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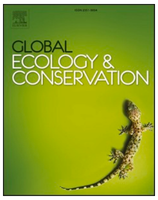

Ants in space and time: Spatiotemporal niche changes facilitate species coexistence in semi-natural ecosystem complexes

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ABSTRACT

Semi-natural farming systems with high conservation value offer a valuable opportunity to meet biodiversity conservation goals without compromising agricultural production. The high conservation value of such systems often roots in their increased local or landscape-level heterogeneity, which facilitates the coexistence of different species on a small spatial scale. Gaining a comprehensive understanding of the coexistence mechanisms operating in such systems is essential to mark future conservation trajectories. To facilitate this process, in this study, we aimed to uncover the interactive effects of spatial and temporal heterogeneity on community structuring mechanisms in wood-pastures, Europe's widespread and heterogeneous semi-natural land-use form. Using ants as bioindicators, we connected species occurrence data with fine-scale measurements of local microclimatic conditions and quantified the seasonal niche breadths and overlaps of ant species forming communities in the four different habitat types (grasslands, solitary trees, forests, and forest edges) of three Central European wood-pastures. The niche quantification (performed for 28 ant species in total) was based on four-dimensional hypervolumes, with solar irradiation, air and soil temperature, and air humidity values of every species occurrence. Our results show that despite being located close to one another, the ant communities of the four different habitat types exhibited distinct patterns of seasonal realized niche dynamics, leading to community-wide temporal changes in niche hypervolumes and hypervolume overlaps (i.e., realized niche breadths and niche overlaps). The hypervolumes of dominant ants (characterized by high behavioral and ecological dominance) were mainly determined by the favorability of environmental conditions throughout the year, and in turn, their values shaped the realized niche breadths and overlap patterns of the intermediate and subordinate species. Importantly, the niche expansions and retractions of the dominant group changed the competitive pressure within the communities (quantified by hypervolume overlaps), opening up empty ecological niches to intermediate and subordinate species during periods characterized by suboptimal environmental conditions. Moreover, the niche dynamics showed a varying pattern across the different habitat types, implying that habitat structure and the associated environmental conditions interact with the effects of seasonality even on a small spatial scale. Our results uncover the interactive effects

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of spatial and temporal heterogeneity on coexistence mechanisms within wood-pastures. Given the distinct patterns in community dynamics and different community structuring mechanisms of the individual habitat types, wood-pastures and other complex landscapes have the potential to sustain different communities on a small spatial scale and thus boost landscape-level biodiversity.

1. Introduction

Aligning biodiversity conservation efforts with the continuously increasing agricultural utilization of landscapes is a challenging, yet crucially important task of our century (Foley et al., 2011). While the conservation of natural ecosystems should be prioritized for preserving biodiversity, in human-dominated landscapes, where their number is scarce, farming systems with high conservation value can offer a viable alternative (Fischer et al., 2017; Tscharntke et al., 2021). In Europe, wood-pastures are among the most abundant land use forms with significant conservation value, covering approximately 4.7 % of the total land area of the European Union (Plieninger et al., 2015). Wood-pastures are semi-natural habitats characterized by the presence of solitary trees, which are scattered in a grazed grassland matrix (Hartel et al., 2013). These trees are commonly in the focus of scientific research, as they provide a multitude of ecosystem services (Garrido et al., 2017; Tölgyesi et al., 2023) and have been shown to promote the diversity of different organisms (Hartel et al., 2014; Falk, 2014; Gaytán et al., 2021). From a landscape perspective, however, wood-pastures can be considered "ecosystem complexes" (Bergmeier et al., 2010), as they accommodate four different habitat types on a small spatial scale, namely grasslands, solitary trees, nearby forests, and forest edges. These habitat types pose unique microclimatic and structural characteristics and host ecologically distinct plant and animal communities (Gallé et al., 2017; Tölgyesi et al., 2018).

The increased landscape-level heterogeneity of wood-pastures is generally thought to facilitate species coexistence by promoting niche differentiation among species on a small spatial scale (Plieninger et al., 2015; Lőrincz et al., 2024). While spatial heterogeneity is key in facilitating species coexistence (Stein et al., 2014; Barton et al., 2024), temporal heterogeneity may also play a pivotal role in this process through various niche-based mechanisms (Fretwell, 2020; White and Hastings, 2020). Seasonal changes in ecologically relevant characteristics impact resource availability (McMeans et al., 2015; Fuirst et al., 2023) and alter biotic interactions (Williams et al., 2017), thereby affecting organisms both directly and indirectly. Thus, to cope with seasonal changes in abiotic and biotic conditions (e.g., changes in environmental favorability, or quality and quantity of available food sources and habitats), many species were shown to exhibit temporal changes along certain axes of their realized niche breadth, which can also influence their niche overlap patterns (Albrecht and Gotelli, 2001; Roy and Thomas, 2003; Houadria and Menzel, 2020). Such niche descriptors are regularly employed to gain insights into the structuring mechanisms of communities, as the inferred patterns may signal niche partitioning (overdispersed niches with low overlaps) or environmental filtering (aggregated niches with high overlaps) (Gotelli et al., 2010; Fowler et al., 2014; Seoane et al., 2021; Salas-López et al., 2022). However, long-term studies addressing the seasonal changes of such niche metrics, especially on a community level are scarce (but see Albrecht and Gotelli, 2001), hindering our ability to fully understand the coexistence and structuring mechanisms operating on an annual scale in diverse landscapes.

The variable nature of realized niche breadth and niche overlap patterns is highlighted by several studies, as populations can modify these metrics according to different ecological factors, such as environmental favorability or the availability of limiting resources (Hofer et al., 2004; Alexander et al., 2022). The context-dependency of niche descriptors has been studied along ecological gradients, such as elevation (Bastianelli et al., 2017; Seoane et al., 2021), or ecosystem productivity (Lesser et al., 2020). However, studies addressing this issue on a small spatial scale are still lacking, therefore, the extent to which different habitat conditions interact with the effects of seasonality to influence realized niche dynamics and community assembly patterns remains to be explored. Scrutinizing these questions would enhance our understanding of the interactive effects of spatial and temporal heterogeneity on coexistence mechanisms within wood-pastures and other complex landscapes, and thus offer a holistic view that reaches beyond the well-documented mechanisms of species coexistence. A comprehensive approach integrating both the spatial and temporal components of environmental heterogeneity is crucial for future decision-making and conservation efforts to maximize biodiversity preservation in heterogeneous landscapes.

