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ORIGINAL ARTICLE

Annual dynamics of subterranean ants (Hymenopetra: Formicidae) in a cork oak forest in Morocco (Northwest Africa)

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Abstract. Subterranean ants play a critical role in soil ecosystems, yet their cryptic lifestyle and the challenges associated with their sampling hinder comprehensive understanding of their biodiversity. This study examines the seasonal dynamics of subterranean ant communities in a cork oak forest in northwestern Morocco. We employed an adapted soil-washing method. that enabled the collection of 1,318 individuals from 17 species, of which 41.18% were identified as hypogaeic. The analysis revealed significant differences in community composition across seasons, with summer exhibiting notably higher species richness and worker abundance. Non-hypogaeic ants showed strong positive correlations with temperature and negative correlations with rainfall, while hypogaeic ants exhibited weak and non-significant responses to climatic variables, likely due to their ecological specialization. These results suggest that climatic factors distinctly influence ant subgroups and highlight the ecological relevance of subterranean ants in soil biodiversity. The study underscores the importance of tailored sampling methodologies for capturing the diversity and dynamics of these often-overlooked communities.

INTRODUCTION

Hypogaeic ant species are known to nest, forage, and migrate underground, where environmental conditions impose significant constraints on their morphology and behavior i.e. ants that can be found in the soil and are specifically adapted to a primarily underground existence (Wong & Guénard, 2017). Within these habitats, they exhibit distinct adaptations that reflect their specialization to life in low-light environments with limited space for movement. These adaptations include reduced or absent eyes, pale or depigmented cuticles, compact body structures, and shortened appendages, which facilitate their navigation and survival in confined and stable underground ecosystems (Fowler & Delabie, 1995; Silva & Silvestre, 2004; Eguchi et al., 2006, 2010; Weiser & Kaspari, 2006; Andersen & Brault, 2010; Zryanin, 2015). Their cryptic lifestyle and unique adaptations to specific environmental conditions, such as complete darkness and limited fluctuations in temperature and humidity, make them fascinating subjects for ecological research (Culver & Pipan, 2014; Mammola et al., 2016; Nitzu et al., 2018).

In forest ecosystems, subterranean ants play a crucial ecological role, particularly in decomposition processes, soil formation, and trophic networks (Kalule-Sabiti, 1980; Lavelle, 1997; Folgarait et al., 1998; Underwood & Fisher, 2006; Culliney, 2013). Despite their ecological importance, the cryptic nature of these ants, combined with the difficulties involved in their sampling, has limited the collection of comprehensive data on their ecology and biology, resulting in limited understanding and fragmented knowledge about their roles in subterranean ecosystems (Culver & Pipan, 2014; Wong & Guénard, 2017; Martins et al., 2020; Houadria & Menzel, 2021). Research suggests that their diversity and abundance are likely underestimated (Longino & Colwell, 1997; Cagniant, 2006).

The cork oak forest in Morocco (Northwest Africa) provides a particular environment for studying subterranean ant communities due to its specific biodiversity and distinct microclimatic features (Villemant & Fraval, 1993; Afi et al., 2005; Zouaki et al., 2018; Samih et al., 2024). This study aims to explore the seasonal dynamics of subterranean ant communities within this habitat using an improved soil-washing methodology, avoiding bait usage as implemented in several previous studies (Wong & Guénard, 2017). Traditional methods are limited in accurately assessing the spatial and temporal structure of hypogaeic ant communities (Ryder Wilkie et al., 2007). Our methodological approach effectively captures ants inhabiting soil. These environments include both interstitial spaces between soil particles and cavities within the rocky substrate,

