



## Ant diversity and species assemblages along an elevational gradient in the arid area of Central Iran

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**ABSTRACT.** Ants (Hym., Formicidae) have been recognized as vital components of arid ecosystems. Determining the diversity patterns of ants and the ecological factors behind these patterns is expected to improve our understanding of the functioning of arid ecosystems. Here, we explored patterns of ant species diversity and community composition along an elevational gradient (800 to 2800 m) in the arid area of Central Iran. The elevational gradient in ant diversity and the effects of environmental factors on various indices of ant diversity and species composition were investigated using generalized linear mixed models and variance partitioning analysis. We recorded 34 ant species of 12 genera and 8 tribes from 120 surveyed quadrats. Climate variables were the most important predictors of ant community structure. Indices of ant alpha diversity including Hill numbers and taxonomic diversity increased with elevation. Hill numbers were negatively influenced by temperature, while they were positively affected by precipitation. The observed diversity pattern could be explained by the diversity-productivity hypothesis. In our study area, the maximum primary productivity and consequently the maximum species diversity occurred at high elevations, where precipitation is high and temperature is lower than the extremes that could limit plant productivity. Ant assemblages are expected to become increasingly composed of warm-tolerant species in response to warmer and drier conditions driven by climate change. The distribution of species with lower heat tolerance will be limited to high-elevation areas in Central Iran. These areas could act as refuges for ants and should be considered priorities for conservation.

**Key words:** Altitude, biodiversity, desert, Formicidae, hill numbers, Middle East

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## INTRODUCTION

Concerns about the impacts of climate change on biodiversity have created an urgent need to understand the patterns of species diversity and the ecological processes that produce these patterns. Compared to humid regions, arid regions which cover approximately one-third of the planet's surface seem to be more vulnerable to climate change (Xu & Yang, 2017). Mostly because arid regions have

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scarce freshwater resources and any disruption in precipitation patterns or increased evaporation due to climate change can exacerbate water scarcity, impacting ecosystems and biodiversity. Thus predicting the response of arid regions' biodiversity to the main drivers of global change is of special interest (Moradmand & Yousefi, 2022). However, the biodiversity of arid regions in Africa, the Middle East, and Central Asia is not well documented and these regions are considered gaps in the global biodiversity information (Peterson & Soberón, 2018). This knowledge gap is even more severe when considering Arthropods. Even though Arthropods make up the majority of terrestrial animal diversity and have considerable functional importance in ecosystems (Rader et al., 2016; Gibb et al., 2019).

Among arthropods, ants (Hym., Formicidae) are a globally dominant faunal group (Dröse et al., 2021) that have been recognized as vital components of arid ecosystems (Li et al., 2011). They could perform a range of ecosystem functions as ecosystem engineers (Bybee et al., 2016), seeds dispersers (Wolff & Debussche, 1999), scavengers (Holway & Cameron, 2021), predators (Philpott & Armbrecht, 2006), and herbivores (Herz et al., 2007). Furthermore, due to the sensitivity of ants to environmental change, they are known as indicators of ecosystem change (Andersen, 2019). Therefore, determining the diversity patterns of ants and the ecological factors behind these patterns is expected to improve our understanding of the functioning of arid ecosystems. This would also give us more information on the general trend of biodiversity change and could be effectively used in conservation decision-making. In this study, we will focus on the diversity patterns of ants in an elevational gradient in the arid area of central Iran.

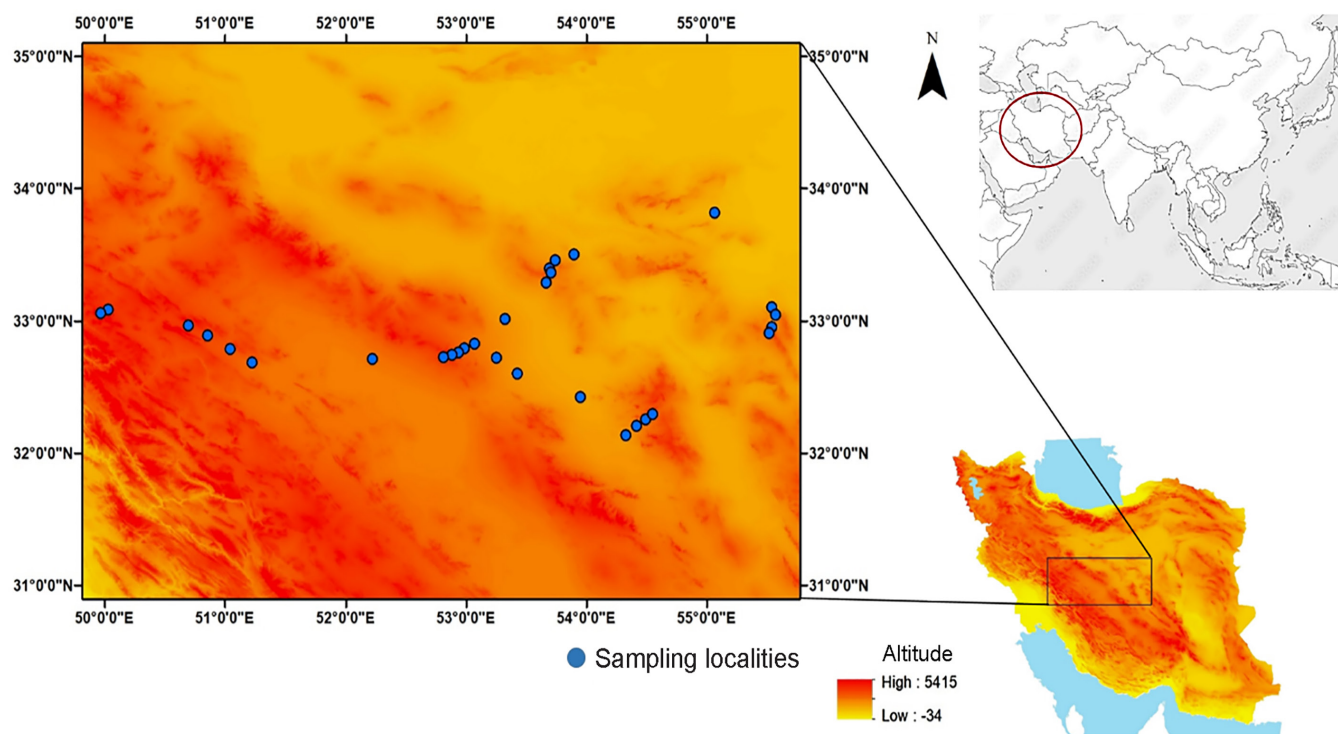
Elevation gradients encompass highly contrasting environmental conditions over short geographical distances. Therefore they are one of the most suitable models for investigating the ecological drivers of biodiversity (McCain & Grytnes, 2010). Numerous studies have investigated elevational patterns in species diversity. The observed trend varies among different taxa and across different geographical regions. The most commonly observed patterns are decreasing richness with increasing elevation and a hump-shaped pattern with the highest richness occurring at intermediate elevations (Grytnes & McCain, 2007). Studies of ant diversity along elevational gradients also reported various results. For instance, many studies in temperate and tropical regions have documented a decline in species richness with increasing elevation (Reymond et al., 2013; Kwon et al., 2014; Liu et al., 2018; Marathe et al., 2021; Kunene et al., 2022). A mid-elevation peak in species richness also has been frequently reported (Smith et al., 2014; Nowrouzi et al., 2016; Flores et al., 2018). To date, only a small number of studies have examined ant diversity in arid regions. These studies also reported variable richness patterns (Szewczyk & McCain, 2016), and even increases in richness with elevation (Sanders et al., 2003). Despite the conducted studies, many questions remain unanswered regarding the patterns of ant diversity across elevation gradients. For example, the information about the combined effects of climate and habitat conditions such as soil properties in shaping elevational patterns of ant diversity is limited. Furthermore, it remains unclear whether adopting a multi-dimensional approach and using various diversity indices could improve our understanding of biodiversity changes across elevation gradients.