To facilitate this process, we set out to monitor the community-wide seasonal niche changes of an insect group, whose ecological dominance is ubiquitous on wood-pastures and most terrestrial ecosystems worldwide, and possess several advantageous properties for uncovering spatiotemporal niche patterns – the ants (Hölldobler and Wilson, 1990). Ants are fierce competitors and have been shown to divide up the niche space in various dimensions, such as their use of food resources (Grevé et al., 2019), or their daily and seasonal activity (Albrecht and Gotelli, 2001; Houadria et al., 2015). Furthermore, being ectothermic animals, ants are highly sensitive and responsive to changes in microclimatic conditions (Perfecto and Vandermeer, 1996; Retana and Cerdá, 2000), allowing for the direct quantification of their niche metrics under field conditions. Moreover, ant communities often show a hierarchical organization with distinct levels of competition (Savolainen and Vepsäläinen, 1988; Parr and Gibb, 2010), enabling us to rely on groups of species with similar competitive abilities and roles within communities, rather than focusing on individual species, thereby uncovering general trends in their community dynamics.

In the present study, we aimed to quantify the realized niche breadths and niche overlaps of ant species sampled throughout three seasons (spring, summer, and autumn) in the four different habitat types of wood-pastures (grasslands, solitary trees, forests, and forest edges). Considering that seasonality might differently affect species along the dominance hierarchy (Fellers, 1987), we focused on the realized niche changes of ant groups occupying different hierarchical positions (dominant, intermediate, and subordinate) in the studied communities to further enhance the resolution of our study. We specifically hypothesized that I) due to the varying environmental favorability during the seasons, the different ant groups show substantial seasonal niche changes, leading to community-wide changes in niche breadths and overlaps. These fluctuations are II) expected to alter niche overlaps (competitive relationships) within communities, thereby promoting species coexistence and leading to the diversification of communities. Furthermore, we also hypothesized that III) by posing different microclimatic characteristics, habitat structure interacts with the large-scale effects of seasonality on niche dynamics, thus we expect different patterns for communities of the four different habitat types. By simultaneously quantifying seasonal niche changes of whole ant communities living on the different habitat types of wood-pastures, our study proposes to uncover the interactive effects of temporal and spatial heterogeneity on coexistence mechanisms within complex landscapes such as wood pastures or other human-dominated farming systems.

2. Materials and methods

2.1. Study sites

We chose three wood-pastures of Central and Eastern Europe for our study, spanning a 390 km transect within the Pannonian Basin (Table 1). On each wood-pasture, we sampled four different habitat types that pose unique microclimatic conditions and host distinct ant communities (cf. Lőrincz et al., 2024), namely: grasslands, solitary trees, forest edges, and forests (Fig. 1). Each wood-pasture is situated within a hilly terrain characterized by oak-hornbeam forests. The dominant solitary trees are mainly oaks (*Quercus petraea* and *Q. robur*), but pear (*Pyrus pyraster* and *P. communis*) and hornbeam (*Carpinus betulus*) also occur (Hartel et al., 2018). The grassland matrices are dominated by perennial grasses (*Agrostis capillaris, Festuca pseudovina,* and *F. rubra*) and are subject to moderate grazing by sheep, but in Romania cattle and buffalo are also used (see also Hartel et al., 2018; Tölgyesi et al., 2018). The field sampling was carried out in 2022 under clear weather conditions in three months (April, June, and September), representing three different seasons (spring, summer, and autumn, respectively) in Central-Europe with sufficient ant activity.

2.2. Sampling design

We set up four fixed sampling sites (separated by at least 20 m) on all four habitat types of each wood-pasture (i.e., 16 sampling sites/wood-pasture; 48 in total/season). The same sampling sites were used for the three different seasons. The three wood-pastures were sampled within a 10-day sampling window in each season, with the sampling of the four different habitat types carried out simultaneously along a sampling day (i.e., 9 sampling days in total).

In woody habitat types (forests, forest edges, and solitary trees), each sampling site contained a central oak tree. In forests, to exclude any potential edge effects, we selected trees located at least 50 m from the forest edges, whereas in forest edges, trees from the outermost tree lines were used. Solitary trees were oaks embedded into the grassland matrix at least 50 m from the nearest forest edges. Within grasslands, the sampling sites were organized in a rectangular pattern and positioned at a minimum distance of 50 m from the nearest forest edge or solitary tree. The sampling design was consistent with our previous study on wood-pastures (cf. Lőrincz et al., 2024).

During all three seasons, we used non-invasive baiting to assess the relative abundance of different ant species and their community composition. Each sampling site consisted of five bait stations, arranged in a cross-shaped pattern: four stations were placed in the cardinal directions 3 m away from the central oak, whereas one station at breast height (~1.5 m) on the north-facing side of the central oak's trunk (i.e., 60 bait stations/habitat type/season, 720 in total). In grasslands, the central bait station was placed on the ground (cf. Lőrincz et al., 2024). We monitored the ant foraging activity on baits (1:3 mixture of tuna:honey placed on a plastic disk of Ø 8 cm) every 30-min during three observation periods: 7:30 a.m. – 9:30 a.m., 11:30 a.m. – 2:00 p.m., and 4:00 p.m. – 6:30 p.m. (i.e., 17 observations/bait station/day), corresponding to the main activity periods of diurnal ant species in similar habitats (e.g., Tăuşan et al., 2017; Maák et al., 2020; Lőrincz et al., 2024). In spring, however, the first observation period started at 8:30 a.m., as ant activity was too low during the earlier hours. During each observation, we noted the number of workers per ant species and the interactions among them (e.g., biting and charging; see also Maák et al., 2020; Lőrincz et al., 2024). Baits were available *ad libitum*. Ants were identified to morphospecies or genus level in the field, and workers 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.