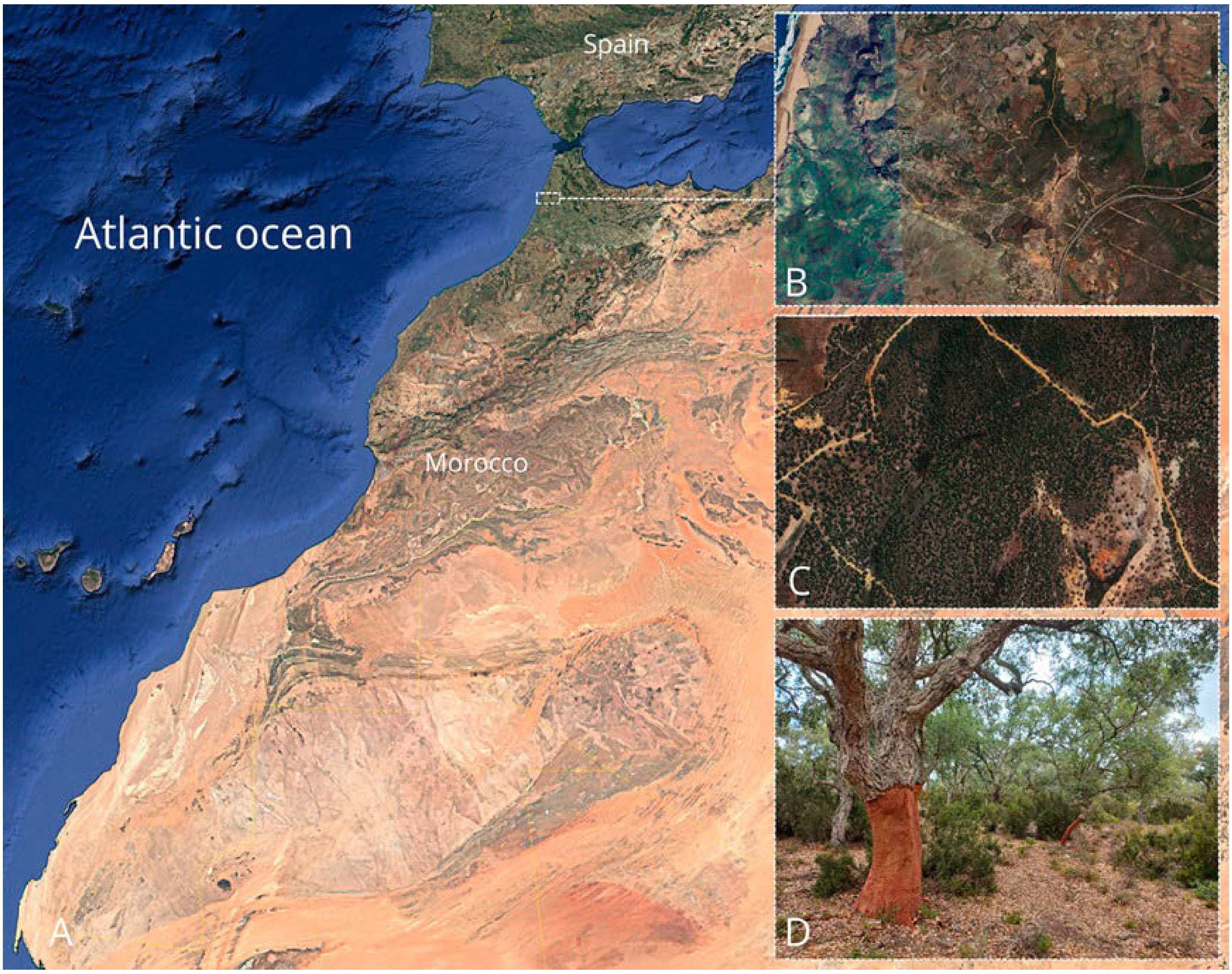

Fig. 1. Multiscale representation of the study site, illustrating the geographic context from the map of Morocco (A), the Krimda region (B), the surveyed cork oak forest (C), and a detailed view of a sampled station prototype (D).

which serve as climatic and reproductive refuges for several species due to reduced temperature extremes throughout the year (Nitzu et al., 2010, 2014, 2018; Mammola et al., 2016), as well as biogeographical corridors to deeper ecosystems (Ortuño et al., 2013; Jiménez-Valverde et al., 2015). Indeed, Wong & Guénard (2017) highlighted that subterranean ant communities are not only distinct from those of upper strata but also remarkably diverse, with up to 113 species recorded in certain studies and uniqueness levels reaching 44%. Similarly, Martins et al. (2020) reported 149 species sampled using the TSBF method, of which 36 were considered hypogaeic. These findings underscore the critical importance of developing and applying sampling methods tailored to the study of these cryptic populations.

We hypothesize that seasonal variations in environmental and microclimatic conditions within the cork oak forest induce significant changes in the composition and abundance of subterranean ant communities. Additionally, we propose that specific climatic factors, namely temperature (T_{Max} and T_{min}) and rainfall, have a direct influence on the abundance patterns of these subterranean ants. These changes are expected to reflect the ants' adaptations to fluctuations in resource availability and environmental constraints. Our null hypothesis (H0) is that no significant variation exists in the composition and abundance of subterranean ant communities between seasons. By testing this hypothesis, our study aims to contribute to a deeper understanding of subterranean ant ecology and their roles in ecosystem processes, thereby highlighting their importance in subterranean biodiversity.

