Wood-pastures promote environmental and ecological heterogeneity on a small spatial scale

Ádám Lőrincz [a,b,*], Alida Anna Hábenczyus [a,b,c], András Kelemen [a], Bonita Ratkai [a], Csaba Tölgyesi [a,c], Gábor Lőrinczi [a], Kata Frei [a,d], Zoltán Bátori [a,c], István Elek Maák [a,e]

[a] Department of Ecology, University of Szeged, Közép fasor 52, Szeged 6726, Hungary
[b] Doctoral School of Biology, University of Szeged, Közép fasor 52, Szeged 6726, Hungary
[c] MTA-SZTE Lendület Applied Ecology Research Group, University of Szeged, Közép fasor 52, Szeged 6726, Hungary
[d] Doctoral School of Environmental Sciences, University of Szeged, Rerrich Béla tér 1, Szeged 6720, Hungary
[e] Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw 00-679, Poland

HIGHLIGHTS

- Wood-pastures accommodate four different habitat types on a small spatial scale.
- We showed that the habitat types differ in a range of microclimatic parameters.
- These peculiar microclimatic conditions shaped the ant interspecific interactions.
- This led to unique ant activity and community organization patterns.
- Complex landscapes can host distinct communities and promote biodiversity.

GRAPHICAL ABSTRACT
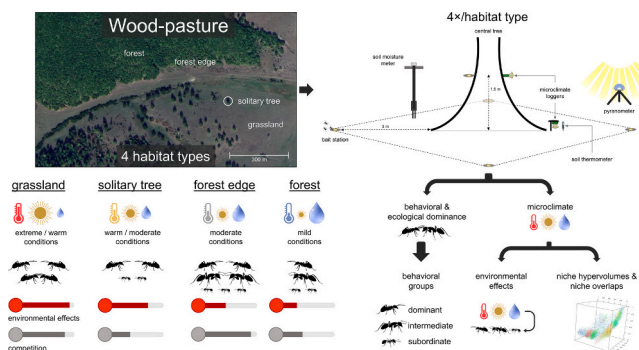
ARTICLE INFO

ABSTRACT

Wood-pastures harbor critical natural and social values and are among the most ancient land use forms of Europe. The crucial conservation value of these silvopastoral systems is generally contributed to their characteristic landscape elements, the solitary trees, which provide microhabitats for a variety of organisms. However, by accommodating four habitat types (grasslands, solitary trees, forests, and forest edges) on a relatively small spatial scale, wood-pastures might host functionally and compositionally distinct arthropod communities, thus enhancing the landscape-level biodiversity. To test this, we assessed the fine-scale microclimatic conditions of the four different habitat types of three wood-pastures and investigated the effects of these conditions on ant activity and community organization patterns. Besides microclimate, niche breadths (quantified by four-dimensional niche hypervolumes), niche overlaps, and interspecific interactions were also considered to assess the importance of interspecific competition in shaping the studied ant communities. The four habitat types showed notable differences in the previous aspects, which resulted in different patterns of ant activity and community organization. Posing ideal conditions (high solar irradiance and temperatures above 25 °C) for ant activity, the grasslands were monopolized by usually 2–3 dominant species with large hypervolumes, while the

subordinates mostly occurred under environmental extremities. Despite their vicinity to the grasslands, solitary trees showed a different pattern, where in total 8 subordinate species associated with specific microclimates were present. The forest edges hosted the most species-rich communities, with 18 species in total, where interspecific interactions played a major role in shaping the activity patterns. A similar result was obtained for forests, although the mild environmental conditions of these habitat types resulted in low overall ant activity. Our results unveil that by posing various microclimatic and structural conditions, wood-pastures enable the coexistence of four ecologically and functionally distinct communities, which makes them ideal targets for biodiversity conservation.

1. Introduction

Wood-pastures are among the most ancient land use forms in Europe, their origins dating back to the Neolithic (Luick, 2008; Bergmeier and Roellig, 2014). Due to the wide geographic range and different management types of these silvopastoral systems (Plieninger et al., 2015), their physiognomy can differ considerably from pastures with scattered trees or shrubs to closed-canopy grazed woodlands (Manning et al., 2006; Bergmeier et al., 2010). Nevertheless, the term generally refers to semi-natural environments, where solitary trees are sparsely distributed in a grazed grassland matrix (Hartel et al., 2013; Plieninger et al., 2015).

These large, often very old trees provide microhabitats for a wide range of species, such as birds (Hartel et al., 2014; Horak et al., 2014), bats (Galindo-González et al., 2000; Lumsden and Bennett, 2005), arboreal and ground-dwelling arthropods (Dunn, 2000; Majer et al., 2000; Falk, 2014; Sebek et al., 2016), saproxylic beetles and flies (Falk, 2014; Lindman et al., 2023), but also to lichens or fungi (Horak et al., 2014). Furthermore, by altering the microclimatic and physicochemical properties of their environment (Rhoades, 1996; Manning et al., 2006), these trees greatly influence the composition of their understory plant communities (Garbarino and Bergmeier, 2014; López-Sánchez et al., 2016). For these reasons, solitary trees within this habitat can be considered keystone structures, as their ecological significance is disproportionally large relative to their spatial extent (Manning et al., 2006; Tölgyesi et al., 2018).

The presence of solitary trees, however, is not the sole factor contributing to the high ecological and conservation value of wood-pastures. The grasslands embedding the solitary trees are traditionally managed as extensively grazed pastures, thus supporting a rich flora and fauna (Rosenthal et al., 2012). Furthermore, as the origin of wood-pastures is linked to the opening-up of woodlands (Bergmeier et al., 2010), closed-canopy forests of various sizes can usually be found in the surrounding landscape. These forests – besides providing habitat for forest-associated species (Horak et al., 2014; Tăuşan et al., 2021) – form edges with the pasture's grasslands, thus creating an ecotone that may host functionally and ecologically distinct communities (Ries et al., 2004; Erdős et al., 2014; Frasconi Wendt et al., 2021). The individual habitat types (solitary trees, grasslands, forests, and their edges) of wood-pastures have the potential to create diverse microclimatic and abiotic conditions, thus enhancing the environmental heterogeneity of the whole system. This, in turn, might enable the coexistence of species with different environmental preferences on a small and intermediate scale (Stein et al., 2014), thus increasing landscape-level biodiversity. By accommodating four habitat types, wood-pastures are good representatives of heterogenous semi-natural habitat mosaics maintained by human activity, and as such, offer an ideal framework to study the underlying mechanisms that enable the coexistence of different communities at small and intermediate spatial scales with a variety of habitat and environmental conditions. Considering the ongoing anthropogenic habitat change, gaining a comprehensive understanding of the interplay between environmental and biotic conditions and the rules governing community organization in semi-natural habitats becomes increasingly relevant for sustaining biodiversity.

We chose ants as our model organisms as they are highly sensitive and responsive to changes in climatic (Gibb et al., 2015) and microclimatic conditions (Perfecto and Vandermeer, 1996; Retana and Cerdá, 2000), and react dynamically to changes in their habitat structure (Farji-Brener et al., 2002; Gallé et al., 2016). Due to the sessile nature of most ant colonies (Wilson, 1971), workers are less likely to move between distant habitats, consequently, their presence is a more accurate indication of site conditions as compared to more mobile animals (Stephens and Wagner, 2006). Furthermore, the competition between ant colonies is confined to well-defined zones (Andersen, 1991), ensuring reliable detection of agonistic interactions between individuals.

The purpose of our research was dual: firstly, we intended to scrutinize the microclimatic differences between the four different habitat types of wood-pastures, and thus uncover the main environmental factors influencing community organization. Secondly, we aimed to investigate the effects of these microclimatic differences and interspecific interactions on the functional and community composition, as well as the activity patterns of an ecologically dominant group of organisms in wood-pastures. Coupling fine-scale microclimatic measurements and observations of interspecific interactions with occurrence data allowed us to take a deeper insight into the underlying mechanisms that structure the communities of these highly heterogenous habitats. We specifically hypothesized that I) the four different habitat types will differ in the measured microclimatic parameters, and II) that these latter will profoundly affect the ant interspecific interactions. Thus, we also hypothesized that III) the microclimate and interspecific interactions will jointly influence the composition and activity patterns of ants, leading to the coexistence of compositionally and functionally distinct ant communities.

2. Materials & methods

2.1. Study sites

Our study was carried out in three wood-pastures of Central and Eastern Europe: 1) Erdőbénye (Zemplén-Mts, North-East Hungary) (N 48.276, E 21.319; 215–245 m a.s.l.), 2) Deuşu (Cluj County, North-West Romania) (N 46.916, E 23.505; 420–490 m a.s.l.), and 3) Rupea, (Braşov County, Central Romania) (N 46.019, E 25.223; 500–580 m a.s.l.) (Fig. 1A). The wood-pastures are of comparable sizes (215 ha, 250 ha, and 393 ha, respectively), and share similar environmental characteristics. The climate is continental with a mean annual precipitation of 600, 600, and 650 mm, and a mean annual temperature of 9.5, 8.3, and 8.2 °C, respectively. Each wood-pasture is embedded into a hilly landscape with gentle slopes and connected to oak-hornbeam forests. Oaks (*Quercus petraea,* and *Q. robur*) are the most common solitary trees, but pear (*Pyrus pyraster,* and *P. communis*) and hornbeam (*Carpinus betulus*) also occur. The surrounding grasslands are dominated by perennial graminoids (*Agrostis capillaris, Festuca pratensis, F. pseudovina,* and *F. rubra*) and are subjected to moderate grazing by sheep (Erdőbénye location), supplemented by cattle and buffalo (Deuşu, Rupea locations) (Fig. 1B).