Determining the range of environmental conditions experienced by ant species at the different habitat types requires the simultaneous monitoring of ant activity and fine-scale environmental conditions. To achieve this, we monitored the changes in four key environmental parameters at each sampling site, which are considered primary factors influencing ant activity: soil and air temperature, relative air humidity, and solar irradiance (Perfecto and Vandermeer, 1996; Retana and Cerdá, 2000; Azcárate et al., 2007). At

Table 1
Location and general characteristics of the three wood-pastures selected for the study.

Location	Area (Ha)	Elevation (m a.s.l.)	Mean annual precipitation (mm)	Mean annual temperature (°C)	GPS coordinates
Erdőbénye, Hungary	215	215–245	600	9.5	N 48.276, E 21.319
Deușu, Romania	250	420–490	600	8.3	N 46.916, E 23.505
Rupea, Romania	393	500–580	650	8.2	N 46.019, E 25.223

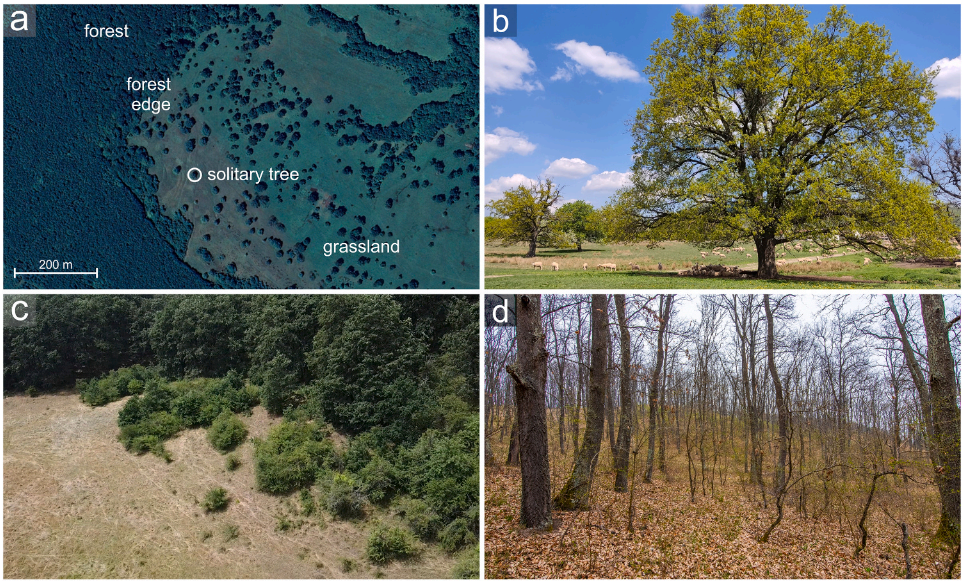

Fig. 1. (a) Aerial view of a wood-pasture (Rupea, Romania), with the four encompassing habitat types: (b) solitary trees and the surrounding grasslands, (c) forest edges, (d) forests.

each observation period, we recorded the soil temperature (°C) in the upper 10 cm of the soil using digital penetration probe thermometers (TFA pocket-digitemp 30.1018; 2640 measurements in total). Local air temperature (°C) and relative air humidity (%) were monitored at 5-min intervals using Optin Ambient Data Loggers (ADL-TH3; 17424 measurements in total). The loggers were encased in a radiation shield and suspended at 10 cm above the ground (Frei et al., 2023; Lőrincz et al., 2024). For sampling sites of woody habitat types, we installed an additional data logger at breast height (~1.5 m) on the south-facing side of the tree trunk, close to the bark to monitor the environmental conditions experienced by ants foraging on bait stations located on the tree trunk. We chose this side to avoid interference with the microclimate loggers during our observations of the bait stations. The intensity of solar irradiance (W/m^2) was monitored at one location per habitat type at 5-min intervals using Kipp & Zonen SMP3 pyranometers (4356 measurements 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 prevent shading by our activities (see also Lőrincz et al., 2024).

2.3. Species grouping

Similarly to our previous study on wood-pastures (Lőrincz et al., 2024), the species grouping was based on two indices that reflect the two components of ant dominance: behavioral and ecological dominance (Cerdá et al., 1997; Parr and Gibb, 2010). To measure behavioral dominance, we calculated an aggression index (A) for each species, which is defined as the proportion of aggressive interactions (e.g., charging, biting, and expulsion) directed toward heterospecific workers (Fellers, 1987; Bestelmeyer, 2000). For ecological dominance, an evenness value was calculated for each species 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 type of the respective wood-pasture (for the activity ranges, see Table S4). The Shannon-diversity value (H) of a species is based on a modified form of the Shannon-diversity index:

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

where Oc is the number of bait stations occupied by a given species, and pi is the proportion of workers present in the i^{th} of O_c observations (Retana and Cerdá, 2000; Lőrincz et al., 2024). Based on these two indices, ant species were grouped into three categories: dominant (high behavioral and ecological dominance), intermediate (high behavioral, but lower ecological dominance, or vice versa), and subordinate (low behavioral and generally low ecological dominance) (see Table S1 for species list and Supplementary material further details of the species grouping).

2.4. Data analysis

2.4.1. Microclimatic conditions

To test how the four different habitat types of wood-pastures affect the large-scale effects of seasonality on local microclimate, we tested the effects of the three seasons on the measured environmental parameters (soil and air temperature, relative air humidity, and solar irradiation) by using linear mixed-effect models (LMMs, Gaussian error, maximum likelihood fit). Before 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. For solar irradiation, we log-transformed the data to achieve normality. In the full models, habitat type, season, 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. In the model for solar irradiation (only one pyranometer/habitat type), only the location was included as a random factor.