This research contributes to a better understanding of subterranean biodiversity and its seasonal dynamics, a field still underexplored but essential for future conservation planning (Villemant & Fraval, 1993; Verdinelli et al., 2017). By clarifying the relationships between subterranean ant communities and climatic variables, we also aim to contribute to conservation efforts for these unique habitats and their exceptional biodiversity.

MATERIAL AND METHODS

Study area

The study area is situated in the province of Larache (35.291, –6.067), in northwest Morocco (Fig.1A). The climate is characterized as Mediterranean, classified as Csa according to the Köppen-Geiger system (Kottek et al., 2006). Larache experiences an average temperature of 17.9°C, with an annual precipitation of 779 mm (Climate Data, 2021).

The surveyed forest belongs to the group of "subhumid cork oak forests on sand" (Sauvage, 1961). Locally, it is dominated by mature *Quercus suber* L., 1753 trees, with canopy cover ranging from 50% to 75% (Fig. 1B, C). The understory, covering less than 50%, is mainly composed of *Erica arborea* L., 1753, *Pistacia lentiscus* L., 1753, *Cistus crispus* L., 1753, *Cistus monspeliensis* L., 1753, and *Chamaerops humilis* L., 1753.

The maximum temperature, minimum temperature, and precipitation variables for Larache were obtained from meteorological data available on the Weather Spark website (2022) for inclusion in this study.

Sampling method

The sampling was based on the use of the "soil washing method" for collecting subterranean ants. The method was developed by Normand (1911) for capturing subterranean beetles. It allows researchers to catch very specialized ants living underground and rarely found otherwise (Wong & Guenard, 2017; Castro et al., 2018). Sampling unit was 18,750 cm^3 (0.25 × 0.25 m and 0.30 m depth), sieved at 5 × 5 mm. This unit was chosen following the methodology suggested by the Tropical Soil Biology and Fertility Program (TSBF) for soil macrofauna collection (Anderson & Ingram, 1990) and the study of Wong & Guénard on subterranean ants sampling methods (2017). The surface humus layer was removed before soil collection to minimize contamination by non-hypogaeic species. Additionally, a depth of 30 cm has been shown to be effective in encompassing the entire assemblage of subterranean ant species within a tropical ecosystem (Lavelle & Spain, 2001; Ryder Wilkie et al., 2007). The extracted soil was sieved through sieves of 5 mm mesh. This sieving is mainly used to remove large unnecessary particles and to separate the soil from the roots of the plants (Lemagnen, 2009). The sifted soil is poured carefully into a large bucket, 75% of which is filled with water. Then the substrate which has fallen into the bucket is stirred by hand. After 10 min of settling, heavy and inert matter sinks to the bottom, as living things rise to the surface, often attaching themselves to small, light organic fragments. Subsequently, the supernatant is taken with a fine mesh sieve strainer and packed in several layers of recycled newsprint for 2 days in the open air in the shade, and to have a suitable desiccation without the formation of solid crusts.

During the year 2022, we systematically collected 10 soil samples each month, maintaining a consistent spacing of 10 m between them along a 100 m transect. A total of 120 soil samples were taken and analyzed (i.e. 2.25 m^3 of soil analyzed). After extraction, the ants were stored in 70% ethanol for subsequent identification. Specimens were sorted and identified to species level using standard taxonomic keys relevant to the Mediterranean ant fauna. The following keys were applied according to genus: Cagniant & Espadaler (1997) for *Temnothorax*; Cagniant (1996) for *Aphaenogaster*; Cagniant (2005) for *Crematogaster*; Cagniant (1997) for *Tetramorium*; Sharaf et al. (2011) for *Plagiolepis*; Bolton (2000) for *Strumigenys*; Bolton & Fisher (2011) for *Hypoponera*; Taylor (2015) for *Dorylus*; Kugler & Ionescu (2007) for *Anochetus*; and Borowiec & Salata (2022) for *Stigmatomma*.