2.2. Sampling design

Four sampling sites were established in all four habitat types (grasslands, solitary trees, forest edges, and forests; Fig. 1C) from every
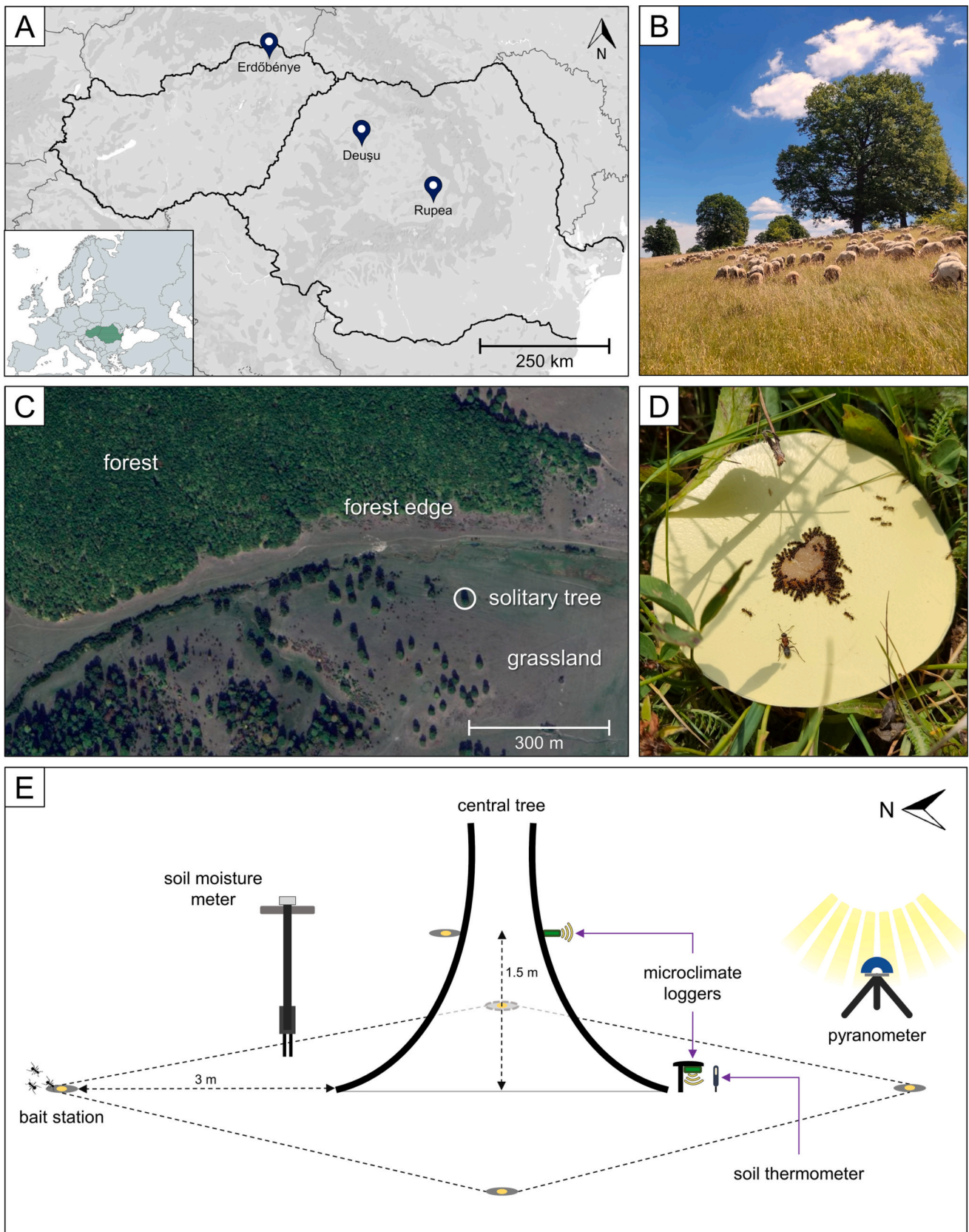
Fig. 1. Study sites and study design. (A) Location of the studied wood-pastures in Hungary and Romania. (B) General physiognomy of a wood-pasture (Deuşu, Romania). (C) Aerial view of a wood-pasture (Deuşu, Romania) with the studied habitat types. (D) Workers of *Tetramorium* cf. *caespitum* and *Formica rufibarbis* on a bait station. (E) Sampling design of the study.

wood-pasture (16 sampling sites in every wood-pasture, i.e., 48 sites in total). The sampling sites were located at least 20 m from each other. Except for grasslands, each sampling site contained a central oak tree. In forests, the central trees were located at least 50 m from the forest edges to exclude any edge effects, meanwhile, in edges, the trees were selected from the outermost tree line. The orientation of forest edges were similar within each wood-pasture with only a slight difference in one location due to the slightly different landscape composition (forest edges facing south-west in Erdőbénye, and south-east in Deuşu and Rupea). Accordingly, we selected solitary oaks embedded in the grassland matrix located at least 50 m from the nearest forest edges. In grasslands, the sampling sites were placed in a rectangular pattern, and each site was located at least 50 m from the nearest forest edge or solitary tree. The field sampling was carried out under fair weather conditions in June 2022, within a 10-day sampling window. In each wood-pasture, the sampling of the four different habitat types was carried out simultaneously, within one sampling day. The three wood-pastures, however, were sampled in five day intervals.

We used non-invasive baiting to assess the species composition and relative abundance of ants (Fig. 1D). In each sampling site, five bait stations were placed in a cross-shaped pattern: four stations were situated 3 m away from the central oak following the cardinal directions (20 bait stations/habitat, 240 in total), and one station at a height of 1.5 m on the north-facing side of the central oak's trunk (Fig. 1E). In grasslands, the central bait station was placed on the ground. Each bait station consisted of a plastic disk (8 cm in diameter) and a quarter-teaspoon of a 1:3 mixture of tuna and honey as bait material. Foraging activity on baits was monitored every 30 min during three observation periods: 7:30 a.m. – 9:30 a.m.; 11:30 a.m. – 2:00 p.m.; 4:00 p.m. – 6:30 p.m. (17 observations/bait station). Based on previous works (e.g., Tăușan et al., 2017; Maák et al., 2020), the selected observation periods corresponded to the main activity periods of diurnal species in similar habitats. During each observation, the number of workers of each ant species on the bait, as well as the interactions between them (e.g., biting, and charging) were recorded. Baits were available ad libitum. Ants were identified to morphospecies or genus level in the field, and representatives were collected and preserved in 95 % ethanol for later species identification in the laboratory using the keys of Czechowski et al. (2012) and Seifert (2018). The specimens were deposited at the Department of Ecology, University of Szeged. The nomenclature follows Bolton's catalogue (Bolton, 2020) and the Hymenoptera Name Server (Johnson, 2007).

To assess the microclimatic differences between the four habitat types, we monitored the changes in a range of abiotic conditions at each sampling site (from 7:30 a.m. to 6:30 p.m.). Air temperature (°C) and relative air humidity (%) were recorded at 5-min intervals using Optin Ambient Data Loggers (ADL-TH3) (145 measurements/device, 12,180 in total). The loggers were encased in a radiation shield and were suspended 10 cm above the ground. In the sampling sites with a central tree (solitary trees, forests, and forest edges), we installed an additional data logger at a height of 1.5 m on the south-facing side of the tree trunk. We chose this side to avoid interfering with the microclimate loggers during our observations of the bait stations installed on the tree trunks. Soil temperature (°C) was recorded in the upper 10 cm of the soil using digital penetration probe thermometers (TFA pocket-digitemp 30.1018). The measurements were conducted at the beginning of each observation period (17 measurements/sampling site, 816 in total). Soil moisture (volumetric water content – VWC%) was also measured at four locations within each sampling site using a FieldScout TDR 350 Soil Moisture Meter. We also recorded the solar irradiance (W/m²) at one location per habitat type every 5 mins using Kipp & Zonen SMP3 pyranometers (145 measurements/device, 1740 in total). The sensors were attached to tripod stands at 50 cm height and were placed at least 20 m from the nearest sampling site to avoid shading by our activities (Fig. 1E).