The central part of Iran is extremely hot and arid. Future projections also foresee a warmer and drier climate for the future of this area (Madani et al., 2016). The biodiversity of this area is increasingly threatened by a wide range of disturbances, including climate change and anthropogenic habitat alterations. In this situation, understanding biodiversity patterns and their drivers is essential to develop effective conservation programs. So far only a few studies have been carried out regarding the diversity patterns of Arthropods in the central part of Iran. Most of these studies have focused on charismatic insects such as dragonflies (Eslami Barzoki et al., 2020a, 2020b, 2021). Ant diversity also has been the subject of a few studies. These studies have mainly investigated ant species richness and composition patterns along a latitudinal gradient in Iran (Paknia, 2011; Paknia & Pfeiffer, 2011, 2012, 2014; Mohseni & Rad, 2021; Farajollahzadeh et al., 2023). Nevertheless, still, many aspects of ant ecology remain unexplored, especially in the central parts of Iran. In the present study, we explored patterns of ant species diversity and community composition along an elevational gradient in the arid area of Central Iran. Specifically, we address the following questions: (1) What is the relationship between ant species diversity and elevation? (2) Are there distinct local communities at different elevations? (3) Which environmental factors contribute to shaping the spatial distribution of ant species in Central Iran?

## MATERIAL AND METHODS

**Study areas.** The studied area is located in central Iran (latitude 32°08.107" N to 33°49.334"N, longitude 49°57.775"E to 55°32.287"E) (Fig. 1) which has a semi-arid and arid climate. The east and central parts of the area are located in the Central Persian Desert basins ecoregion where annual precipitation is less than 100 mm and the extreme maximum temperature can reach 42°C. The west part of the area is located in the Zagros Mountains Forest steppe ecoregion. The annual precipitation in this ecoregion reaches 800 mm and the temperature can fall below -25°C in the winter (Zohary, 1973). The area exhibits a drop in elevation in an eastern direction, with the highest point being altitudes 2800 m in the west and decreasing to 800 m in the east.

**Sampling design.** Thirty sampling sites were distributed along the elevational gradient. All of them were located in pastures, away from residential or agricultural areas. Ant sampling was conducted on sunny days between 10:00 and 17:00, once in each sampling season (spring, summer, and autumn) in 2019 and 2020. In each sampling site, four 20 × 20 m<sup>2</sup> quadrats were placed at a distance of more than 300 m from each other to avoid pseudoreplication. All quadrats had at least 200 meters distance from the main road. Wide plastic frames were positioned on either side of the quadrats to block ants from entering or leaving the quadrats during the sampling process. Then, each quadrat was surveyed using vacuum sampling and hand search-collecting methods for approximately 60 minutes. In each quadrat, the ant specimens that were visible on the soil surface or plant bushes were collected using a rechargeable vacuum cleaner (Lach et al., 2010). Vacuum sampling was followed by hand sampling during which rocks were turned over, and objects like dried bushes and debris were checked to find hidden nests or individuals (Salyer et al., 2014). Later, ant specimens that have been observed during soil sampling (see Predictor variables section) also have been collected. If there was an ant nest entrance inside the quadrat and hundreds of individuals of a single species were observed, only 20 to 30 individuals were collected.



**Figure 1.** The map demonstrates the elevational gradient in Central Iran, with the location of the sampling sites.

**Identification of specimens.** Specimens collected from each quadrat were kept in separate containers. Some of the collected specimens of each species were kept in 96% ethanol for future molecular studies, and some were kept in 75% ethanol for identification and taxonomic studies. Species identified to species level using identification keys such as Collingwood and Agosti (1996), Ward et al. (2016), Khalili-Moghadam et al. (2021), Salata et al. (2021). Additionally, the identification of some samples has been carried out with the help of Dr. Jonathan Romiguier and Yannick Juve from Université de Montpellier. The species lists resulting from all seasons were pooled in a single list to use in downstream analysis.