2.4.2. Niche hypervolume estimation

Our sampling design enabled us to link ant occurrence data to fine-scale measurements of local microclimatic conditions, and therefore, estimate the range of environmental conditions experienced by each species in each habitat type under field conditions (i.e., realized niche breadth). This approach provides more realistic representations of the key factors determining activity and distribution patterns (Arnan and Blüthgen, 2015; Guo et al., 2020; Haesen et al., 2023). The estimation was based on the construction of four-dimensional hypervolumes (Blonder et al., 2014), which are defined by the bounds of scaled and centered environmental factors, in our context, solar irradiance, air and soil temperature, and relative air humidity (Blonder et al., 2018). The hypervolume construction was performed using the support vector machine method (svm, with a default γ parameter value of 0.5), which provides a smooth fit around the data and allows for outlier inclusion, hence it is appropriate for realized niche modeling applications (Blonder, 2018; Blonder et al., 2018). Before the analysis, environmental data were separately min-max normalized across each habitat type. This way we ensured that the hypervolume values are unbiased by the different variability of environmental parameters of the four habitat types (cf. Lőrincz et al., 2024). Ant species with less than ten occurrences were excluded from the analysis to ensure the reliability of hypervolume construction (Blonder et al., 2014). The analyses were carried out for the three different seasons (spring, summer, autumn) separately.

To investigate whether seasonal changes in species niche hypervolumes impact the degree of niche overlaps within communities, we calculated the shared volume between hypervolumes of species pairs in each season and habitat type (i.e., niche overlap, Blonder et al., 2018). Jaccard's similarity index was used to quantify niche overlaps between species pairs, which ranges from 0 (no overlap) to 1 (complete overlap). As every species had only one hypervolume value per season and habitat type, the hypervolume and Jaccard values were not compared statistically. Instead, we calculated the median values and interquartile ranges of these metrics for the different ant groups and assessed their percentage changes over the seasons to quantify seasonal changes in realized niche breadths and overlaps. In each habitat type, the largest niche change was set as a reference, and the rest of the niche shifts were calculated relative to this change. In the forest edges and forests, representatives of all three ant groups (dominant, intermediate, subordinate) occurred in sufficient numbers to allow for the quantification of seasonal changes in their realized niche metrics. In grasslands and solitary trees, however, only the dominant and subordinate groups could be considered, as intermediate species were not present in grasslands, and only one species with a few occurrences was found in solitary trees.

It is important to note that our approach operates with presence/absence data, as under field conditions, the number of ant workers observed on bait stations are influenced by several factors that are very difficult to control for (e.g., distance between the bait and nest (s), colony size, nest density, and different foraging strategies of species), leading to significant noise in the detected numbers. However, we performed the niche hypervolume construction and hypervolume overlap calculations also with abundance-weighted data to test the congruency between the two approaches. As all the general trends and patterns were consistent between the two approaches (see Supplementary material for the implementation of abundance-weighting and results), we opted for the former to avoid any bias introduced by the abovementioned factors influencing worker numbers.

2.4.3. Ant community structure and diversity metrics

To gain a general understanding of the ant community composition of the four different habitat types of wood-pastures, we calculated species richness and the proportion of occupied baits by the representatives of each behavioral group at each season. To calculate species richness, we pooled the data for each habitat type and determined the number of species found during each observation (i.e., 15 values for spring, and 17 for summer and autumn for each habitat type), thereby accounting for species turnovers between different sampling sites and locations. We used linear mixed-effect models (LMMs, Gaussian error, maximum likelihood fit) to compare the species richness of the different habitat types and seasons. In the models, the habitat type (space) or season (time) was included as a fixed factor, whereas the observation period was included as a random factor. Additional analyses regarding community structure (NMDS with fitted environmental vectors, PERMANOVA) and diversity metrics (Shannon diversity index) were also performed and are included in the Supplementary material.

2.4.4. Implementation of the statistical analysis

All statistical analyses were carried out using the R software (R Core Team, 2022). LMMs were performed using the *lmer* function of the 'lme4' package (Bates and Maechler, 2013). The *emmeans* function of the 'emmeans' package was used for sequential post-hoc comparisons among factor levels (Lenth, R., 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 of the 'hypervolume' package (Blonder et al., 2014).

3. Results

In total, we estimated the seasonal niche breadths and overlap patterns of 28 ant species belonging to three subfamilies (Formicinae: 16; Myrmicinae: 10; Dolichoderinae: 2 species). Of the four habitat types, forest edges hosted the most species-rich ant communities throughout the year (LMM $t>5.39$; $p<0.001$), while the grasslands were the most species-poor habitat types ($t>3.46$; $p<0.006$; Fig. S5**;** Table S4). The solitary trees and forests had intermediate species numbers with no significant differences between them ($t<2.24$; $p>0.125$; Fig. S5). Although species richness patterns were consistent across the different habitat types throughout the year, each habitat type experienced seasonal fluctuations in species numbers. The lowest numbers were detected during spring in all four habitat types ($t>5.04$; $p<0.001$; Fig. 2; Table S5), while there was no significant difference between summer and autumn in this aspect ($t<1.89$; $p>0.152$; Fig. 2) – except for forests, where the species number significantly decreased from summer to autumn ($t=5.20$; $p<0.001$). Based on the two indices reflecting behavioral and ecological dominance, eight species were placed into the dominant, five species into the intermediate, and 15 species into the subordinate groups (see Table S1 for the species list). The abundance and relative proportion of representatives of the different behavioral groups varied both in space (i.e., across habitat types) and time (i.e., across seasons) (Fig. 3), in concordance with the favorability of environmental conditions throughout the year.

3.1. *Effects of seasonality on microclimate*

Seasonality had a strong influence on the measured microclimatic parameters (Fig. S1). However, the different habitat types showed slightly varying patterns, suggesting that habitat structure interacts with the effects of seasonality to influence microclimate on a small spatial scale. The highest air temperatures were recorded during summer in all four habitat types ($z>39.99$; $p<0.001$). The difference between spring and autumn, however, varied: autumn was warmer in grasslands ($z=4.42$; $p<0.001$), there was no significant difference in solitary trees and forest edges between these seasons ($z<0.96$; $p>0.217$), whereas, in forests, higher temperatures were detected during spring ($z=6.21$; $p<0.001$) (Fig. S1a). Soil temperatures showed a more uniform pattern, with the highest values