2.3. Species grouping

To enhance the generalizability of our data and to account for the differences in the species pool of the three studied wood-pastures, ant species were grouped into different behavioral categories. Since the behavioral status of an ant species can be context and habitat-dependent (Punttila et al., 1996; Lach et al., 2010), instead of relying on the literature, we used direct observations and measurements for the construction of behavioral groups. The grouping process was based on two indices that reflect the two components of dominance in ants: behavioral and ecological dominance (Cerdá et al., 1997; Lach et al., 2010). To quantify the behavioral dominance, an aggression index (*A*) was calculated for each species, which is defined as the proportion of aggressive interactions (e.g., charging, biting, and expulsion) directed toward heterospecific workers. Similar indices are commonly used in ant community ecology and are the basis of mapping dominance hierarchies in ant communities (Fellers, 1987; Cerdá et al., 1997, 1998; Bestelmeyer, 2000). To measure ecological dominance, we calculated an evenness value for each species at each habitat type. The evenness values are based on Pielou's J' index:

$$J' = \frac{H}{ln A_v}$$

where H is the Shannon-diversity value of a species and A_v is the number of potentially available bait stations for the same species, i.e., (1) air temperature and relative air humidity measured at the bait station is within the determined activity range of the species, and (2) workers were found at the given habitat of the respective wood-pasture (for the activity ranges, see Table S1). The Shannon-diversity value (*H*) of a species is based on a modified form of the Shannon-diversity index:

$$H = -\sum_{j=1}^{Oc} p_i ln p_i$$

where *Oc* is the number of bait stations occupied by a given species, and *pi* is the proportion of workers present in the ith of *Oc* observations.

Based on the aggression and evenness values, ant species were grouped into three behavioral categories: dominant, intermediate, and subordinate (for the characteristics of the three behavioral groups, see Table 1, for the species list, see Supplemental data). The dominant group consisted of behaviorally and ecologically dominant ant species. The representatives of this group (e.g., *Formica gagates,* and *Lasius niger*) were very abundant in multiple habitat types of the studied wood-pastures, recruited large numbers of workers to the occupied baits, and showed great levels of aggression toward heterospecific workers. Similarly, high aggressivity was shown by the representatives of the intermediate group (e.g., *Camponotus ligniperda,* and *Formica sanguinea*). These ants often outcompeted even the members of the dominant group, although their ecological dominance was less pronounced: they sporadically monopolized some baits but were not abundant throughout their habitats. A similar group is used in the literature – mainly in arid Australian ecosystems – for species that can be locally abundant, but whose occurrence depends on certain physical factors such as climate and soil properties (Andersen, 1986). Although showing a different pattern, one additional

Table 1

Simplified list of the characteristics of ant species belonging to the three behavioral groups. For the species list and index values, see Supplemental data.

Behavioral group	Aggression index (behavioral dominance)	Evenness value (ecological dominance)	Abundance at baits	Occurrence on wood-pastures
Dominant	High	High	High	High
Intermediate	High	Intermediate	Various	Sporadic
Subordinate	Low	Mostly low	Low	Low

species, *Myrmica ruginodis* was also placed into the intermediate category. This species showed a relatively high ecological dominance in woody habitats, although the outcome of its interspecific interactions was context-dependent. The subordinate group consisted of behaviorally and ecologically subordinate species, which were among the rarest ant species in wood-pastures. The representatives of this group (e.g., *Camponotus atricolor,* and *Temnothorax affinis*) were often associated with certain microclimates or microhabitats, showed low levels of aggression, and were easily excluded from the baits by dominant or intermediate species.

2.4. Data analysis

2.4.1. Species number and microclimatic conditions

We used a generalized linear mixed-effect model (Poisson error, maximum likelihood fit) to compare the number of species found in the four different habitat types. The number of species found in different locations and sites within each habitat type was summed for every observation. In the full model, the habitat type was included as a fixed factor, whereas the observation period as a random factor.

To test the effects of the four different habitat types on the measured environmental parameters (soil and air temperature, soil moisture, relative air humidity, and solar irradiation), linear mixed-effect models (Gaussian error, maximum likelihood fit) were used. Prior to analysis, the data of the two microclimate loggers (measuring air temperature and relative air humidity) installed in the same sampling site were averaged for each measurement. In the full models, the habitat type, the three observation periods (morning, midday, and afternoon), and the interaction of the two variables were included as fixed factors, whereas the location (wood-pasture) and the sampling sites within each habitat type were included as nested random factors. However, in the model for solar irradiation, only the location was included as a random factor, as we used only one pyranometer per habitat type. For soil moisture, a separate linear mixed-effect model (Gaussian error, maximum likelihood fit) was built to test the effect of the other microclimatic components (soil and air temperature, relative air humidity, and solar irradiation) on this variable. In the full model, all other scaled microclimatic variables were included as explanatory variables, whereas the location and the sampling sites within each habitat type were included as nested random factors. As this variable was in strong relationship with other microclimatic variables (GLMM, soil temperature: $z = 5.57$; $p < 0.001$; solar irradiation: $z = 10.37$; $p < 0.001$; and air humidity: $z = 6.05$; $p < 0.001$) and was not monitored throughout the day due to the lack of diurnal changes, it was not included in further GLM models, unless tested separately.

2.4.2. Niche hypervolume estimation

In addition to quantifying the fine-scale microclimatic conditions in the four different habitat types, we estimated the breadth of conditions utilized by each species through the construction of multidimensional hypervolumes (Blonder et al., 2014). Hypervolumes represent the niche breadth of each species within a given habitat type and are defined by the bounds of scaled and centered environmental factors (Blonder, 2018). Using the irradiance, air temperature, relative air humidity, and soil temperature values of each occurrence data, four-dimensional hypervolumes were constructed for each species per habitat type. The support vector machine (svm) method (with a default γ parameter value of 0.5) was chosen as it provides a smooth fit around the data and allows for outlier inclusion, hence it is appropriate for fundamental niche modeling applications (Blonder, 2018). Prior to constructing hypervolumes, environmental data were separately min-max normalized across each habitat type. This way, besides accounting for the different measurement units and axis scales, it is ensured that the hypervolume values are unbiased by the different variability of environmental parameters in the four habitat types. Ant species with less than ten occurrences were excluded from the analysis to ensure the reliability of

hypervolume construction (Blonder et al., 2014).

The applied framework also allows for the estimation of the shared volume between two hypervolumes, which is interpreted as the niche overlap of the corresponding species. We used the Jaccard similarity index to quantify the pairwise overlap between hypervolumes for each habitat type. The index ranges from 0 (no overlap) to 1 (complete overlap). As every species had only one hypervolume value per habitat type, the hypervolume and Jaccard values were not further analyzed statistically. Instead, mean values and standard deviations were calculated to quantify the differences between the communities of the four habitat types.

2.4.3. Effects of habitat type, observation period, and competitive interactions

After assigning each ant species to one of the three behavioral groups (dominant, intermediate, subordinate), the abundances of the species belonging to the same group were summed for each observation. To test the effect of the different habitat types on the abundances of the three behavioral groups, GLMMs (Poisson error, maximum likelihood fit) were used. In model over-dispersion, a negative binomial error term was used (Lindén and Mäntyniemi, 2011). In the models, the habitat type and the three observation periods, as well as their interaction were included as fixed factors, whereas the location and sampling site were included as nested random factors. For the intermediate group, only the forest edges and forests could be compared, as there were no intermediate species on grasslands, and only one species (with few occurrences) was present on solitary trees (*Camponotus vagus*, $N = 13$).

We determined the effects of environmental parameters and intergroup interactions on the activity of the ants belonging to the three behavioral groups by using generalized linear mixed-effect models (Poisson error, maximum likelihood fit). We built separate models for each behavioral group at each habitat type. In the models, the scaled environmental parameters and the scaled abundances of the superior groups (if relevant, e.g., dominant and intermediate groups for the subordinates) were included as explanatory variables, whereas the sampling site and the observation period were included as random factors. For the reasons mentioned above, we could include the intermediate group only in the models of forest edges and forests. In every model, we calculated the variance inflation factor (VIF) of each variable to check for multicollinearity. The variable(s) with a VIF value around 5 or above were removed, and a new model was constructed without this variable (James et al., 2013).

2.4.4. General details of the statistical analysis

All statistical analyses were carried out in the R Statistical Environment (R Core Team, 2022). GLMMs were performed using *glmer* and *glmer.nb* functions of the 'lme4' package (Bates and Maechler, 2013). The *emmeans* function ('emmeans' package) was used for sequential post-hoc comparisons among factor levels when performing LMM and GLMM analyses (Lenth, 2020). The four-dimensional hypervolumes were constructed using the *hypervolume_svm* function of the 'hypervolume' package (Blonder et al., 2014). Pairwise hypervolume overlaps were calculated with the *hypervolume_overlap_statistics* function ('hypervolume' package, Blonder et al., 2014).