Within each quadrat, the percent of vegetation cover was recorded. Furthermore, one or two specimens of every plant species within each quadrat were collected. The samples were pressed, dried, and later identified by expert botanists in Isfahan University Herbarium. Within each quadrat, five soil samples were collected at random from the surface (top 5–10 cm of the soil), and an additional five samples were collected from a depth of 30–40 cm. Samples from surface and depth were mixed to have one surface and one depth soil sample from each quadrat. The physical (soil texture) and chemical (pH, salinity, EC, water content) characteristics of these 240 samples were measured in the laboratory following the approach of Ryan et al. (2001).

**Predictor variables.** Two groups of environmental predictors were used: **1.** Bioclimatic variables with a spatial resolution of 1 km for the period of 1970–2000 were obtained from the WorldClim database (Fick & Hijmans, 2017). To avoid the multicollinearity problem, 19 bioclimatic variables were divided into subsets related to precipitation and temperature. Then, for each subset principal component analysis (PCA) was applied, using the base R stats package. This way uncorrelated synthetic variables were generated that represent the original precipitation and temperature variables. The results showed that the first principal component (PC1) explained 72.2% of the variation in the temperature subset. This number was 82.7% for the precipitation subset. Therefore, subsequent analyses were performed using only PC1<sub>temperature</sub> and PC1<sub>precipitation</sub>. Almost all variables were positively correlated with PC1 and had large weights and highly contributed to PC1. The exceptions were Isothermality, Temperature Annual Range, and Mean Diurnal Range, which had weights <30 and were negatively correlated with PC1. Therefore, any interpretation using PC1<sub>Temperature</sub> and PC1<sub>Precipitation</sub> should largely reflect the broad variation in terms of temperature and precipitation occurring across central Iran. From now on, we will refer to PC1<sub>temperature</sub> as temperature and PC1<sub>precipitation</sub> as precipitation. **2.** Habitat predictors included physical and chemical characteristics of depth and surface soil (percent of clay, silt, and sand, pH, salinity, and wet reserve ability) as well as plant richness and plant coverage. For each set of soil characteristics related to the surface and depth, PCA was used to reduce variables to a smaller number of non-correlated PCs. The first two PCs derived from each PCA served as surface and depth soil characteristics variables (supplementary material S1).

**Alpha diversity.** To estimate the alpha-diversity of ants in each sampling site, Hill numbers of order 0 ( $Q = 0$ , species richness), 1 ( $Q = 1$ , exponential of Shannon's entropy), and 2 ( $Q = 2$ , inverse of Simpson concentration) (Jost, 2006) were calculated with the help of R package SpadeR (Chao et al., 2016). A taxonomic tree was constructed using Linnaean classification for all recorded species. With the help of this tree, taxonomic diversity ( $\Delta$ ), taxonomic distinctness ( $\Delta^*$ ), and average taxonomic distinctness ( $\Delta^+$ ) were calculated using the R package vegan (Oksanen et al., 2013). These indices are similar to Hill numbers but they have an added component of taxonomic separation, which is the path length through the taxonomic tree connecting every pair of species (Warwick & Clarke, 1995; Clarke & Warwick, 1998, 2001).  $\Delta$ ,  $\Delta^*$ , and  $\Delta^+$  are usually used to take into account the taxonomic distance among the species composing an assemblage. Elevational and longitudinal gradients in ant diversity were analyzed using generalized linear mixed models (GLMs). Response variables in these models were the first three Hill numbers,  $\Delta$ ,  $\Delta^*$ , and  $\Delta^+$ . Explanatory variables were the fixed effects of elevation and longitude. The effects of environmental factors on ant diversity were modelled using GLMs. Response variables were the first three Hill numbers,  $\Delta$ ,  $\Delta^*$ , and  $\Delta^+$ , while fixed variables were temperature, precipitation, and principal components of soil characteristics. Since plant richness and percentage of plant cover were strongly correlated with precipitation, we excluded them from GLMs. A model selection procedure

was performed based on the second-order Akaike information criteria corrected for a small sample size (AICc). This model selection was carried out using “dredge” function in the R package MuMIn which performs automated model selection with every possible combination of predictor variables (Barton, 2023).

**Species composition.** Based on the altitudinal variation of the studied area, sampling sites were classified as low-altitude ( $800 \leq A1 < 1470$ ), middle-altitude ( $1470 \leq A2 < 2140$ ), and high-altitude ( $2140 \leq A3 < 2800\text{m}$ ). To compare the composition of ant species between elevation classes, a one-way permutational multivariate analysis of Variance, (PERMANOVA) was applied using the Bray–Curtis dissimilarity index and 9999 permutations. We used nonmetric multidimensional scaling (NMDS) to visualize the variation of ant species composition between elevation classes. This analysis was performed with the Bray–Curtis dissimilarity index on two axes. We are aware that by using unequal group sizes in comparing species composition, the results might be deviated, however, for our data this test was the best available choice. The relationship between the geographical distance between sampling sites and Bray–Curtis dissimilarity was analyzed using a Mantel test (10,000 permutations). These analyses have been performed using the R package vegan (Oksanen et al., 2013). The importance of environmental variables and geographical distance, in explaining the variation in species composition among sampling sites, was determined using variance partitioning analysis through the function ‘varpart’ of the R package vegan. This function partitions the variation in community data with respect to explanatory tables (here: climate variables, geographical distance, and habitat variables), using adjusted  $R^2$  in redundancy analysis ordination (RDA). All packages employed for statistical analyses and the “ggplot2” package (Wickham et al., 2016) used for graph building are incorporated in the R-software version 4.1.2 (R Development Core Team, 2021). The level of significance used in all analyses was set to  $p < 0.05$ .