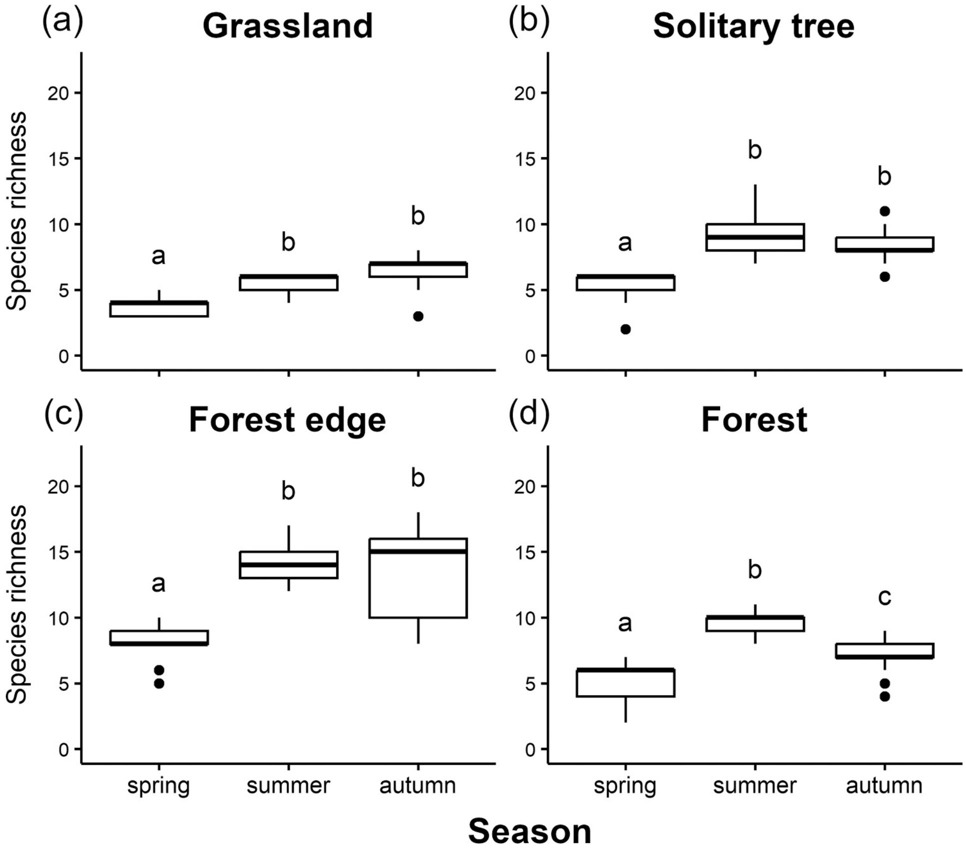

Fig. 2. Species richness of ant communities recorded during three seasons (spring, summer, autumn) in the four different habitat types of wood-pastures: a) grasslands, b) solitary trees, c) forest edges, d) forests. Different lowercase letters indicate significant differences among seasons ($p<0.05$).

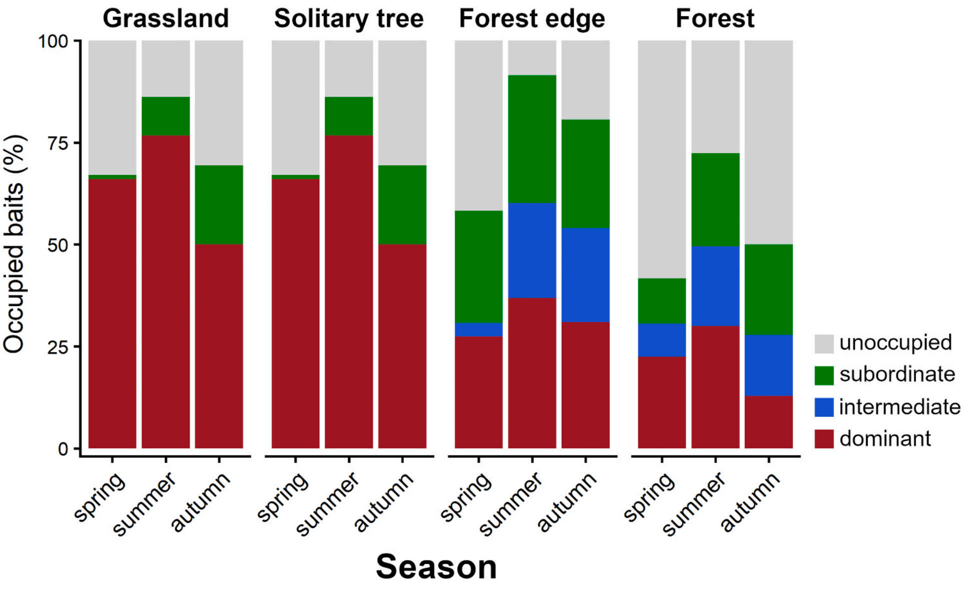

Fig. 3. Seasonal changes in the proportion of occupied baits by representatives of the three ant behavioral groups (dominant, intermediate, subordinate) across the four habitat types of wood-pastures.

during summer, followed by autumn and spring in all four habitat types ($z>4.18$; $p<0.001$) (Fig. S1b). Relative air humidity was highest during autumn in all the habitat types, followed by summer and spring in woody habitat types ($z>9.04$; $p<0.001$). In grasslands, however, higher values were detected during spring compared to summer ($z=13.46$; $p<0.001$) (Fig. S1c). In woody habitat types, solar irradiance was the most intensive during spring, followed by summer and autumn ($z>8.45$; $p<0.001$). In grasslands,