3. Results

In total, 15,855 ant workers belonging to 27 species and three subfamilies were recorded in the three studied wood-pastures (Formicinae: 15 species; Myrmicinae: 10 species; Dolichoderinae: 2 species; see Table S1 for the species list). The number of species were the highest in forest edges ($z > 4.05$; $p < 0.001$), and the lowest in grasslands ($z > 3.99$; $p < 0.001$) (Fig. 2). The difference in species numbers between the solitary trees and forests was not significant ($z = 0.17$; $p = 0.99$). Based on the two indices reflecting behavioral and ecological dominance presented above, eight species were placed into dominant, five species
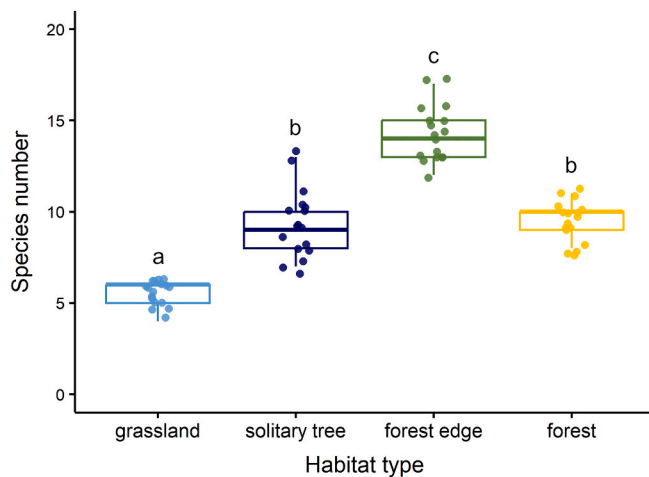
Fig. 2. Number of ant species recorded in the four different habitat types of wood-pastures. Lowercase letters indicate significant differences among habitat types.

into intermediate, and 14 species into subordinate behavioral groups (see Supplemental data).

3.1. Microclimatic parameters

The four habitat types of wood-pastures differed considerably in terms of the measured microclimatic parameters (Fig. 3). We detected the highest air temperatures in the grasslands, regardless of the time of observation ($z > 30.26$; $p < 0.001$) (Fig. 3A). Among the woody habitat types, during the morning and afternoon hours (1st and 3rd periods) the temperatures were the highest underneath the solitary trees, followed by the forest edges and forests. The differences between these two latter habitat types were significant ($z > 3.26$; $p < 0.01$). During the midday hours (2nd period), however, the temperatures were significantly lower underneath the solitary trees as compared to the forest edges ($z = 2.58$; $p = 0.049$), and marginally significantly lower as compared to the forests ($z = 2.50$; $p = 0.06$). The differences between the forests and the forest edges were not significant in this respect ($z = 0.08$; $p = 0.999$).

The relative air humidity followed a reverse pattern, with the grasslands having the lowest values ($z > 15.03$; $p < 0.001$) (Fig. 3B). Among the remaining habitat types, during the morning and afternoon hours air humidity was lowest underneath the solitary trees, followed by the forest edges and forests ($z > 2.62$; $p < 0.044$). At the midday hours, however, there were no significant differences between the three woody habitats ($z < 2.57$; $p > 0.05$).

The solar irradiance generated a similar pattern to that of the air temperature (Fig. 3C). Without shading, the grasslands received the highest solar irradiation, regardless of the time of observation ($z > 15.94$; $p < 0.001$). During the morning and afternoon hours, the highest values among the woody habitats were detected underneath the solitary trees, followed by the forest edges and forests ($z > 6.56$; $p < 0.001$). The differences between the forests and forest edges were not significant during the morning period ($z = 0.22$; $p = 0.996$). During the midday hours, the irradiance was significantly higher in forest edges as compared to the forests ($z = 3.90$; $p < 0.001$), and there were no significant differences between the rest of the woody habitats ($z < 2.41$; $p > 0.075$).

Regardless of the time of the day, soil temperatures were the highest on the grasslands ($z > 12.06$; $p < 0.001$), followed by the solitary trees ($z > 2.53$; $p < 0.05$) (Fig. 3D). There was no significant difference between the forest edges and forests ($z < 1.17$; $p > 0.644$). On the other hand, the highest soil moisture values were detected underneath the solitary trees, being significantly higher as compared to the forest edges and forests ($z > 3.25$; $p < 0.008$), but not significant as compared to

grasslands ($z = 2.08$; $p = 0.164$) (Fig. 3E). The values of grasslands were significantly higher as compared to the forests ($z = 2.75$; $p = 0.033$). There was no significant difference between the grasslands and the forest edges ($z = 0.73$; $p = 0.887$), nor between the forest edges and forests ($z = 2.34$; $p = 0.098$).

3.2. Niche hypervolumes and hypervolume overlaps

The niche hypervolume values showed notable differences among the four habitat types, indicating the presence of species with various degrees of ecological specialization. The highest hypervolume values were detected in grasslands ($\mu = 0.017$; SD $= 0.013$), followed by forest edges, ($\mu = 0.014$; SD $= 0.016$), solitary trees ($\mu = 0.005$; SD $= 0.006$), and forests ($\mu = 0.005$; SD $= 0.005$) (Fig. 4A). The differences in the niche breadths resulted in different degrees of niche overlaps. Similarly to the niche hypervolumes, the highest Jaccard similarity values were detected in grassland communities ($\mu = 0.255$; SD $= 0.124$), followed by the forest ($\mu = 0.139$; SD $= 0.139$), forest edge ($\mu = 0.105$; SD $= 0.146$), and solitary tree communities ($\mu = 0.065$; SD $= 0.082$) (Fig. 4B).

3.3. Effect of habitat type on ant activity patterns

The number of workers of the three behavioral categories showed consistent differences between the individual habitat types throughout the day. The dominant group was represented in highest numbers on grasslands, followed by solitary trees, forest edges, and forests (Fig. S1A). The differences between the habitat types were significant ($z > 3.29$; $p < 0.01$), except in the morning period, when the solitary trees and forest edges did not differ regarding the activity of this group ($z = 1.40$; $p = 0.5$). During the midday hours, however, due to the extreme environmental conditions, the activity of the dominant ants dropped in the grasslands, resulting in a non-significant difference between grasslands and solitary trees ($z = 0.53$; $p = 0.95$). The subordinate group showed the highest abundance in the forest edges throughout the day ($z > 3.43$; $p < 0.05$) (Fig. S1B). Among the other habitat types, the highest subordinate worker numbers were detected in the forests ($z > 3.23$; $p < 0.05$). However, the activity of this group showed a descending pattern in this habitat type, which resulted in a non-significant difference compared to grasslands in the afternoon period ($z = 1.79$; $p = 0.28$). There was no significant difference between grasslands and solitary trees in terms of the abundance of subordinate ants throughout the day ($z < 1.36$; $p > 0.52$). As detailed above, the representatives of the intermediate group were present only in the forest edges and forests. Of the two, the forest edges had significantly higher numbers of workers, regardless of the observation period ($z > 2.18$; $p < 0.05$) (Fig. S1C).

