also influenced the abundance of forest ants according to the GLMs. The structural parameters influenced the abundance of nonforest ants as well (presence of tree trunks: $Z = -4.790$, $P < 0.001$, $n = 15$; vegetation cover: $Z = 2.929$, $P = 0.003$, $n = 15$; average height of the herbaceous vegetation: $Z = -3.343$, $P < 0.001$, $n = 15$), although forest age had no detectable effect on them.

The results of the significant redundancy analysis model showed that the age of the forests ($F = 5.825$, $P = 0.004$, $N = 15$), the cumulative length of fine ($F = 4.021$, $P = 0.040$, $N = 15$) and coarse ($F = 7.176$, $P = 0.008$, $N = 15$) woody debris had a significant role in shaping the composition of the studied ant assemblages (Fig. 1).

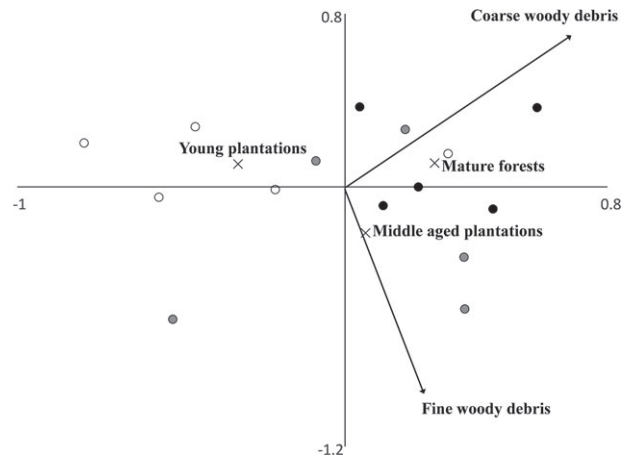


Figure 1 The result of the non-metric multidimensional scaling model. The symbols indicate the age of the forests. Open circles, young plantations; grey circles, middle-aged plantations; black circles, mature plantations. The significant parameters of the redundancy analysis models are fitted passively onto the diagram. The crosses represent the age classes of the plantations.

Discussion

The present study, in line with our hypothesis, showed that both forest age and habitat structure significantly influenced the ant assemblages. The effect was different for forest specialist species and for nonforest species; forest age was significant for forest species, although we did not find differences in nonforest ant abundances among the forest stages.

The indicator species analysis (IndVal procedure) showed that one ant species, *T. caespitum*, was specific to young plantations, whereas other species were typical of mature stands. *Tetramorium caespitum* is a semixerophilous species and it is common on dry sandy soils with sparse vegetation. This species defends food resources and nests (Cerdá *et al.*, 2009) and *T. caespitum* is at the high level of the dominance hierarchy in young plantations as a result of the low abundance of red wood ants. The analysis also showed that *T. crassispinus* and *T. unifasciatus* were characteristic of mature stands, confirming that both species have a strong affinity to forest habitats (Czechowski *et al.*, 2012).

Numerous studies have documented significant changes in invertebrate assemblages after clear-cutting (Koivula, 2011; Magura *et al.*, 2015). Forestry practices and soil preparation destroy microhabitats required by forest specialist species, causing the disappearance of most of these species from young stands (Magura *et al.*, 2003). A rapid initial colonization of generalist and open habitat specialist invertebrates takes place after the disturbance of the habitat (Bröring & Wiegler, 2005; Gallé *et al.*, 2014a). Besides generalist and open habitat species with good colonizing abilities, some forest specialist species can also persist, which results in an increased abundance or diversity in young forest stands (Koivula *et al.*, 2002). Several studies have reported that forest ant assemblages change dramatically within 2 years after clear-cutting (Sorvari & Hakkaraïnen, 2005; Neuvonen *et al.*, 2012); old-growth forest specialists almost disappear, presumably because of the loss of arboreal food resources (Punttila *et al.*, 1991), although Gibb and Johansson (2010)

found that ant workers collected similar amounts of hemipteran honeydew from recently clear-cut sites and the different aged forest stands, suggesting an optimization of foraging effort.

In the present study, we also found that forest age had an effect on the species composition of ant assemblages but that species richness did not differ among forest age classes. We did not find a higher diversity of ants in the young stands and forest age did not have a significant effect on the abundance of nonforest ants. The change in species composition was presumably a result of the colonization by forest ant species.

Regional species pool and landscape structure are also important factors in shaping local diversity. The species composition of invertebrates in recently clear-cut habitats is strongly affected by the presence of the source populations of the potential colonizers (Koivula, 2011); thus, the surrounding matrix and landscape composition have a pronounced effect on recently established habitats. In the present study, the surrounding landscape mainly consisted of different aged forests with various species composition; thus, the source populations of forest specialist species were undoubtedly present in the surrounding landscape.

In accordance with our results, several studies emphasize that the species composition of ant assemblages also responds to structural changes of the habitats (Bestelmeyer & Wiens, 1996; Lubertazzi & Tschinkel, 2003; Lassau & Hochuli, 2004). Several environmental conditions probably change in parallel to changes in the herbaceous vegetation and canopy closure; differences in ground-shading and plant transpiration can create temperature, soil and humidity gradients (Lubertazzi & Tschinkel, 2003). The increasing numbers of fallen and decaying branches can serve as suitable nesting sites for ants (Alvarado, 2000), especially for *F. fusca*, which is the most abundant ant species in the present study.

In general, only a small number of ant species are able to live in closed forests (Holec & Frouz, 2005). Only eight of the collected species were forest specialists, and the abundance of forest ants was lower in the young plantations than in the middle-aged and mature stands. Poplar forests have a relatively open canopy compared with non-native plantations (Gallé *et al.*, 2014b). Generalist and open habitat specialist ant species also occurred in the sampled poplar forests: in the present study, 14 of the 22 species collected had no pronounced prevalence in forests. Other studies emphasize a consistent pattern of insect species composition change in the early stages of the forestry cycle. After canopy closure, the number and abundance of generalist and open habitat species decline (Buddle *et al.*, 2006; Taboada *et al.*, 2008; Oxbrough *et al.*, 2010). However, most studies have been conducted in situations where the mature forests have a closed canopy (e.g. conifer plantations). Our analysis did not show significant differences in the abundance of nonforest species among forest age classes, indicating that, in forest stands with a relatively open tree canopy, these species also persist in later stages of the forestry cycle.

Interference competition has an increasing significance in advanced successional stages (Gallé *et al.*, 1998; Gibb, 2011). In the later stages of succession, changes in habitat properties and the appearance of dominant, aggressive species can lead to the exclusion of early colonizing ant species (Vepsäläinen *et al.*, 2000). Besides foraging on the forest floor, redwood ants also forage efficiently on tree trunks (Lenoir, 2002; Neuvonen *et al.*,

2012) and, in the present study, there was a low abundance of the *F. rufa* group, which might be explained by a weak effect of interference competition in shaping assemblage composition of the forest stands studied.

The present study confirmed the correlation between habitat structure, forest age and ground-dwelling ant assemblages. Besides the forest specialist ants, most generalist species meet their habitat requirements in mature stands. Our results also suggest that the abundance of dominant ants has little effect on the number of species in these ant assemblages, and that forest age is probably more important than interference competition in the case of lowland poplar plantations.

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Supporting information

Additional Supporting information may be found in the online version of this article under the DOI reference: 10.1111/afe.12148

Appendix S1. The location of the study sites.

Appendix S2. Spearman correlation matrix of numeric habitat parameters.

Appendix S3. The list of the collected species and habitat requirements. F, forest specialist; Non-F, non-forest species.

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