Data analysis

In this study, we analyzed the monthly dynamics of ant populations in a cork oak forest, focusing on the interaction between climatic variables and ant biodiversity over a one-year period. The variables examined included maximum temperature (T_{Max}), minimum temperature (T_{min}), Rainfall, total number of species per month (TNS/M), and the total number of workers per month (TNW/M), in addition to the Monthly Shannon diversity index (MSH).

We categorized the captured ants into two groups: hypogaeic ants, characterized by small body size, reduced or absent eyes, short legs, and depigmented bodies, as described by Andersen & Brault (2010); and non-hypogaeic ants, which lack at least one of these characteristics and are generally found foraging in leaf litter or are arboreal. Individuals in the latter category were either encountered near their ground nests or accidentally captured, thus contaminating the collection equipment. We then analyzed the monthly variation in the abundance of these two ant categories using the Kruskal-Wallis test, which is suited for non-normal distributions.

To visualize seasonal patterns in species richness and abundance of the different ant groups (subterranean, non-hypogaeic, and hypogaeic), we performed a circular (radar) analysis.

The analysis was then continued with the construction of a Pearson correlation matrix to identify linear relationships between the variables, excluding the month, for subterranean ant species. The same approach was then applied separately for hypogaeic species and non-hypogaeic species. Subsequently, a simple linear regression model was used to assess TNW/M as a function of T_{Max}, T_{min}, and Rainfall. To assess the dispersion and diversity of ant communities across different seasons, a pairwise PERMANOVA (Permutational Multivariate Analysis of Variance) was conducted

Table 1. Monthly distribution and abundance of captured ants. 1 – January, 2 – February, 3 – March, 4 – April, 5 – May, 6 – June, 7 – July, 8 – August, 9 – September, 10 – October, 11 – November, 12 – December, * – hypogaeic species.

Species	1	2	3	4	5	6	7	8	9	10	11	12	Total	%
Plagiolepis schmitzii Forel, 1895	0	0	1	0	4	116	93	104	141	0	0	1	460	34.90
**Solenopsis* sp.	0	0	2	0	0	158	0	88	0	10	0	0	258	19.58
Temnothorax pardoi (Tinaut, 1987)	16	0	0	0	0	68	73	12	4	0	4	33	210	15.93
**Hypoponera eduardi* (Forel, 1894)	0	11	45	2	4	9	23	1	0	0	1	39	135	10.24
Temnothorax curtulus (Santschi, 1929)	0	0	0	2	0	0	0	0	0	55	15	0	72	5.46
**Strumigenys argiola* (Emery, 1869)	17	0	10	0	20	5	0	0	2	1	1	0	56	4.25
Pheidole pallidula (Nylander, 1849)	0	0	0	4	0	37	0	0	0	0	0	0	41	3.11
**Stigmatomma denticulatum* Roger, 1859	8	3	3	0	0	0	0	0	1	3	3	1	22	1.67
**Dorylus fulvus* (Westwood, 1839)	0	0	18	0	0	0	0	0	0	0	0	0	18	1.37
Aphaenogaster mauritanica Dalla Torre, 1893	0	0	0	0	7	0	3	0	0	0	0	0	10	0.76
Tetramorium semilaeve André, 1883	0	0	0	0	0	7	0	2	0	0	0	0	9	0.68
**Hypoponera ragusai* (Emery, 1894)	0	0	0	0	0	0	0	0	2	0	6	0	8	0.61
**Strumigenys baudueri* (Emery, 1875)	0	5	1	0	0	0	0	1	0	0	0	0	7	0.53
Aphaenogaster senilis Mayr, 1853	0	0	0	2	1	1	0	0	0	0	0	1	5	0.38
Crematogaster scutellaris (Olivier, 1792)	0	0	0	2	0	0	0	0	1	0	0	1	4	0.30
Anochetus ghilianii (Spinola, 1851)	0	0	0	0	0	0	0	0	2	0	0	0	2	0.15
Plagiolepis sp.	0	0	0	0	0	0	0	1	0	0	0	0	1	0.08