3.4. Effect of microclimatic parameters and competitive interactions on ant activity patterns

Based on our results, both microclimatic conditions and interspecific interactions had a strong influence on ant activity patterns in the studied habitat types (Table 2). The effects of the two components, however, showed a varying pattern across the habitat types, indicating the differing importance of environmental conditions and interspecific interactions in shaping the activity patterns of the four different ant communities. The microclimatic parameters included in our models showed varying effects across habitats and behavioral groups. Air temperature has proven to be the most important microclimatic factor influencing ant activity patterns and is the only parameter showing a significant effect in every habitat type. The interactions between the different behavioral groups also showed varying effects across habitat types, although in most cases a dominance hierarchy was present (Table 2).
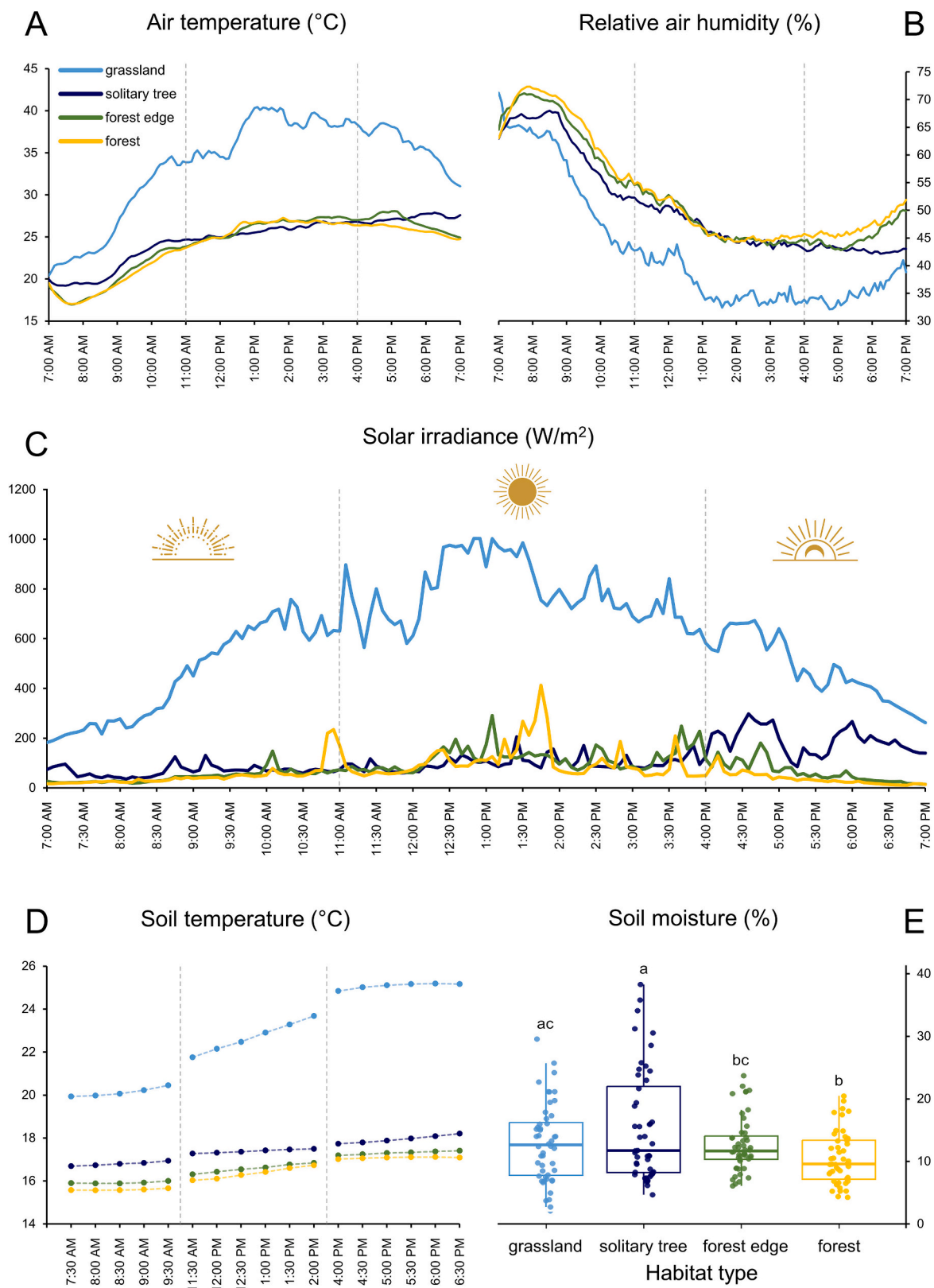
Fig. 3. Measured abiotic parameters in the four different habitat types (grasslands, solitary trees, forest edges, forests) of wood-pastures. Data from the three studied wood-pastures (Deușu, Rupea, Erdőbénye) are pooled, and in figs. A-D the values are averaged over the sampling sites. In fig. E, lowercase letters indicate significant differences among habitat types. The dashed vertical lines mark the three observation periods (morning, midday, afternoon). The color coding is consistent throughout the figures.
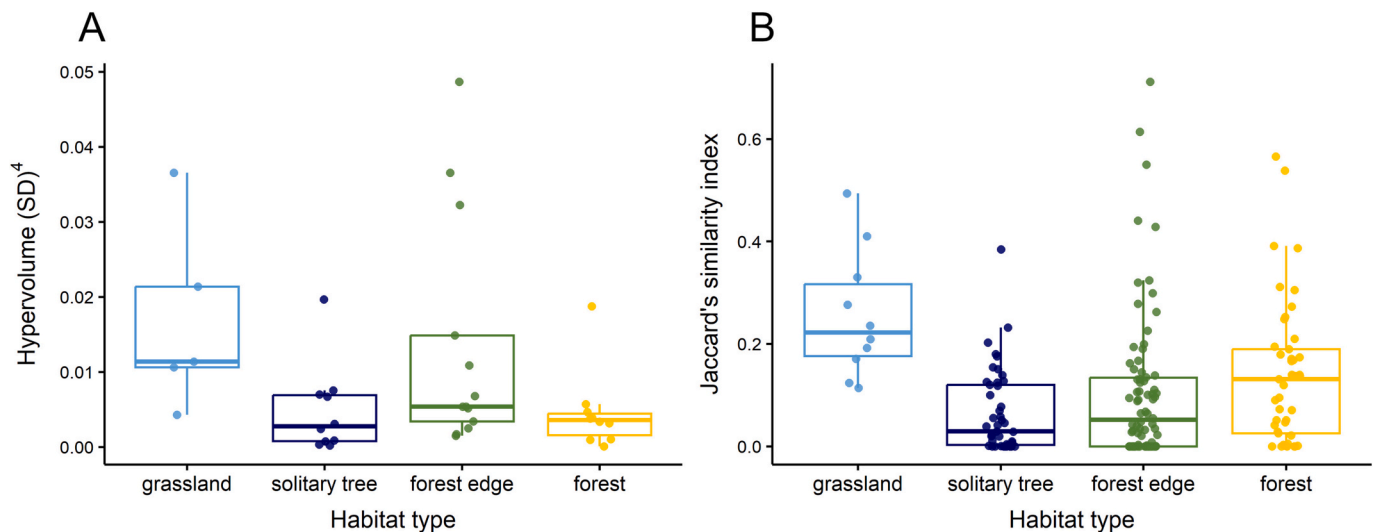
Fig. 4. Niche hypervolume (A) and Jaccard similarity values (B) of the ant communities in the four different habitat types of wood-pastures.

Table 2
The effect of different microclimatic parameters and competitive interactions on the activity patterns of ants in the three studied wood-pastures. The three behavioral categories used were established prior to the statistical analyses. Arrows indicate the direction of the significant effects found by fitting generalized linear mixed-effect models. Significant results are shown with bold font.

Habitat	Behavioral group	Microclimatic parameters						Interactions			
		Air temperature		Air humidity		Irradiance		Dominant		Intermediate	
		Effect	*p*-value	Effect	*p*-value	Effect	*p*-value	Effect	*p*-value	Effect	*p*-value
Grassland	Dominant	↘	**<0.001**	↘	**<0.001**	↘	**<0.001**				
	Subordinate	↗	**<0.001**			↘	**<0.001**	—	0.252		
Solitary tree	Dominant	↗	**<0.001**	—	0.383	↘	**0.027**				
	Subordinate	↗	**<0.001**			—	0.721	↗	**<0.001**		
Forest edge	Dominant	↗	**<0.001**	↘	**<0.001**	↘	**<0.001**				
	Intermediate	—	0.847	↗	**0.007**	—	0.242	↘	**<0.001**		
	Subordinate	—	0.883	—	0.287	—	0.563	↘	**<0.001**	↘	**0.034**
Forest	Dominant	—	0.382	—	0.982	—	0.286				
	Intermediate	↘	**<0.001**	↗	**0.025**	—	0.951	—	0.851		
	Subordinate	—	0.403	↘	**0.046**	—	0.828	↗	**0.023**	↘	**<0.001**

4. Discussion

The four studied habitat types of wood-pastures (grasslands, solitary trees, forest edges, and forests) showed remarkable differences in the measured microclimatic parameters, thereby creating different environmental conditions for ants within a relatively small spatial scale. Importantly, the microclimatic conditions influenced the occurrence and activity of ant species, and together with the observed interspecific interactions, resulted in varying species occurrence patterns across habitat types and behavioral groups. These results indicate the interplay between microclimatic factors and interspecific interactions and suggest that the organization of the studied ant communities is driven by these interacting underlying principles. The studied grasslands hosted the least species-rich ant communities, characterized by high abundances of aggressive, ecologically dominant ants, high niche hypervolumes, and consequently, high niche overlaps. This combination implies that these grasslands were monopolized by a few dominant species that occurred under a wide range of environmental conditions (i.e., generalists), and experienced high levels of competition. This result is consistent with previous studies addressing ant community organization patterns in open habitats (e.g., Andersen, 1992; Trigos-Peral et al., 2016) and seems to provide further evidence for the presence of dominance-richness relationships in ant communities. Dominant species have been shown to control the small-scale (often referred to as "momentary") diversity in a range of different biomes and ecosystems (e.g., Savolainen and

Vepsäläinen, 1988; Andersen, 1992; Retana and Cerdá, 2000; Parr et al., 2005), and although not ubiquitous, a general negative relationship seems to prevail between small-scale species richness and dominance. It is important to note, however, that the regulation of momentary diversity by dominant ants does not necessarily scale up to the community level in all ecosystems, hence, the role of competitive exclusion in structuring ant communities can be habitat specific (Arnan et al., 2011, 2018).

The high irradiance and air temperature during the midday hours had a negative effect on the activity of the dominant group, while the temperature had a positive effect on the subordinate species. The three subordinate species found in the studied grasslands (*Camponotus atricolor*, *Tapinoma subboreale*, and *Formica rufibarbis*) showed peak activity at high temperatures (40.5; 35.6; 35.5 °C, respectively), and were often the only species active during these periods. This pattern is consistent with the dominance-thermal tolerance trade-off, which implies the existence of an inverse relationship between behavioral dominance and thermal tolerance in ants (Bestelmeyer, 2000). By sustaining their foraging activity under severe environmental conditions, subordinates are able to acquire resources otherwise monopolized by dominant species. This mechanism has proven to be a fundamental component influencing ant community organization and diversity (reviewed in Cerdá et al., 2013), and seems to be of primary importance in the studied grasslands as well. Interestingly, dominant species did not directly affect the activity patterns of subordinates in these grasslands, as found in

open Mediterranean habitats by Cerdá et al. (1998), who concluded that the foraging activity of subordinate species is more influenced by thermal conditions than by interspecific competition. However, this pattern can be interpreted as an indirect product of interspecific competition, as thermophily can also be viewed as an adaptation to avoid interference with dominant ants that are active at cooler temperatures (Harkness and Wehner, 1977; Hoffmann, 1998).