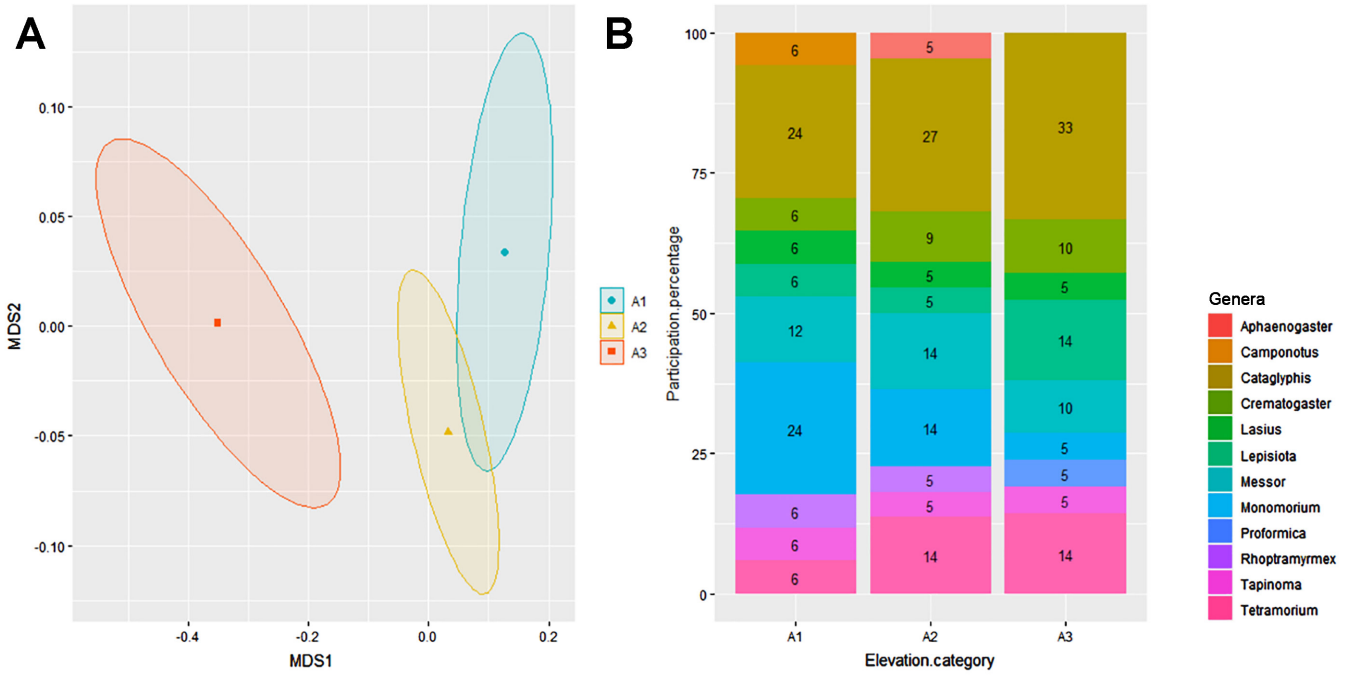
## RESULTS

In total, 34 ant species of 12 genera and 8 tribes were identified from 120 sampled quadrats (supplementary material S2). This represents 12.5 % of the total number of species recorded from Iran so far (280 species). The species belonged predominantly to the genus *Cataglyphis* Förster, 1850 with 9 species. The number of species per site ranged from 2 to 11, with an average of  $6 \pm 2.88$  (SD). The Bray–Curtis dissimilarity was positively correlated with the distance (Mantel test;  $r=0.39$ ,  $P=0.0001$ ). The results of the PERMANOVA test showed that the composition of ant species varied significantly between elevation classes ( $F= 1.71$ ;  $P=0.0021$ ). The pairwise comparison demonstrated that the most distinct species composition belongs to high-altitude sites (A3) (Table 1). These results were also shown by the NMDS analysis (Fig. 2A). In all three elevation classes, the ants of the genus *Cataglyphis* were dominant (Fig. 2B). Also, based on the cluster analysis sites lower than 2400 m altitude formed a cluster that was distinct from a cluster containing higher elevation sites (Fig. 3).