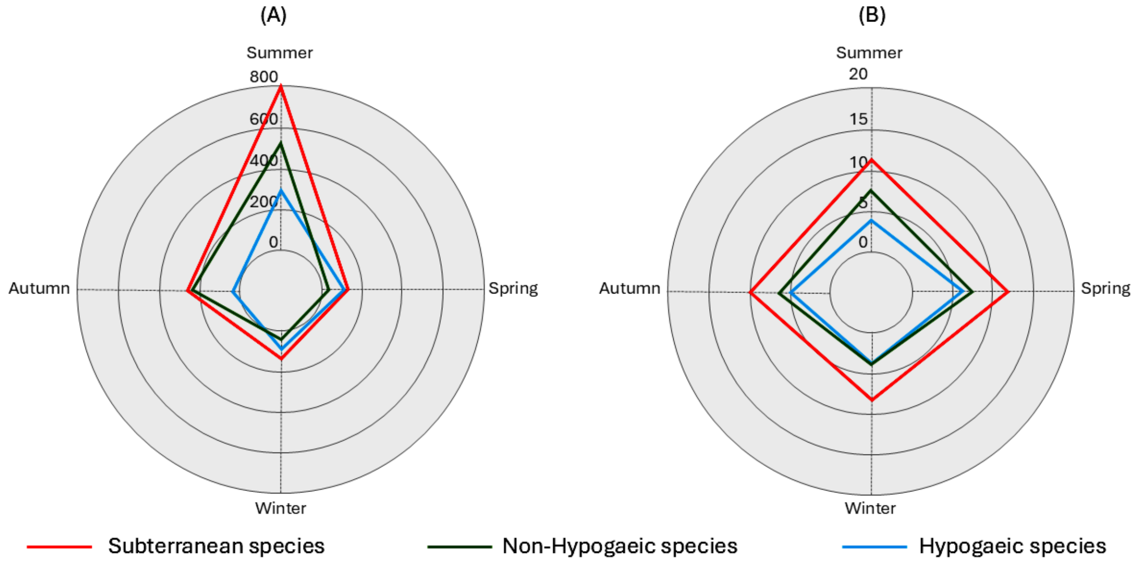

Fig. 2. Seasonal dynamics of ant abundance (A) and ant species richness (B) represented in radar plots.

using the function adonis () from the vegan package (Oksanen et al., 2024), and a multivariate dispersion analysis was performed using the function betadisper () from the same package. All the statistical analyses and plots were made with R version 4.4.0 (R Core Team, 2024), with visualization produced using the ggplot2 package (Wickham, 2016).

RESULTS

We collected a total of 1,318 ant workers, comprising 17 species across 12 genera. Seven species (41.18%) met the criteria for hypogaeic species (Table 1). The analysis of relative abundance among Formicidae species over a 12-month period reveals that four of the 17 captured species had an abundance exceeding 10%. Notably, *Plagiolepis schmitzii* Forel, 1895, emerged as the dominant species with 460 individuals, accounting for 34.9% of the total captures. This species primarily occurs during the warm period between June and September and is almost absent during the winter. The second species, *Solenopsis* sp., exhibiting a relative abundance of 19.57%, follows a pattern like that of *P. schmitzii*. Meanwhile, the third and fourth species, *Temnothorax pardoi* (Tinaut, 1987) and *Hypoponera eduardi* (Forel, 1894), with relative abundances of 15.93% and 10.24% respectively, are equally prevalent during both the cold and warm months. *Dorylus fulvus* (Westwood, 1839) was exclusively recorded during the spring season (in March), whereas *Hypoponera ragusai* (Emery, 1894) was observed during the autumn months (September and November). Both hypogaeic species are regarded as rare in this study.

Radar plots depicting the seasonal dynamics of ant communities show distinct annual patterns (Fig. 2). The abundance of subterranean ants shows clear seasonal variation, peaking in summer with 802 individuals and dropping to a low of 122 individuals in spring. Similarly, non-hypogaeic species are the most abundant in summer (517 individuals) and least abundant in spring (36 individuals). Hypogaeic species also display seasonal fluctuations, with their highest abundance recorded in summer (285 individuals) and the lowest in autumn (30 individuals). The species richness of subterranean ants is highest in spring (12 species) and lowest in winter (8 species). Similarly, non-hypogaeic species show maximum richness in spring and summer (7 species), and minimum richness in winter (4 species). In contrast, hypogaeic species exhibit peak richness in spring (6 species) and the lowest richness in both summer and winter (4 species).The correlation matrix (Table 2) including hypogaeic species and non-hypogaeic species reveals that TNS/M had moderate positive correlations with T_{Max} (r = 0.40, p = 0.201) and T_{min} (r = 0.44, p = 0.156), though neither correlation was statistically significant. For rainfall, TNS/M had a weak but non-significant negative correlation (r = –0.35, p = 0.261). In contrast, TNW/M exhibited

Table 2. Correlation matrix of species abundance, species richness and climatic factors. T_{Max} – maximum temperature, T_{min} – minimum temperature, TNS/M – total number of species per month, TNW/M – total number of workers per month, MSH – Monthly Shannon index.