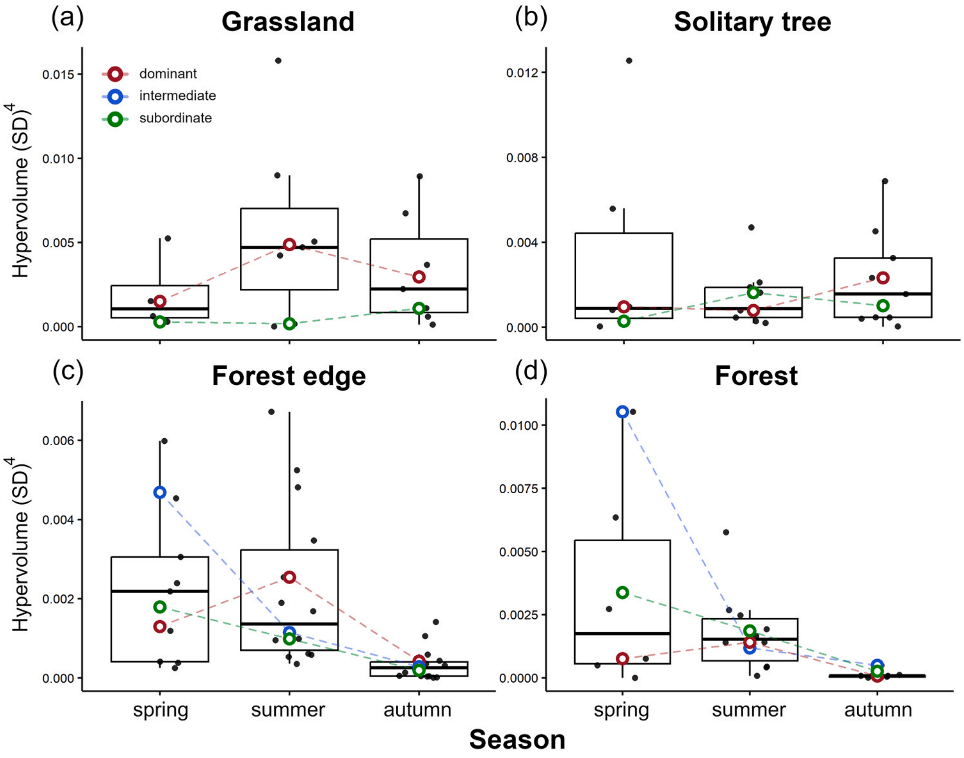

Fig. 4. Seasonal changes in niche hypervolumes of ant communities in the four different habitat types (grasslands, solitary trees, forest edges, and forest) of wood-pastures. Plots show medians, lower and upper quartiles, min-max values, and outliers, whereas colored circles within indicate the median value of the corresponding ant behavioral group (red–dominant, blue–intermediate, and green–subordinate).

however, the highest values were detected during summer, followed by spring and autumn ($z > 5.75$; $p < 0.001$) (Fig. S1d).

3.2. Seasonal changes in niche hypervolumes

In concordance with the changes in abundance, ants belonging to the three groups (dominant, intermediate, and subordinate) showed substantial changes in their realized niche breadths throughout the seasons, having different patterns in the four studied habitat types (Fig. 4, Table S6). In grasslands, the niche hypervolume of the dominant group showed an optimum curve, increasing substantially from spring to summer (100 % increase, i.e., largest detected niche expansion), and decreasing from summer to autumn by 42.9 %, taking an intermediate value. Meanwhile, the hypervolumes of the subordinate group were consistently lower throughout the seasons, with smaller and opposing inter-seasonal variability (3.6 % decrease from spring to summer, and 27.2 % increase from summer to autumn) (Fig. 4a). In solitary trees, the niche hypervolume of the dominant group decreased slightly from spring to summer (11.2 %), and increased drastically from summer to autumn (100 % increase). The hypervolumes of the subordinate group showed an opposite pattern, increasing from spring to summer (86 %), and decreasing from summer to autumn (39.7 %; Fig. 4b). In forest edges and forests, niche hypervolume changes of the different behavioral groups followed identical patterns throughout the seasons. In both habitat types, the values of the intermediate group underwent the largest decrease from spring to summer (100 % decrease), and a further decrease was observed from summer to autumn (24.3 % in forest edges, and 7.3 % in forests, respectively). The values of the subordinate group followed a similar pattern, decreasing from spring to summer (22.7 % in forest edges, and 16.3 % in forests), and further decreasing from summer to autumn (22.4 % in forest edges, and 17.1 % in forests). The values of the dominant group, however, showed an optimum curve, increasing from spring to summer (35.1 % in forest edges, and 6.9 % in forests), and decreasing from summer to autumn (59.9 % in forest edges, and 14.2 % in forests; Fig. 4c,d), similarly to the grasslands.

3.3. Seasonal changes in niche hypervolume overlaps

Similarly to the niche hypervolumes, the niche (hypervolume) overlap patterns of the different ant groups varied across habitat types (Fig. 5). In grasslands, the niche overlaps showed an increasing trend for all the behavioral group combinations along the seasons (i.e., the dominant ants exhibited growing niche overlaps with both other dominant and subordinate ants, while subordinate species also displayed increasing overlaps with other subordinate species; Fig. 5a). The highest overlaps were detected between dominant species, while subordinates exhibited lower niche overlaps with other subordinate or dominant species throughout the seasons (see