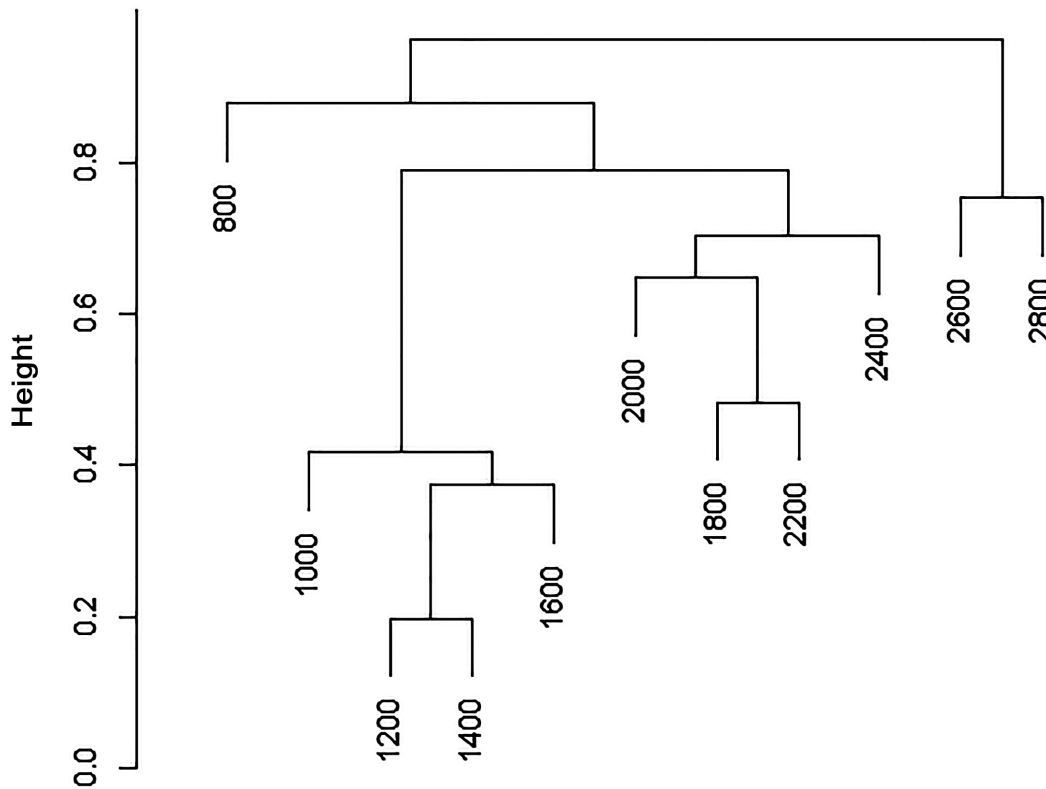
Based on the variance partitioning analysis 53% of the variance in ant community structure could be explained by variables related to climate, habitat, and geographical distance. Climate variables were the most important predictors of ant community structure and explained 8% of the variation in the ant community data. Habitat variables and geographical distance explained 3% and 2% of the variance, respectively (Fig. 4).

**Table 1.** Results of pairwise PERMANOVA test for differences in ant species composition between three elevation classes in Central Iran. A1: low altitude, A2: middle altitude, A3: high altitude.

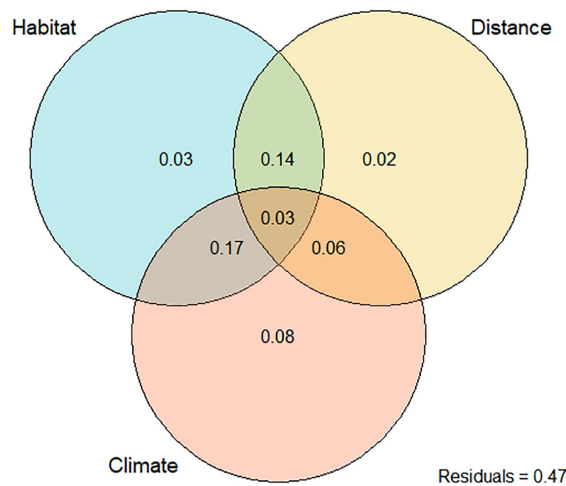
	F.Model	R2	p Value	p Adjusted
A1 vs A2	3.946	0.152	0.004	0.012
A1 vs A3	9.96	0.356	0.001	0.003
A2 vs A3	10.25	0.422	0.001	0.003



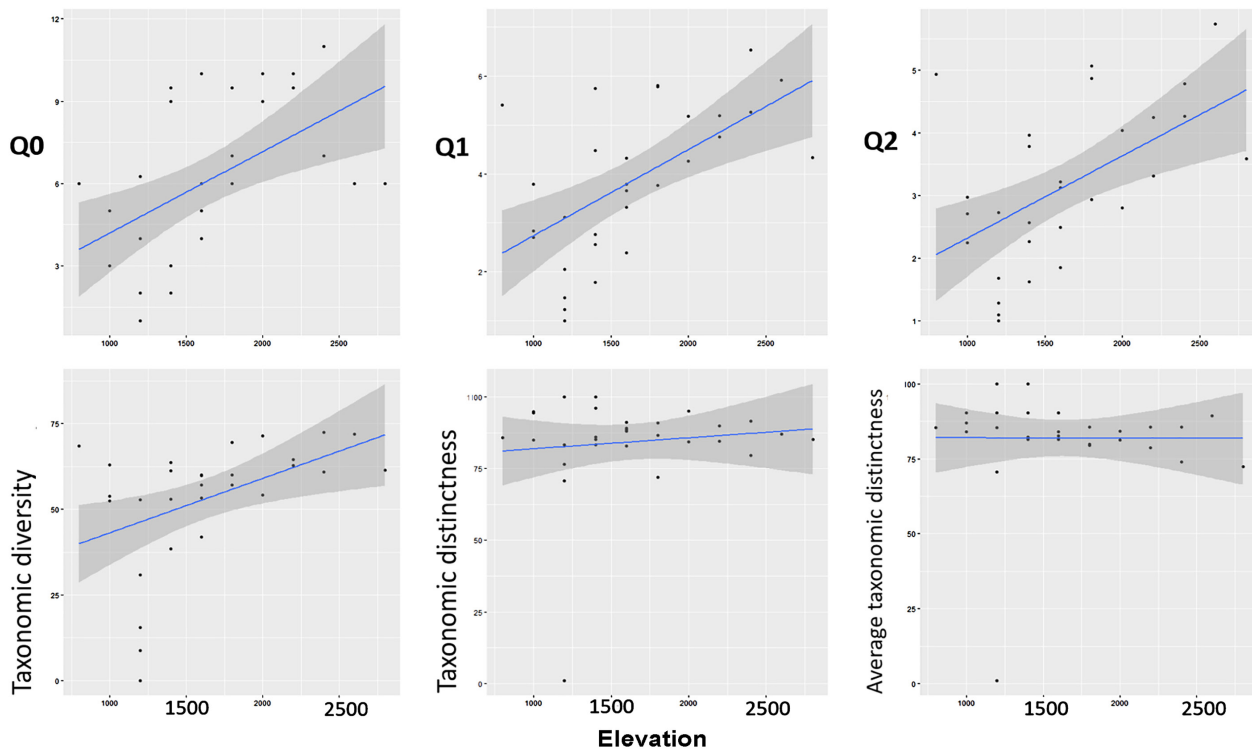
**Figure 2.** Comparing ant assemblages composition in three elevation classes in Central Iran. **A.** NMDS ordination plots based on Bray-Curtis dissimilarity index; **B.** Participation percentage of each genus (based on the number of species) in ant assemblages composition. A1: low altitude, A2: middle altitude, A3: high altitude.