	T_{Max}	T_{min}	Rainfall	TNS/M	TNW/M	MSH
T_{Max}	1.00	0.99***	–0.85***	0.40	0.69*	–0.28
T_{min}		1.00	–0.81**	0.44	0.70*	–0.28
Rainfall			1.00	–0.35	–0.68*	0.08
TNS/M				1.00	0.60*	0.10
TNW/M					1.00	–0.07
MSH						1.00

Statistically significant (*), highly significant (**), very highly significant (***).

Table 3. Correlation matrix for hypogaeic species. T_{Max} – maximum temperature, T_{min} – minimum temperature, TNS/M – total number of species per month, TNW/M – total number of workers per month.

	T_{Max}	T_{min}	Rainfall	TNS/M	TNW/M
T_{Max}	1.000	0.994***	–0.852***	–0.170	0.289
T_{min}		1.000	–0.814**	–0.126	0.291
Rainfall			1.000	0.172	–0.409
TNS/M				1.000	0.321
TNW/M					1.000

Highly significant (**), very highly significant (***).

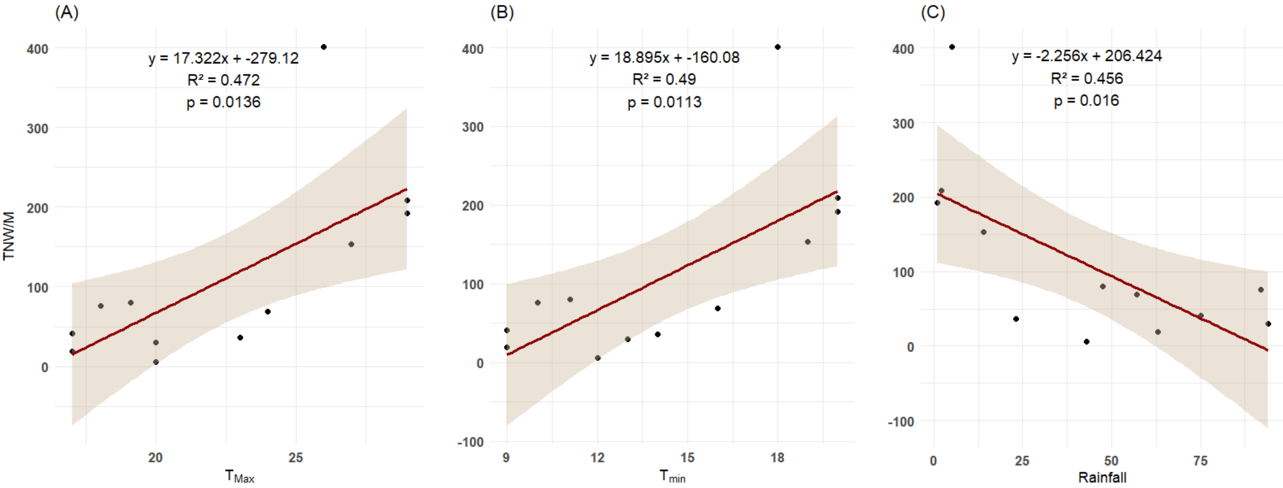

Fig. 3. Simple Linear Regression of TNW/M (total number of workers per month) based on T_{Max} (maximum temperature), T_{min} (minimum temperature), and Rainfall in a Cork Oak Forest.

moderate and strong, statistically significant positive correlations with T_{Max} (r = 0.69, p = 0.013) and T_{min} (r = 0.70, p = 0.011), and a moderate negative correlation with rainfall (r = –0.68, p = 0.016). By considering only the hypogaeic species (Table 3), TNS/M showed weak, non-significant correlations with all climatic variables (T_{Max}, T_{min}, and rainfall), with r values ranging from –0.17 to 0.17 ($p \geq 0.592$). Similarly, TNW/M exhibited weak to moderate, but non-significant correlations with these variables (r = –0.41 to 0.29, $p \geq 0.186$). For non-hypogaeic species (Table 4), TNS/M showed moderate positive correlations with both T_{Max} and T_{min}, though these did not reach conventional statistical significance (r = 0.55, $p \geq 0.059$), and a moderate negative non-significant correlation with rainfall (r = –0.51, p = 0.090). TNW/M, in contrast, exhibited strong positive correlations with T_{Max} and T_{min}, both statistically significant (r = 0.81 and 0.83, respectively, p = 0.001), and a strong negative correlation with rainfall (r = –0.72, p = 0.008).We investigated the relationships between TNW/M and temperature (T_{Max} and T_{min}) using simple linear regression models. The analysis revealed significant positive trends for both T_{Max} (R^2 = 0.472 p = 0.013) and T_{min} (R^2 = 0.490, p = 0.011), suggesting that ant abundance tends to increase with rising maximum and minimum temperatures. These relationships are visually represented in Fig. 3A, B.