Although being embedded into grasslands, we found very different patterns of ant activity and community organization under solitary trees, which, in part, can be linked to their unique microclimatic characteristics. By buffering the environmental extremities of the grasslands, solitary trees ensured continuous ant activity throughout the day. Furthermore, due to the high solar irradiation during the morning and evening hours, these trees provided warmer temperatures than the forest edges and forests, thereby having a positive effect on the activity of both the dominant and subordinate groups. Similar to grasslands and forest edges, however, the high levels of solar irradiation influenced negatively the activity of dominant ants, probably due to the higher chance of desiccation. It is important to note, however, that the high activity of dominant ants did not result in the impoverishment of these communities, as it is often observed in similar habitats of arid regions (Andersen, 1992; Cros et al., 1997). The low niche hypervolume and Jaccard values indicate the presence of specialist ant species that can be associated with specific microhabitats and microclimatic conditions, thus are able to coexist with generalist grassland species. This result is also supported by previous studies that have demonstrated the positive effect of solitary trees on the species number and community composition of local ant communities (Reyes-López et al., 2003; Gaytán et al., 2021; Tăușan et al., 2021).

The structural complexity of solitary trees provides a wide range of microhabitats (e.g., tree hollows, cracks, galls, patches of bark loss, lichens, and dead branches with decomposing deadwood), which tend to accumulate over time (Regnery et al., 2013; Horak et al., 2014; Sebek et al., 2016). Furthermore, the canopy structure of these trees creates a diverse illumination regime, which has been shown to promote ant diversity (Dolek et al., 2009). It is likely that all these factors contributed to the high niche differentiation, and therefore, high number of observed subordinate species in solitary trees. Interestingly, the presence of dominant ants had a positive influence on the activity of subordinate species. A similar result was found by Arnan et al. (2011), who attributed this pattern to the differential interference competition among dominant, intermediate (in their study "subdominant"), and subordinate ants. According to the authors, dominants show varying activity within their patchy territories in more heterogeneous habitat types, having a stronger pressure on intermediates and promoting opportunistic foraging strategies. By recruiting in small numbers and showing low levels of aggression, subordinate species are able to insinuate themselves among dominant workers or exploit patches with lower activity, thus gaining important food sources. However, subordinates might still compete with the intermediate species, as their representatives exploit resources in local patches more intensively than the dominant ants (Maák et al., 2020). In the solitary trees from our study, only one species (*C. vagus*) with very few occurrences belonged to the intermediate group. Nevertheless, it is quite likely that subordinates still suffered interspecific competition by certain dominant or other subordinate ants. Therefore, forming indirect associations with ecologically and behaviorally dominant species might be beneficial for them through the exclusion of their competitors.

Of the four habitat types, forest edges hosted the most diverse ant communities. Both the niche hypervolume and Jaccard values showed the greatest spread in these habitats, indicating the presence of species with various niche breadths and degrees of specialization. Indeed, besides the dominant generalist species of the adjacent forests and grasslands, intermediate and subordinate species with lower hypervolume values were also observed in high numbers. The increased diversity of ant assemblages in forest edges has also been documented in other

studies (e.g., Pinheiro et al., 2010; Gallé et al., 2014), and is probably linked to the unique microhabitats and microclimatic conditions created by the complex vegetation structure (Risser, 1995). It is likely that the high abundances of intermediate and subordinate ants are linked to these factors. Their activity patterns, however, seem to be influenced primarily by competitive interactions rather than microclimatic conditions. Unlike in other habitat types, in forest edges a linear hierarchical pattern was observed, where the intermediate species were negatively influenced by dominants, while the subordinate species were negatively influenced by both the dominant and intermediate species. This pattern implies that interspecific competition might play a major role in determining the ant activity patterns in this habitat type. The hierarchical organization of ant communities is well documented by Savolainen and Vepsäläinen (1988) and Pisarski and Vepsäläinen (1989) in boreal ecosystems with similar species compositions. According to the authors, the hierarchy consists of three main competition levels, with territorial, aggressive species on the top, encounter (intermediate) species with no territorial behavior in the middle, and submissive species yielding to stronger competitors in the bottom. Despite the slight differences in the establishment of the three behavioral groups, our results bear strong resemblance to this concept, suggesting the important role of interspecific competition in shaping the ant communities of the studied forest edges. Regarding the environmental parameters, air humidity had a positive effect on the activity of intermediate species, while a negative effect on dominant species. Thus, the association with humid conditions may be a strategy for intermediate species to avoid competition with dominant ants. For the latter group, the rest of the environmental parameters had a similar effect as in the solitary trees.

As could be expected, the fourth habitat type (forests) provided the coolest environmental conditions throughout the day due to their closed canopy structure. These mild conditions, however, can be suboptimal for ant activity, as their proper metabolic rate depends on adequate temperatures and solar irradiation (Hölldobler and Wilson, 1990). The cooler microclimates probably contributed to the observed low levels of ant activity in the studied forests. Similar to the other habitat types, the environmental parameters had varying effects on the activity of the different behavioral groups. The activity of intermediate species was negatively influenced by temperature, but positively influenced by air humidity, indicating their association with colder, humid environments. This result should be interpreted in the light that *M. ruginodis* was by far the most abundant species of the intermediate group. Previous studies have shown that this species, like other *Myrmica* ants, tends to forage at low temperatures to avoid competition with dominant ants (Mabelis, 1983; Vepsäläinen and Savolainen, 1990), as it was probably the case also in these habitat types. The environmental parameters, however, showed no effect on the activity of dominant species, suggesting that – at least during daytime – other factors influence their activity patterns. The lack of extreme environmental conditions, coupled with the continuous food availability in the form of our baits might be a potential explanation. As indicated by the low niche hypervolume values, specialist species belonging to the subordinate group were well represented in the forests. Their activity patterns, however, were primarily influenced by interspecific interactions rather than environmental parameters. The intermediate group had a negative, meanwhile the dominant group had a positive effect on the activity of these ants. The explanation of this pattern could be similar to that described in solitary trees: forming indirect associations with dominant ants might help to reduce competition with intermediate species, which exploit and defend local food sources more intensely than dominants (Arnan et al., 2011). Despite the low niche hypervolume values, substantial niche overlaps were observed in the studied forests. This pattern reflects the patchy distribution of ants in these habitats, resulting in the aggregation of species in particular sampling sites. The causes of patchy distributions are various, but food and nest site availability, preference for certain microclimatic conditions, and associations with other species are probably of primary importance (Kaspari, 1996; Kaspari and Majer, 2000; Maziarz et al.,

2021).

Our study provides an integrative approach for understanding the underlying processes that shape the ant communities of wood-pastures, a highly heterogenous semi-natural habitat found throughout Europe (Plieninger et al., 2015). By connecting ant occurrence data with fine-scale changes in the local microclimatic conditions, we were able to uncover the main environmental factors influencing ant activity patterns in the four different habitat types of wood-pastures. Additionally, the direct link between species occurrence and microclimate allowed us to apply the hypervolume framework and quantify the niche overlaps between species pairs at each habitat type. This, together with the observed interspecific interactions provided useful insights into the role of interspecific competition in the four different ant communities. Both microclimatic conditions and interspecific interactions showed varying effects across habitat types and behavioral groups, indicating that the organization of the studied ant communities is governed by both underlying principles. The structural and microclimatic heterogeneity of these silvopastoral systems ensures the coexistence of four ecologically distinct ant communities on a relatively small spatial scale. Although not addressed in the present study, it is likely that other assemblages also track the environmental heterogeneity of the different habitat types of wood-pastures, as microclimate plays a major role in shaping the occurrence patterns of most organisms (Willmer, 1982; Stein et al., 2014).

Given the pressing need to protect and preserve biodiversity in the face of habitat loss and climate change, the conservation of habitats with high environmental heterogeneity becomes increasingly relevant. While the preservation of natural ecosystems is the preferred approach to sustain biodiversity, such efforts frequently encounter obstacles and confront a multitude of challenges (Rands et al., 2010). Therefore, semi-natural habitats harboring high environmental heterogeneity should also be considered in conservation efforts, especially in heavily modified landscapes, where natural habitats are scarce. With their ability to accommodate four distinct habitat types on a relatively small spatial scale, wood-pastures represent a valuable opportunity for sustainable land use that benefits both people and biodiversity.

CRediT authorship contribution statement

Ádám Lőrincz: Conceptualization, Methodology, Investigation, Data curation, Formal analyses, Original draft preparation, Reviewing and Editing; **Alida Anna Hábenczyus:** Investigation, Reviewing and Editing; **András Kelemen:** Investigation, Reviewing and Editing; **Bonita Ratkai:** Investigation, Reviewing and Editing; **Csaba Tölgyesi:** Conceptualization, Investigation, Reviewing and Editing; **Gábor Lőrinczi:** Investigation, Reviewing and Editing; **Kata Frei:** Investigation, Reviewing and Editing; **Zoltán Bátori:** Investigation, Reviewing and Editing; **István Elek Maák:** Conceptualization, Methodology, Investigation, Formal analyses, Original draft preparation, Reviewing and Editing.