**Figure 3.** Cluster analysis of species composition of ants found in Central Iran. Based on the Bray-Curtis dissimilarity index. Numbers are the altitude of sites.



**Figure 4.** Venn diagram resulting from variance partitioning analysis with predictor variables that may affect the ant community structure. See the text for a full description of each set of variables.



**Figure 5.** The relationship between ant species diversity indices and elevation in Central Iran, based on generalized linear mixed models.

Based on our findings, indices of ant alpha diversity including Q0, Q1, Q2, and  $\Delta$  increased with elevation (likelihood ratio test; Q0:  $R^2=0.28$ ,  $p=0.002$ ; Q1:  $R^2=0.34$ ,  $p=0.001$ , Q2:  $R^2=0.29$ ,  $p=0.002$ ;  $\Delta$ :  $R^2=0.20$ ,  $p=0.016$ ). Richness peaked at 2200–2500 m and was lowest at 1000–1200 m. There were no significant elevational patterns in  $\Delta^*$  and  $\Delta^+$  (Fig. 5). Neither of the calculated diversity indices showed a significant longitudinal pattern. Q0, Q1, and Q2 were negatively influenced by temperature, while they were positively affected by precipitation. The percentage of sand in the surface soil (PC1's highest load) also negatively affects Q1 and Q2. Taxonomic diversity is negatively affected by temperature. Neither of the selected variables had significant impacts on taxonomic distinctness ( $\Delta^*$ ) and average taxonomic distinctness ( $\Delta^+$ ) (Table 2).

**Table 2.** Factors that significantly affect ant diversity indices, based on the best model obtained from model selection by dredge function in MuMIn package.

	Coefficient	p-Value	Null deviance	Residual deviance	AIC
<b>Q0</b>			241.58	137.31	138.77
Temperature	-1.528	<0.001	-	-	-
Precipitation	1.293	<0.001	-	-	-
<b>Q1</b>			68.890	34.22	99.1
Temperature	-0.720	0.00110	-	-	-
Precipitation	0.639	0.01891	-	-	-
Sand percentage in surface soil	-0.411	0.01970	-	-	-
<b>Q2</b>			45.193	24.05	91.857
Temperature	-0.450	0.012	-	-	-
Precipitation	0.359	0.105	-	-	-
Sand percentage in surface soil	-0.366	0.014	-	-	-
<b>Taxonomic diversity</b>	-	-	9410.6	7350.2	256.17
Temperature	-2.992	0.009	-	-	-

## DISCUSSION

In this study, patterns of ant species diversity and community composition along an elevational gradient in the arid area of Central Iran were explored. We believe that by using both vacuum sampling and hand sampling in three seasons, we were able to compile a comprehensive list of species. As the habitats we studied were open and had low complexity it was easy to spot ants efficiently through visual scanning. The vacuum method enabled us to catch individuals that are hard to catch by hand such as fast-running species and species on thorny bushes. While the pitfall technique has been used successfully in many studies, we opted not to use this technique due to time constraints. Surveying 30 stations (120 quadrats) in a vast area within limited time frames of one month (in each season) made pitfall traps impractical for us. Furthermore, our pilot study in five arid locations, where both pitfall and hand-vacuum sampling were employed, demonstrated that hand-vacuum sampling led to the discovery of more species (Hajian et al., *unpublished data*). Similar findings were reported by Fotso Kuate et al. (2015). Diversity indices including Q0, Q1, Q2, and taxonomic diversity tended to increase with increasing elevation. This pattern is similar to what is reported by Sanders et al. (2003) who studied the richness of ant species along an elevational gradient (1000–2500 m) in an arid ecosystem. Paknia and Pfeiffer (2012) also studied ant species richness in the Central Persian Desert Basins, covering an elevational range of 1000–1900 meters. They reported an independent relationship between elevation and species richness. Other studies conducted in different climatic regions also show different results. A mid-elevation peak is the most frequently reported pattern of ant species richness along elevational gradients (Subedi & Budha, 2020). This pattern has been reported in various ecosystems including the Australian Wet Tropics (Nowrouzi et al., 2016), the Mediterranean mountain range (Flores et al., 2018), and the tropical forest (Smith et al., 2014). Another observed pattern is a monotonic decrease in species richness along with an increase in elevation. This pattern has also been reported from different climatic zones such as temperate regions (Reymond et al., 2013; Kwon et al., 2014; Liu et al., 2018) and tropical regions (Marathe et al., 2021; Kunene et al., 2022). This inconsistency between the observations of different studies could be explained by changes in the climate-elevation relationship over space (Sanders et al., 2003). The association between temperature and precipitation may differ along similar elevation ranges in different climatic zones. For example, precipitation generally decreases with elevation in tropical regions, while precipitation increases along with increasing elevation in many temperate and arid habitats (Sanders et al., 2003). Therefore, if there is a relationship between species richness and climate, this relationship should also change over space.



Consistent with this hypothesis, Ward (2000) conducted a widespread survey to study the leaf litter ant diversity and found that species richness peaked at mid-elevations in the tropics, but decreased continuously with elevation in temperate regions.