Similarly, we analyzed the relationship between TNW/M and rainfall using a simple linear regression model. The analysis revealed a significant negative association between rainfall and ant abundance (R^2 = 0.456, p = 0.016), suggesting a decrease in ant abundance with increasing rainfall. This relationship is presented in Fig. 3C.

In addition, the PERMANOVA results revealed significant differences (adjusted p-values ranging from 0.006 to 0.030) between the following seasons: Winter and Summer, Spring and Summer, Spring and Autumn, Winter and Autumn, and Summer and Autumn. Summer shows a strong distinction compared to Winter, with more pronounced differences observed in pairs involving Summer, suggesting that this season is more distinct from the others. Between Winter and Spring, the difference was not statistically significant (adjusted p-value = 0.120), therefore, no statistically significant difference was found between these two seasons (Table 5).

DISCUSSION

Ants are widely recognized as excellent environmental indicators due to their remarkable diversity and essential functional roles in terrestrial ecosystems (Andersen et al., 2002; Andersen & Majer, 2004; Ellison, 2012; Fisher et al., 2014; Verdinelli et al., 2017). This capacity is particularly evident in cork oak woodlands, where, for instance, 25 species were recorded in Gallura, Italy, 18 in Maâmora, and 25 in Bab Taza, Morocco (Taheri et al., 2014; Verdinelli et al., 2017). However, most studies highlighting their bioindicator potential rely on traditional capture methods, such as pitfall traps, which target ants active in the litter or on the soil surface. In contrast, our soil washing method detected 17 species, including 7 hypogaeic species, shedding

Table 4. Correlation matrix for non-hypogaeic species. T_{Max} – maximum temperature, T_{min} – minimum temperature, TNS/M – total number of species per month, TNW/M – total number of workers per month.

	T_{Max}	T_{min}	Rainfall	TNS/M	TNW/M
T_{Max}	1.000	0.994***	–0.852***	0.555	0.815**
T_{min}		1.000	–0.814**	0.559	0.833***
Rainfall			1.000	–0.510	–0.722**
TNS/M				1.000	0.627*
TNW/M					1.000

Statistically significant (*), highly significant (**), very highly significant (***).

Table 5. Pairwise Seasonal Comparisons (PERMANOVA).

Pairs	Df	S.Sqs	F.Model	R^2	p. value	p.adj
Winter vs Spring	1	0.847	2.096	0.053	0.039	0.234
Winter vs Summer	1	1.387	3.487	0.066	0.001	0.006**
Winter vs Autumn	1	1.230	2.964	0.063	0.004	0.024*
Spring vs Summer	1	1.149	2.882	0.064	0.001	0.006**
Spring vs Autumn	1	1.263	3.013	0.075	0.001	0.006**
Summer vs Autumn	1	1.048	2.562	0.049	0.005	0.030*

Statistically significant (*) Highly significant (**).

light on less explored components of ant communities. Hypogaeic ants constitute one of the least-known frontiers for Formicidae (Ryder Wilkie et al., 2007; Schmidt & Solar, 2010). Because their apparent rarity often reflects methodological sampling artefacts (Schmidt & Solar, 2010), accurately characterizing subterranean assemblages requires efficient, specialized methods, notably TSBF monolith extraction and hypogaeic pitfall traps, which are crucial for documenting rare species (Berghoff et al., 2003; Martins et al., 2020).