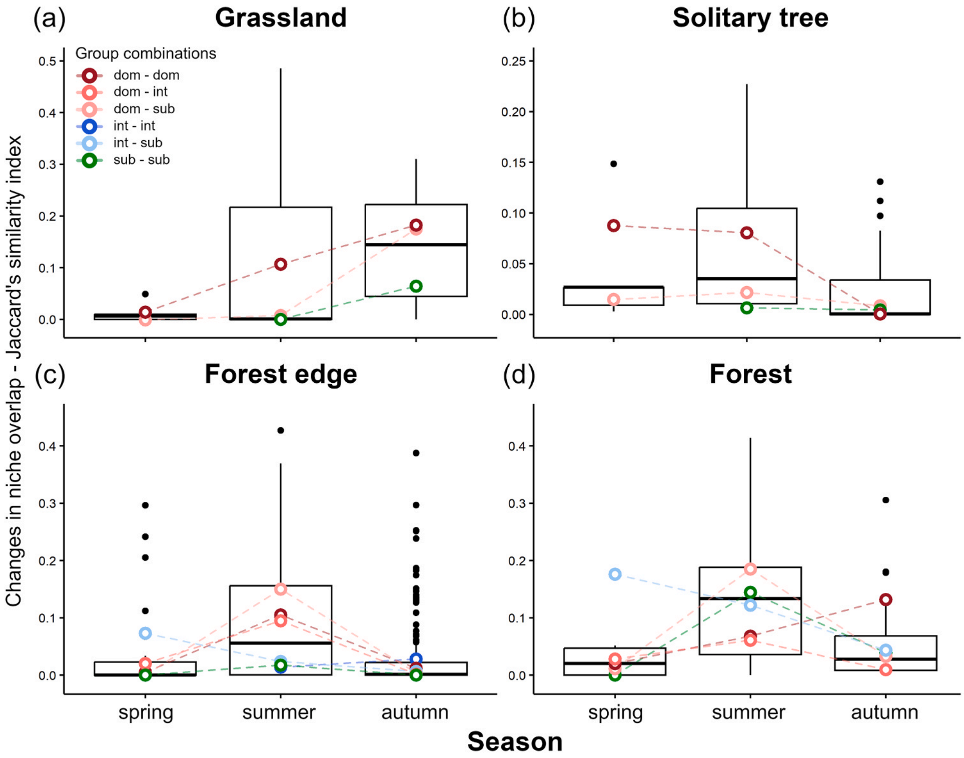

Fig. 5. Seasonal changes in the realized niche overlaps (quantified by Jaccard similarity values) of ant species in the four different habitat types (grasslands, solitary trees, forest edges, and forest) of wood-pastures. Plots show medians, lower and upper quartiles, min-max values, and outliers, colored circles within indicate the median value of the corresponding ant behavioral group combination. Values range from 0 (no overlap) to 1 (complete overlap). Legend abbreviations: dom=dominant; int=intermediate; sub=subordinate.

Table S7 for the Jaccard similarity values and percentage changes). For solitary trees, the overlaps between dominant species showed a slight decrease from spring to summer, and a large decrease from summer to autumn, while the niche overlaps of the other behavioral group combinations (dominant–subordinate, and subordinate–subordinate) showed lower values and remained relatively unchanged throughout the seasons (Fig. 5b). For forest edges and forests, the identical hypervolume changes resulted in similar changes in the niche overlap patterns. From spring to summer, all behavioral groups showed increased niche overlaps with the dominant group, while the overlaps decreased from summer to autumn. In forests, however, the niche overlaps between the dominant ants further increased from summer to autumn. This unimodal pattern also applied to subordinate ants, whereas the niche overlaps between the subordinate and intermediate groups gradually decreased throughout the seasons (Fig. 5c,d).

4. Discussion

Our results strongly support the "ecosystem-complex" approach of wood-pastures proposed by Bergmeier et al. (2010), and highlight their potential to boost landscape-level biodiversity by sustaining distinct communities on a small spatial scale. Despite being in close proximity to each other, the ant communities of the four different habitat types exhibited unique patterns of seasonal realized niche dynamics, implying that the relative importance of different community structuring mechanisms differs among them. The dominant, intermediate, and subordinate ant groups showed substantial changes in their realized niche breadths and niche overlaps throughout the year, resulting in community-wide temporal changes. The realized niche breadths of the dominant species generally influenced the values of the intermediate and subordinate ant groups, and were driving the level of niche overlaps (used as a proxy for competition). This spatiotemporal variability in competitive pressure opened up empty ecological niches to species belonging to the intermediate and subordinate groups, promoting their coexistence with dominant ants, and thus diversifying the studied ant communities.

The range of environmental conditions experienced by different ant species (i.e., hypervolume) was strongly influenced by the levels of solar irradiation, temperature, and humidity, which are considered primary determinants of ant activity (Hölldobler and Wilson, 1990; Porter and Tschinkel, 1993). Being the most exposed habitat types, the grasslands posed favorable environmental conditions throughout the year, contributing to the high abundance and prevalence of dominant species. However, during spring, their activity was restricted to a narrow range of environmental conditions, as indicated by the low hypervolumes and species numbers. This is likely to be the result of low soil and air temperatures, which constrain the activity of many ant species (Crist and Williams, 1999; Azcárate et al., 2007). As solar irradiation and temperatures increased from spring to summer, dominant ants expanded their realized niches and foraged under a much broader spectrum of environmental conditions, which, similarly to other studies, led to their higher prevalence (Cros et al., 1997; Retana and Cerdá, 2000). This expansion, however, inevitably resulted in increased niche overlaps among dominant species, which was even more pronounced during autumn. The milder environmental conditions during autumn forced dominant ants to restrict their activity (lower hypervolumes and percentage of occupied baits as compared to summer), which, based on our results, led to high niche overlaps during the favorable periods. On the other hand, the niche hypervolumes and overlaps of the subordinate species were consistently lower throughout the year, with smaller inter-seasonal variability. Many subordinate species have been shown to forage under suboptimal environmental conditions to minimize competition with behaviorally dominant ants, a phenomenon known as dominance-thermal tolerance trade-off (Cerdá et al., 1997). The inverse relationship between dominance and thermal tolerance is an important mechanism of coexistence in both heat- and cold-limited environments (Bestelmeyer, 2000; Lessard et al., 2009; Lőrincz et al., 2024), and likely explains the observed low hypervolumes of subordinate grassland species. It is important to note, however, that high niche overlaps do not always indicate elevated levels of competition within communities. Such disruption may occur under conditions of low competition caused by strong environmental filtering (e.g., at high latitudes and altitudes, Arnan et al., 2017; Silvestre et al., 2021) or by an elevated abundance of resources (Connell, 1983). However, due to the lack of similar conditions in our study sites, and the direct observations of numerous aggressive interspecific interactions and species turnovers, we believe that in our study the use of niche overlap as a proxy for competition is well supported.

The solitary trees posed distinct microclimatic conditions throughout the year, resulting in different patterns of ant activity and niche dynamics compared to the surrounding grasslands. Similarly to grasslands, the constraining effect of cold springtime conditions limited the activity of both dominant and subordinate behavioral groups, resulting in low hypervolumes and a low percentage of occupied baits in this season. The spring-summer transition, however, did not result in a drastic niche expansion of dominant ants, as observed in grasslands. Both the hypervolumes and hypervolume overlaps remained relatively unchanged for the dominant group, thus they did not monopolize and dominate the trees, but rather occupied some preferred baits. Besides these baits, dominant ants focused their foraging efforts on grasslands, where the conditions were generally more appropriate for their activity (higher percentage of occupied baits on grasslands). Subordinate species, on the other hand, benefited from the heterogeneity provided by the solitary trees and expanded their hypervolumes during summer, without increasing the niche overlaps with the dominant ants. The increased structural and microclimatic heterogeneity of solitary trees thus likely explains the higher species numbers of this habitat type, as it was also demonstrated in other studies (e.g., Regnery et al., 2013; Horak et al., 2014; Sebek et al., 2016). In autumn, unlike the spring-summer transition, dominant ants expanded their hypervolumes and foraged under a wider range of environmental conditions, possibly due to the diminishing microclimatic differences between grasslands and solitary trees. However, parallel with this hypervolume increase, the niche overlaps between dominant ants decreased. This pattern is likely to be explained by the fact that during autumn, dominant species rarely co-occurred under the same trees. Although spatial mosaics generated by the non-random distribution of ants might indicate strong competition (Majer et al., 1994), this pattern might also reflect the decreased ant activity during this season or the preferences towards certain microhabitats or microclimatic conditions (Ribas and Schoereder, 2002).