Our multiple regression analysis suggests that ant species richness increases as the temperature decreases and rainfall increases (which coincides with increasing elevation in our study area). In other words, low-elevation sites that are extremely hot and dry have the lowest ant richness compared to high-elevation sites with lower temperatures and higher rainfall. So far studies that have been conducted in arid regions reported diverse responses of ant diversity to climatic factors, including positive (Davidson, 1977; Sanders et al., 2003; Segev, 2010; Paknia & Pfeiffer, 2012; Gibb et al., 2019) and insignificant (Pfeiffer et al., 2003) association with precipitation; negative (Sanders et al., 2003) and insignificant (Segev, 2010) correlation with temperature. Several studies in temperate and tropical regions also reported that species richness responds positively to temperature (Longino & Colwell, 2011; Machac et al., 2011; Kwon et al., 2014; Munyai & Foord, 2015). This disparity in results shows that the diversity-climate relationship could change over space according to habitat factors, community characteristics, the scale of the study, the geological and evolutionary history of the study area, and the level of habitat productivity (Sanders et al., 2007; Dunn et al., 2009).

The diversity-productivity hypothesis could explain the observed diversity pattern in our study. Based on this hypothesis, the density and size of ant colonies increase with increasing productivity and thus the availability of energy and resources. A higher abundance of individuals could decrease the risk of local extinction and lead to higher species richness. In another interpretation, habitats with greater productivity can support a greater diversity of food plants, which in turn enables the evolution of a wider range of specialist species. Furthermore, the higher complexity of more productive habitats allows the coexistence of more species by decreasing competition (Evans et al., 2005; Clarke & Gaston, 2006; Storch et al., 2018). In our study area, there was a strong correlation between precipitation and plant richness and coverage in surveyed quadrats. We can consider this as a positive relationship between precipitation and productivity. Because the production of food resources such as flowers and seeds increases with increasing plant richness and coverage. On the other hand, the high temperatures of arid areas can limit vegetation productivity through an abrupt decrease in gross photosynthesis and a continuous increase in respiration (Waring & Schlesinger, 1985). Therefore, in our study area, the maximum primary productivity and consequently the maximum species richness were expected to occur at high elevations, where precipitation is high and temperature is lower than the extremes that could limit plant productivity.

Our results regarding Q1 and Q2 (indices that take into account species abundance) were similar to the richness pattern. It means that productivity affects not only the presence or absence of species but also the abundance of species. At more productive areas (higher elevations), the relative abundance of species is more evenly distributed. Consistent with our findings, Mohseni and Rad (2021) demonstrated a positive correlation between the abundance of plants in natural habitats and ants abundance and species richness. The fact that taxonomic diversity also followed richness patterns shows that the higher productivity in higher altitudes has led to the evolution of more specialist species and thus phylogenetically more diverse assemblages. Q1 and Q2 also were negatively affected by the sand contents of the surface soil. This pattern could be connected to soil productivity. Sandy soils have a low capacity to retain rainfall water and nutrients in a form available to plants and so are less productive than silt or clay soils (Brady et al., 2008; Delsinne et al., 2010). Also, productive soils with a lower sand content compared to silt favour the establishment of ant nests and provide protection against sand sinking and burial for the nests (Chen et al., 2007; Li et al., 2011). Our results from the variance partitioning analysis showed that climate factors appear to be the most influential factors in shaping species assemblages. Climatic variables are known to be the primary driver of species distributions and changes in species composition across most taxonomic groups (Buckley & Jetz, 2008), including ants (Paknia & Pfeiffer, 2014; Wepfer et al., 2016). The composition of ant species varied significantly between elevation classes. In medium and high altitude sites, ants in the genus *Cataglyphis* were

dominant while in low altitude sites, *Cataglyphis* and *Monomorium* are the most diverse genera. Fast-running thermophilous *Cataglyphis* ants show a set of behavioural (e.g. foraging rhythm), morphological, and physiological (e.g. body size, polymorphism) adaptations that allow them to tolerate extreme conditions in arid areas (Boulay et al., 2017). In high elevations where ant communities are rich, the ability to forage at high temperatures allows *Cataglyphis* to avoid competitors and exploit food resources. *Cataglyphis* ants could also be successful at low elevations where ecosystem productivity and species richness are low because, with their high thermal tolerance, they can escape predation pressure by less thermotolerant species (Boulay et al., 2017).

Contrary to what we observed in high-elevation sites, in low elevations, the species of genus *Monomorium* are as abundant as *Cataglyphis* species. This finding is in line with the study of Pérez-Toledo et al. (2022) in Mexico, who reported that *Monomorium* is highly restricted to the warm conditions found in the lowlands. This could probably resemble the neotropical origin of this genus (Ward et al., 2015). The success of ants in genus *Monomorium* at low-elevation and high temperatures sites might be explained by critical thermal maximum ( $CT_{max}$ ) (Bujan et al., 2020).  $CT_{max}$  is the temperature at which animals lose voluntary muscle control and is considered a measure of heat tolerance. Bujan et al. (2020) measured  $CT_{max}$  and  $CT_{min}$  for 132 species of North American ants. Based on their results  $CT_{max}$  for the *Monomorium* has been estimated at 53°C, while for *Tetramorium* which showed the lowest richness in low-altitude and high-temperature sites,  $CT_{max}$  has been estimated at 46°C (Bujan et al., 2020).

Based on our findings 47% of the deviation in the structure of the ant community remained unexplained, thus we cannot ignore the fact that unmeasured variables also may have significant effects on determining the ant species composition and diversity in Central Iran. We suggest that the geological history of the area is also an important factor that could be investigated in future studies. In conclusion, we have shown that local ant diversity and species composition in the arid area of central Iran depends mainly on climate, and in particular precipitation. Considering future climate change, with a prediction of warmer and drier conditions, ant assemblages are expected to become increasingly composed of warm-tolerant species in lowland areas. The distribution of species with lower heat tolerance will be limited to high-elevation areas. Therefore high-elevation areas can be refuges for ant species and from the conservation perspective, these regions are of priority for conservation.