Declaration of competing interest

The authors declare no competing interests.

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.167510.

References

Andersen, A.N., 1986. Diversity, seasonality and community organization of ants at adjacent heath and woodland sites in southeastern Australia. Aust. J. Zool. 34, 53–64. https://doi.org/10.1071/ZO9860053.

Andersen, A.N., 1991. Responses of ground-foraging ant communities to three experimental fire regimes in a savanna forest of tropical Australia. Biotropica 575–585. https://doi.org/10.2307/2388395.

Andersen, A.N., 1992. Regulation of "momentary" diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. Am. Nat. 140, 401–420. https://doi.org/10.1086/285419.

Arnan, X., Gaucherel, C., Andersen, A.N., 2011. Dominance and species co-occurrence in highly diverse ant communities: a test of the interstitial hypothesis and discovery of a three-tiered competition cascade. Oecologia 166, 783–794. https://doi.org/10.1007/s00442-011-1919-y.

Arnan, X., Andersen, A.N., Gibb, H., Parr, C.L., Sanders, N.J., Dunn, R.R., Retana, J., 2018. Dominance–diversity relationships in ant communities differ with invasion. Glob. Chang. Biol. 24, 4614–4625. https://doi.org/10.1111/gcb.14331.

Bates, D., Maechler, M., 2013. Lme4: linear mixed-effects models using eigen and S4. (1.0-5. R package). http://CRAN.R-project.org/package=lme4.

Bergmeier, E., & Roellig, M. (2014). Diversity, threats and conservation of European wood-pastures. In *European wood-pastures in transition* (pp. 37-56). Routledge.

Bergmeier, E., Petermann, J., Schröder, E., 2010. Geobotanical survey of wood-pasture habitats in Europe: diversity, threats and conservation. Biodivers. Conserv. 19, 2995–3014. https://doi.org/10.1007/s10531-010-9872-3.

Bestelmeyer, B.T., 2000. The trade-off between thermal tolerance and behavioural dominance in a subtropical south American ant community. J. Anim. Ecol. 69, 998–1009. https://doi.org/10.1111/j.1365-2656.2000.00455.x.

Blonder, B., 2018. Hypervolume concepts in niche-and trait-based ecology. Ecography 41, 1441–1455. https://doi.org/10.1111/ecog.03187.

Blonder, B., Lamanna, C., Violle, C., Enquist, B.J., 2014. The n-dimensional hypervolume. Glob. Ecol. Biogeogr. 23, 595–609. https://doi.org/10.1111/geb.12146.

Bolton, B., 2020. An Online Catalog of the Ants of the World. Available online at. http://antcat.org.

Cerdá, X., Retana, J., Cros, S., 1997. Thermal disruption of transitive hierarchies in Mediterranean ant communities. J. Anim. Ecol. 66, 363–374. https://doi.org/10.2307/5982.

Cerdá, X., Retana, J., Manzaneda, A., 1998. The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. Oecologia 117, 404–412. https://doi.org/10.1007/s004420050674.

Cerdá, X., Arnan, X., Retana, J., 2013. Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology. Myrmecological News 18, 131–147.

Cros, S., Cerdá, X., Retana, J., 1997. Spatial and temporal variations in the activity patterns of Mediterranean ant communities. Ecoscience 4, 269–278. https://doi.org/10.1080/11956860.1997.11682405.

Czechowski, W., Radchenko, A., Czechowska, W., Vepsäläinen, K., 2012. The Ants of Poland with Reference to the Myrmecofauna of Europe. Natura optima dux Foundation, Warszawa.

Dolek, M., Freese-Hager, A., Bussler, H., Floren, A., Liegl, A., Schmidl, J., 2009. Ants on oaks: effects of forest structure on species composition. J. Insect Conserv. 13, 367–375. https://doi.org/10.1007/s10841-008-9181-2.

Dunn, R.R., 2000. Isolated trees as foci of diversity in active and fallow fields. Biol. Conserv. 95, 317–321. https://doi.org/10.1016/S0006-3207(00)00025-2.

Erdős, L., Tölgyesi, C., Horzse, M., Tolnay, D., Hurton, Á., Schulcz, N., Körmöczi, L., Lengyel, A., Bátori, Z., 2014. Habitat complexity of the Pannonian forest-steppe zone and its conservation implications. Ecol. Complex. 17, 107–118. https://doi.org/10.1016/j.ecocom.2013.11.004.

Falk, S., 2014. Wood-pastures as reservoirs for invertebrates. In: European Wood-Pastures in Transition. Routledge, Oxfordshire, pp. 132–148.

Farji-Brener, A.G., Corley, J.C., Bettinelli, J., 2002. The effects of fire on ant communities in North-Western Patagonia: the importance of habitat structure and regional context. Divers. Distrib. 8, 235–243. https://doi.org/10.1046/j.1472-4642.2002.00133.x.

Fellers, J.H., 1987. Interference and exploitation in a guild of woodland ants. Ecology 68, 1466–1478. https://doi.org/10.2307/1939230.

Frasconi Wendt, C., Frizzi, F., Aiello, G., Balzani, P., Santini, G., 2021. Ant species but not trait diversity increases at the edges: insights from a micro-scale gradient in a semi-natural Mediterranean ecosystem. Ecol. Entomol. 46, 834–843. https://doi.org/10.1111/een.13020.

Galindo-González, J., Guevara, S., Sosa, V.J., 2000. Bat-and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. Conserv. Biol. 14, 1693–1703. https://doi.org/10.1111/j.1523-1739.2000.99072.x.

Gallé, R., Kanizsai, O., Ács, V., Molnár, B., 2014. Functioning of ecotones – spiders and ants of edges between native and non-native forest plantations. Pol. J. Ecol. 62, 815–820. https://doi.org/10.3161/104.062.0404.

Gallé, R., Torma, A., Maák, I., 2016. The effect of forest age and habitat structure on the ground-dwelling ant assemblages of lowland poplar plantations. Agric. For. Entomol. 18, 151–156. https://doi.org/10.1111/afe.12148.

Garbarino, M., Bergmeier, E., 2014. Plant and vegetation diversity in European wood-pastures. In: European Wood-Pastures in Transition. Routledge, Oxfordshire, pp. 131–149.

Gaytán, Á., Bautista, J.L., Bonal, R., Moreno, G., González-Bornay, G., 2021. Trees increase ant species richness and change community composition in Iberian oak savannahs. Diversity 13 (3), 115. https://doi.org/10.3390/d13030115.

Gibb, H., Sanders, N.J., Dunn, R.R., Watson, S., Photakis, M., Abril, S., Parr, C.L., 2015. Climate mediates the effects of disturbance on ant assemblage structure. Proc. R. Soc. B Biol. Sci. 282, 20150418. https://doi.org/10.1098/rspb.2015.0418.

Harkness, R.D., Wehner, R., 1977. Cataglyphis. Endeavour 1, 115–121. https://doi.org/10.1016/0160-9327(77)90169-7.

Hartel, T., Dorresteijn, I., Klein, C., Máthé, O., Moga, C.I., Öllerer, K., Fischer, J., 2013. Wood-pastures in a traditional rural region of Eastern Europe: characteristics, management and status. Biol. Conserv. 166, 267–275. https://doi.org/10.1016/j.biocon.2013.06.020.

Hartel, T., Hanspach, J., Abson, D.J., Máthé, O., Moga, C.I., Fischer, J., 2014. Bird communities in traditional wood-pastures with changing management in Eastern Europe. Basic Appl. Ecol. 15, 385–395. https://doi.org/10.1016/j.baae.2014.06.007.

Hoffmann, B.D., 1998. Thermophilia in a tropical Australian ant of the *Melophorus aeneovirens* (Lowne) species-group (Hymenoptera: Formicidae). Aust. J. Entomol. 37, 162–167. https://doi.org/10.1111/j.1440-6055.1998.tb01565.x.

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

Horak, J., Vodka, S., Kout, J., Halda, J.P., Bogusch, P., Pech, P., 2014. Biodiversity of most dead wood-dependent organisms in thermophilic temperate oak woodlands thrives on diversity of open landscape structures. For. Ecol. Manag. 315, 80–85. https://doi.org/10.1016/j.foreco.2013.12.018.

James, G., Witten, D., Hastie, T., Tibshirani, R., 2013. An Introduction to Statistical Learning, Vol. 112. Springer, New York, p. 18.

Johnson, N. F. (2007). *Hymenoptera name server (version 1.5)*. Available online at: http://antbase.org/databases/hns.htm.

Kaspari, M., 1996. Testing resource-based models of patchiness in four Neotropical litter ant assemblages. Oikos 76, 443–454. https://doi.org/10.2307/3546338.

Kaspari, M., Majer, J.D., 2000. Using ants to monitor environmental change. In: Ants: Standard Methods for Measuring and Monitoring Biodiversity. Smithsonian Institution Press, pp. 89–98.