While the daily microclimatic conditions differed slightly between the forests and forest edges, their annual variations followed consistent patterns. Accordingly, the niche dynamics of the different ant behavioral groups in these habitat types exhibited similar trends throughout the year, despite the differences in their relative abundances and species numbers. Both in forest edges and forests, the hypervolumes of the intermediate species were exceptionally high during spring, and showed a decreasing trend throughout the year. The same trend was observed for the subordinate species, with less extreme spring maxima in both habitat types. This result should be interpreted in light that *Myrmica ruginodis* was by far the most abundant species of the intermediate group, and other *Myrmica* species were also abundant among subordinates. Previous studies showed that multiple members of this genus tend to forage at low temperatures to avoid competition with dominant ants (Mabelis, 1983; Vepsäläinen and Savolainen, 1990), emphasizing the relevance of the dominance-thermal tolerance trade-off in cold-limited environments (Lessard et al., 2009). During spring, despite the relatively high solar irradiance levels, the soil remained cold throughout the day, inhibiting the activity of many ant species (Pol and de Casenave, 2004). Indeed, we detected the lowest number of species, the lowest proportion of occupied baits, and the lowest hypervolume overlaps with dominant ants, suggesting that species active under suboptimal springtime conditions might experience low levels of competition. Release from interspecific competition has been shown to increase the realized niche breadth of different animal species (Bolnick et al., 2010; Neves et al., 2021), and probably explains the high hypervolumes of the intermediate and subordinate groups in spring.

Communities of forest edges and forests underwent drastic seasonal changes from spring to summer, which is likely attributed to the increased environmental favorability. Similarly to grasslands, with rising temperatures, members of the dominant group expanded their hypervolumes and foraged under a much broader range of environmental conditions, leading to their increased prevalence. This was also observed in the other two groups. These results align with previous studies indicating clustered ant activity during warmer months, possibly due to improved environmental conditions and increased food availability (Dunn et al., 2007; Lessard et al., 2009). The higher prevalence of dominant species, however, led to a concordant increase of niche overlaps between the dominant and other groups during summer, thereby increasing the interspecific competition within the communities. This increased competitive pressure possibly limits the foraging activity of intermediate and subordinate ants (Savolainen and Vepsäläinen, 1989; Arnan et al., 2011), and thus contributes to their decreased hypervolumes.

Similarly to the spring-summer transition, substantial changes were observed in the studied metrics during the summer-autumn transitions in forest edges and forests. The hypervolume of the dominant group decreased in both habitat types, which, again, is probably caused by the constraining effects of cooler temperatures and low irradiance detected during autumn. This hypervolume decrease resulted in lower niche overlaps between the dominant and other groups in both habitat types. However, the two habitat types showed differences in other aspects, which likely can be traced back to their different microclimatic and structural characteristics. In forest edges, the number of co-occurring species further increased from summer to autumn, while the activity remained high (76 % of the baits were occupied, as compared to 50 % in forests). This is likely attributed to the complex vegetation structure and relatively open nature of forest edges, which create diverse microhabitats and microclimatic conditions (Risser, 1995), thus enhancing the diversity of different organisms (e.g., Erdős et al., 2013; Gallé et al., 2014). In contrast, closed forests presented less favorable conditions for ant activity, as their canopy blocked solar irradiation, leading to the lowest detected temperatures. This probably also explains the decreased abundance and species numbers of ants during autumn. Interestingly, dominant species that persisted in forests showed high niche overlaps despite their low hypervolumes – this pattern reflects the observed patchy distribution of these ants, leading to the aggregation of species in particular sampling sites. The patchy distributions can be attributed to a range of factors, but preference for certain microclimatic conditions, food and nest site availability, and associations with other species are probably of primary importance (Kaspari and Majer, 2000; Ribas and Schoereder, 2002; Maziarz et al., 2021).

5. Conclusions

In face of the ongoing and future loss of natural habitats and global climate change, the preservation of semi-natural habitats and land-use forms of high conservation value are of crucial importance to mitigate biodiversity loss (Tscharntke et al., 2021). It is equally important to obtain a holistic understanding of the mechanisms facilitating species coexistence in these systems, as such insights form the basis of both ongoing and future conservation strategies and trajectories. In our study, focusing on one of the most widespread and diverse semi-natural habitats of Europe, we showed that the spatiotemporal variability of environmental conditions on wood-pastures promotes the coexistence of four distinct ant communities by enforcing different community structuring mechanisms. This coexistence is mediated by both temporal (substantial and complementary seasonal niche expansions and retractions of the different ant behavioral groups) and spatial (varying niche composition and dynamics across the four different habitat types) niche-based mechanisms. Given the unique community dynamics and different community structuring mechanisms of the four habitat types, our results strongly support the “ecosystem complex” approach of wood-pastures, and highlight the potential of heterogeneous semi-natural landscapes to conserve high biodiversity on a relatively small spatial scale. Considering their global distribution and multifaceted conservation relevance, wood-pastures of Europe emerge as a promising land-use form to preserve biodiversity without compromising agricultural productivity. However, we strongly believe that whenever possible, such heterogeneous landscapes should be regarded and considered in conservation efforts as a whole, with all the encompassing habitat types to maximize biodiversity preservation.

Ethics approval

All applicable national guidelines for the care and use of animals were followed.

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Declaration of Competing Interest

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Data availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03170.

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