#### AUTHOR'S CONTRIBUTION

The authors confirm their contribution in the paper as follows: M.H., M.E., and S.S. conceived and designed the study having consultation from A.Gh. and M.M. M.H. conducted fieldwork, identified species, analyzed the soil samples, and prepared the databank. Z.E. performed data analyses. M.H. and Z.E. wrote the first draft of the papers. A.Gh., M.M., M.E., and S.S. reviewed the manuscript and helped in finalizing the paper. The authors read and approved the final version of the manuscript.

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#### AVAILABILITY OF DATA AND MATERIAL

Additional supporting information may be found online in the Supporting Information section at the end of the article. The specimens listed in this study are deposited in the Zoological Museum and Collection of Biology Department at Shiraz University (ZM-CBSU), Iran and are available from the curator, upon request.

#### ETHICS APPROVAL AND CONSENT TO PARTICIPATE

Not applicable.

#### CONSENT FOR PUBLICATION

Not applicable.

## CONFLICT OF INTERESTS

The authors declare that there is no conflict of interest regarding the publication of this paper.

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**Supplementary material S1**

**Table S1.** Results of PCA for surface soil characteristics at ants sampling quadrats in Central Iran, showing the contribution of each variable to the loading of the first six components of the PCA.

	PC1	PC2	PC3	PC4	PC5	PC6
<b>Clay (%)</b>	-0.476380	-0.033880	-0.475210	0.624246	-0.306470	-0.249960
<b>Silt (%)</b>	-0.488750	-0.370590	0.154353	-0.449000	0.147348	-0.613720
<b>Sand (%)</b>	0.560319	0.315355	0.027415	0.157126	-0.017490	-0.748900
<b>pH</b>	0.278204	-0.221080	-0.846040	-0.364710	0.157822	0.003878
<b>Salinity</b>	-0.211250	0.604907	-0.118970	-0.499000	-0.571230	0.000961
<b>Wet reserve ability.g</b>	-0.313380	0.589303	-0.140200	0.044845	0.729964	0.000908

**Table S2.** Results of PCA for depth soil characteristics at ants sampling quadrats in Central Iran, showing the contribution of each variable to the loading of the first six components of the PCA.

	PC1	PC2	PC3	PC4	PC5	PC6
<b>Clay (%)</b>	-0.487810	-0.046630	0.361052	-0.702920	-0.282560	0.235738
<b>Silt (%)</b>	-0.537060	-0.253720	-0.094920	0.495319	0.127545	0.613657
<b>Sand (%)</b>	0.589946	0.221242	-0.035480	-0.183510	-0.015130	0.753560
<b>pH</b>	0.235028	-0.277280	0.882654	0.234909	0.183350	-0.000150
<b>Salinity</b>	-0.114390	0.638395	0.247366	0.403706	-0.595980	0.000114
<b>Wet reserve ability.g</b>	-0.239260	0.632511	0.138223	-0.093430	0.717530	-0.000220





## بررسی تنوع و ترکیب گونه‌ای مورچه‌ها در امتداد شیب ارتفاعی در منطقه خشک مرکزی ایران

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**چکیده:** مورچه‌ها (Hym., Formicidae) به عنوان اجزای حیاتی اکوسیستم‌های خشک شناخته شده‌اند. انتظار می‌رود که تعیین الگوهای تنوع مورچه‌ها و عوامل اکولوژیکی موثر در این الگوها درک ما را از عملکرد اکوسیستم‌های خشک بهبود بخشد. در این پژوهش، الگوهای تنوع گونه‌ای و ترکیب گونه‌ای مورچه‌ها در امتداد شیب ارتفاعی (۸۰۰ تا ۲۸۰۰ متر) در منطقه خشک مرکز ایران مورد بررسی قرار گرفت. همچنین اثرات عوامل محیطی بر شاخص‌های مختلف تنوع و ترکیب گونه‌ای مورچه‌ها با استفاده از مدل‌های خطی و تجزیه و تحلیل تقسیم‌بندی واریانس مطالعه شد. در این پژوهش ۳۴ گونه مورچه متعلق به ۱۲ جنس و ۸ قبیله از ۱۲۰ کوادرات بررسی شده ثبت شد. بر اساس نتایج این مطالعه متغیرهای اقلیمی مهم‌ترین عامل در تعیین ترکیب گونه‌ای مورچه‌ها بودند. شاخص‌های تنوع آلفا شامل اعداد Hill و تنوع تاکسونومی با افزایش ارتفاع افزایش یافتند. اعداد Hill به طور منفی تحت تأثیر دما بودند، در حالی که با افزایش بارش این شاخص‌ها افزایش پیدا کردند. الگوی تنوع مشاهده شده را می‌توان با فرضیه تنوع-بهره‌وری (حاصلخیزی) توضیح داد. در منطقه مورد مطالعه، حداکثر حاصلخیزی و در نتیجه حداکثر تنوع گونه‌ای در ارتفاعات بالا رخ می‌دهد، جایی که بارش زیاد است و دما به اندازه ای بالا نیست که تولیدات گیاهی را محدود کند. انتظار می‌رود جوامع مورچه‌ها در پاسخ به شرایط گرم‌تر و خشک‌تر ناشی از تغییرات آب و هوایی به طور فزاینده‌ای از گونه‌های مقاوم به گرما تشکیل شوند. در این شرایط پراکنش گونه‌های با مقاومت کمتر به دمای بالا به مناطق مرتفع در ایران مرکزی محدود خواهد شد. این مناطق می‌توانند به عنوان پناهگاه مورچه‌ها عمل کنند و باید به عنوان اولویت‌های حفاظتی در نظر گرفته شوند.

**واژگان کلیدی:** مورچگان، تنوع زیستی، شاخص Hill، بیابان، ارتفاع، خاورمیانه