Lach, L., Parr, C., Abbott, K. (Eds.), 2010. Ant Ecology. Oxford University Press, Oxford.

Lenth, R., 2020. Emmeans: estimated marginal means, aka least-squares means. R package version 1.4.8. https://CRAN.R-project.org/package=emmeans.

Lindén, A., Mäntyniemi, S., 2011. Using the negative binomial distribution to model overdispersion in ecological count data. Ecology 97, 1414–1421. https://doi.org/10.1890/10-1831.1.

Lindman, L., Öckinger, E., Ranius, T., 2023. Microclimate in hollow trees and how it affects an inhabiting beetle species, *Osmoderma eremita*. Ecol. Entomol. 48, 112–126. https://doi.org/10.1111/een.13206.

López-Sánchez, A., San Miguel, A., López-Carrasco, C., Huntsinger, L., Roig, S., 2016. The important role of scattered trees on the herbaceous diversity of a grazed Mediterranean dehesa. Acta Oecol. 76, 31–38. https://doi.org/10.1016/j.actao.2016.08.003.

Luick, R., 2008. Transhumance in Germany. In: European Forum on Nature Conservation and Pastoralism. European Forum on Nature Conservation and Pastoralism (EFNCP) and University of Applied Sciences Rottenburg/Fachhochschule Rottenburg, Schadenweilerhof, Rottenburg, Germany, pp. 137–154.

Lumsden, L.F., Bennett, A.F., 2005. Scattered trees in rural landscapes: foraging habitat for insectivorous bats in South-Eastern Australia. Biol. Conserv. 122, 205–222. https://doi.org/10.1016/j.biocon.2004.07.006.

Maák, I., Czekes, Z., Erős, K., Pálfi, Z., Markó, B., 2020. Living on the edge: changes in the foraging strategy of a territorial ant species occurring with a rival supercolony – a case study. J. Insect Behav. 33, 59–68. https://doi.org/10.1007/s10905-020-09745-x.

Mabelis, A.A., 1983. Interference between wood ants and other ant species (Hymenoptera, Formicidae). Netherlands J. Zool. 34, 1–20. https://doi.org/10.1163/002829684X00010.

Majer, J.D., Recher, H.F., Ganesh, S., 2000. Diversity patterns of eucalypt canopy arthropods in eastern and western Australia. Ecol. Entomol. 25, 295–306. https://doi.org/10.1046/j.1365-2311.2000.00259.x.

Manning, A.D., Fischer, J., Lindenmayer, D.B., 2006. Scattered trees are keystone structures – implications for conservation. Biol. Conserv. 132, 311–321. https://doi.org/10.1016/j.biocon.2006.04.023.

Maziarz, M., Broughton, R.K., Casacci, L.P., Hebda, G., Maák, I., Trigos-Peral, G., Witek, M., 2021. Interspecific attraction between ground-nesting songbirds and ants:

the role of nest-site selection. Front. Zool. 18, 1–14. https://doi.org/10.1186/s12983-021-00429-6.

Parr, C.L., Sinclair, B.J., Andersen, A.N., Gaston, K.J., Chown, S.L., 2005. Constraint and competition in assemblages: a cross-continental and modeling approach for ants. Am. Nat. 165, 481–494. https://doi.org/10.1086/428292.

Peral, G.T., Markó, B., Babik, H., Tăuşan, I., Maák, I., Pálfi, Z., Ślipiński, P., Czekes, Z., Czechowski, W., 2016. Differential impact of two dominant Formica ant species (Hymenoptera, Formicidae) on subordinates in temperate Europe. J. Hymenopt. Res. 50, 97–116. https://doi.org/10.3897/JHR.50.8301.

Perfecto, I., Vandermeer, J., 1996. Microclimatic changes and the indirect loss of ant diversity in a tropical agroecosystem. Oecologia 108, 577–582. https://doi.org/10.1007/BF00333736.

Pinheiro, E.R., Duarte, L.D.S., Diehl, E., Hartz, S.M., 2010. Edge effects on epigeic ant assemblages in a grassland–forest mosaic in southern Brazil. Acta Oecol. 36, 365–371. https://doi.org/10.1016/j.actao.2010.03.004.

Pisarski, B., & Vepsäläinen, K. (1989). Competition hierarchies in ant communities (Hymenoptera, Formicidae). In Annales Zoologici (Vol. 42, no. 13, pp. 321-329). Państwowe Wydawnictwo Naukowe.

Plieninger, T., Hartel, T., Martín-López, B., Beaufoy, G., Bergmeier, E., Kirby, K., Van Uytvanck, J., 2015. Wood-pastures of Europe: geographic coverage, social–ecological values, conservation management, and policy implications. Biol. Conserv. 190, 70–79. https://doi.org/10.1016/j.biocon.2015.05.014.

Punttila, P., Haila, Y., Tukia, H., 1996. Ant communities in taiga clearcuts: habitat effects and species interactions. Ecography 19, 16–28. https://doi.org/10.1111/j.1600-0587.1996.tb00151.x.

R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rands, M.R., Adams, W.M., Bennun, L., Butchart, S.H., Clements, A., Coomes, D., Vira, B., 2010. Biodiversity conservation: challenges beyond 2010. Science 329, 1298–1303. https://doi.org/10.1126/science.11891.

Regnery, B., Couvet, D., Kubarek, L., Julien, J.F., Kerbiriou, C., 2013. Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. Ecol. Indic. 34, 221–230. https://doi.org/10.1016/j.ecolind.2013.05.003.

Retana, J., Cerdá, X., 2000. Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. Oecologia 123, 436–444. https://doi.org/10.1007/s004420051031.

Reyes-López, J., Ruiz, N., Fernández-Haeger, J., 2003. Community structure of ground-ants: the role of single trees in a Mediterranean pastureland. Acta Oecol. 24 (4), 195–202. https://doi.org/10.1016/S1146-609X(03)00086-9.

Rhoades, C.C., 1996. Single-tree influences on soil properties in agroforestry: lessons from natural forest and savanna ecosystems. Agrofor. Syst. 35, 71–94. https://doi.org/10.1007/BF02345330.

Ries, L., Fletcher Jr., R.J., Battin, J., Sisk, T.D., 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. Annu. Rev. Ecol. Evol. Syst. 35, 491–522. https://doi.org/10.1146/annurev.ecolsys.35.112202.130148.

Risser, P.G., 1995. The status of the science examining ecotones: a dynamic aspect of landscape is the area of steep gradients between more homogeneous vegetation associations. BioScience 45, 318–325. https://doi.org/10.2307/1312492.

Rosenthal, G., Schrautzer, J., Eichberg, C., 2012. Low-intensity grazing with domestic herbivores: a tool for maintaining and restoring plant diversity in temperate Europe. Tuexenia 32, 167–205.

Savolainen, R., Vepsäläinen, K., 1988. A competition hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos 51, 135–155. https://doi.org/10.2307/3565636.

Sebek, P., Vodka, S., Bogusch, P., Pech, P., Tropek, R., Weiss, M., Zimova, K., Cizek, L., 2016. Open-grown trees as key habitats for arthropods in temperate woodlands: the diversity, composition, and conservation value of associated communities. For. Ecol. Manag. 380, 172–181. https://doi.org/10.1016/j.foreco.2016.08.052.

Seifert, B., 2018. The Ants of Central and North Europe. Lutra Verlags-und Vertriebsgesellschaft, Tauer.

Stein, A., Gerstner, K., Kreft, H., 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecol. Lett. 17, 866–880. https://doi.org/10.1111/ele.12277.

Stephens, S.S., Wagner, M.R., 2006. Using ground foraging ant (Hymenoptera: Formicidae) functional groups as bioindicators of forest health in northern Arizona ponderosa pine forests. Environ. Entomol. 35, 937–949. https://doi.org/10.1603/0046-225X.35.4.937.

Tăuşan, I., Dauber, J., Trică, M.R., Markó, B., 2017. Succession in ant communities (Hymenoptera: Formicidae) in deciduous forest clear-cuts-an eastern European case study. Eur. J. Entomol. 114, 92. https://doi.org/10.14411/eje.2017.013.

Tăuşan, I., Muraru, I.M., Öllerer, K., 2021. Monitoring ant assemblages of oak wood-pastures. A case study from Eastern Europe. Biologia 76, 1153–1160. https://doi.org/10.2478/s11756-020-00624-6.

Tölgyesi, C., Bátori, Z., Gallé, R., Urák, I., Hartel, T., 2018. Shrub encroachment under the trees diversifies the herb layer in a romanian silvopastoral system. Rangel. Ecol. Manag. 71, 571–577. https://doi.org/10.1016/j.rama.2017.09.004.

Vepsäläinen, K., Savolainen, R., 1990. The effect of interference by formicine ants on the foraging of Myrmica. J. Anim. Ecol. 59, 643–654. https://doi.org/10.2307/4886.

Willmer, P.G., 1982. Microclimate and the environmental physiology of insects. In: Advances in Insect Physiology. Academic Press, Cambridge, pp. 1–57.

Wilson, E.O., 1971. The Insect Societies. Harvard University Press, Cambridge.