The soil represents a unique habitat, distinct from most other micro-habitats due to two main characteristics: extremely low light levels or complete darkness, and severe spatial constraints resulting from the natural porosity of the substrate and the granulometry of its particles (Eisenbeis & Wichard, 1987). Another difference compared to surface habitats is the reduced amplitude of temperature extremes in MSS sites, which provide a more stable microclimate (Pipan et al., 2010). The lack of correlation between hypogaeic ant occurrence and temperature likely reflects strong soil thermal buffering, which creates stable microclimates; many subterranean ants also exhibit lower thermal tolerances than surface species (Roeder et al., 2021). These conditions have likely driven the emergence of specific morphological and physiological adaptations in hypogaeic ants, reflecting an evolutionary response to this specialized environment. Among these adaptations, significant eye reduction or complete eye loss, along with body depigmentation characterized by pale yellow to almost translucent white coloration, are commonly observed (Eguchi et al., 2006, 2010; Zryanin, 2015). In our study, these morphological characteristics allowed us to classify 41.2% of the species captured using our sampling method as hypogaeic species, primarily belonging to the subfamilies Myrmicinae, Ponerinae, Dorylinae and Amblyoponinae. In Morocco, Cagniant (2006) also reported that the latter three subfamilies, along with the subfamilies Aenictinae, Leptanillinae, Proceratinae, are hypogaeic. However, their discovery remains sporadic and lacks significant insight into their true distribution in the country, likely due to the use of inadequate methods for capturing such species.

Our results demonstrate that maximum and minimum temperatures positively influence subterranean ant species richness and worker abundance, while precipitation exerts a negative effect. These findings are consistent with those of Dunn et al. (2009), who reported a positive correlation between ant species richness and temperature, as well as a negative correlation with precipitation. Similarly, Szewczyk & McCain (2016) highlighted that temperature is a key determinant of ant diversity globally, although precipitation can significantly interact with temperature. The climatic variables selected in this study, namely temperatures and precipitation, are widely recognized as factors influencing ant species richness, as evidenced by studies such as Kaspari et al. (2000, 2004), Majer et al. (2001), and Sanders et al. (2007). These studies have established that annual temperature and annual precipitation are among the most strongly correlated factors with ant diversity. Our findings suggest that, like surface-dwelling ants, subterranean ants, particularly non-hypogaeic species, are influenced by temperature and precipitation variations. In contrast, hypogaeic ants, however, correlations with climatic variables were weak and statistically non-significant, which may indicate a lower sensitivity to seasonal changes or a buffering effect of soil microclimates.

Regarding the seasonal dynamics of subterranean ants, and in the absence of comparative studies, our results revealed a similar pattern to that observed in ants active in the litter or on the soil surface. A significant difference between seasons was observed, with positive correlations between the ant abundance and both maximum and minimum temperatures, and a negative correlation with precipitation. These findings align with those of El Keroumi et al. (2012), who demonstrated in a Moroccan argan forest that the number of ant species, their abundance, diversity, and evenness per argan tree varied significantly across seasons, with higher abundance and richness recorded during summer.

These results are likely explained by the fact that summer is characterized by high temperatures and low rainfall, create favorable conditions for the activity of subterranean ants, particularly for foraging and colonization. In contrast, winter may limit their movements and interactions due to soil saturation and thermal constraints. Additionally, the higher richness and abundance of subterranean ants observed in the soil during the summer suggest a migration of drought-sensitive species to deeper soil layers, where conditions are less extreme than surface environments and conducive to their survival (Jacquemin et al., 2016; Pipan et al., 2010).

These results align with the theory of temperature-dependent kinetics (Rohde, 1992), which predicts that biological activity rates increase with temperature up to species-specific optima. In our study, we observed that ant abundance and diversity increased during summer (warmer season) and decreased during winter (cooler season). As ants are ectothermic organisms, warmer soils accelerate locomotion, recruitment, and foraging, which increases encounter rates and apparent richness. Conversely, cooler winter soils depress activity.

In Mediterranean ant communities, temperature strongly structures temporal niches and competitive hierarchies, with heat-tolerant taxa expanding their activity as environments warm, while heat-intolerant taxa shift to cooler periods (Cerda et al., 1997; Cros et al., 1997). The soil matrix likely buffers extreme heat (analogous to canopy shade), allowing belowground taxa to maintain high summer activity despite surface constraints documented for some primarily surface-foraging species (e.g., *Aphaenogaster senilis*) (Cros et al., 1997; Barroso Rodríguez, 2012). Furthermore, the R^2 values from the PERMANOVA analysis range from 0.049 to 0.075 (i.e., 4.9–7.5% of the total variability), indicating that seasonal differences explain only a small fraction of the variation in subterranean ant communities.

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