

# Geodiversity Increases Biodiversity of Plants in a Semi-arid Region

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## Research Article

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# Abstract

Geodiversity refers to the variety of geological and physical elements as well as to geomorphological processes of the earth surface. Heterogeneity of the physical environment has an impact on plant diversity. In recent years, the relations between geodiversity and biodiversity has gained attention in conservation biology, especially in the context of climate change. In this study, we assessed the effect of hillslope geodiversity – as expressed by stoniness and depth of the soil profile – on plant's community structure. The study was conducted in the Sayeret Shaked LTER station in the semi-arid north-western Negev of Israel. Vegetation survey was conducted for two consecutive years (2016 and 2017), of which the second year was a drier and hotter than the first year. The results show that (1) geodiversity increases vegetation biodiversity, and that (2) the effect of geodiversity on plants' community structure and species richness is greater in the drier year than that in a wetter year. The main insight is that in drylands, hillslopes with higher geodiversity better buffer the effect of drier years, and supported a more diverse plant community than lower geodiversity hillslopes.

## Introduction

Geodiversity is the natural assemblage of abiotic conditions within an ecosystem including its geological, geomorphological, and pedological features [1]. Geodiversity encompasses the substrates, landforms, and physical processes that govern habitat development and sustainability [2]. One of the main components of geodiversity is the soil stoniness. The position of stones on the ground surface regulates hydrological process, as it affects infiltration and evaporation [3–5]. In fact, during rainfall, stones at the soil surface intercept raindrops [3], reducing the splash formed by the impact force of raindrops on the soil [6] with the consequences for processes of water overland flow and soil erosion [7,8]. On the other hand, stones increase water intake rates by preventing surface sealing and crusting [9]. Also, stones on the ground surface act as an isolation by reducing the soil temperature during the day and increasing the temperature during the night [10]. This temperature regulation resulted in effects on soil-water evaporation [11]. These processes are dependent on the stones' size distribution and cover percentage [12].

Heterogeneity of the physical environment, alongside with climatic variables, have a crucial effect on vegetation living conditions and biodiversity [2,13]. It was demonstrated that geodiversity affects the distribution of vegetation [14,15], composition of soil microbes, and the resistance of plant to drought [16–18]. In drylands, understanding the relation between geodiversity-governed water distributions [19] and plants viability is highly important. Recent studies from the semi-arid north-western Negev proposed that heterogeneous land units, dominated with partially-embedded stones in their ground surface, increase the spatial redistribution of water, with the resultant increase in water availability for shrubs [18], improving their durability to prolong drought events [19]. Specifically, mass mortality of *Noaea mucronata* (Forssk.) shrubs was reported for hillslopes with low geodiversity level [18,19]. Overall, better understanding of the effects of geodiversity and plant biodiversity can help in implementing conservation projects of natural ecosystem [1,20,21].

The *N. mucronata* is a perennial shrub that dominates the north-western Negev (Fig. 1), which shows an adaptive response to dryland environments at numerous levels. The adaptation to water-limited environments shaped the plant's metabolism and morphology. Aboveground adaptations comprise changes in leaf morphology, where the small narrow winter leaves shed during the dry season, reducing water loss through transpiration [22]. The green stems transform into grayish fissured bark, which enables the growth of young branches once the wet season starts [23]. The physiological traits of adaptations include the C<sub>4</sub> carbon fixation pathway, which correlates with high efficiency in CO<sub>2</sub> fixation and low transpiration loss under high temperature conditions [24]. Moreover, at the root level, *N. mucronata* adapt in association with ectomycorrhizal fungi, which improves the plants' water and nutrient uptake [25,26]. The *N. mucronata* is considered as a landscape engineer [27–29], which improves habitat conditions and facilitates herbaceous community in its surroundings by modifying microclimate (reduction of temperature stress due to the shading effect) and soil properties (increasing infiltration and reducing evapotranspiration) [27,30–32]. At the same time, it was reported that the *N. mucronata* may impose some negative effects, such as the suppression of annual plants [33] through shading and competition [34].

The study objectives were to (1) assess the effect of hillslope geodiversity on the physiological conditions of *N. mucronata* shrubs, and to (2) study the effect of geodiversity on plant's community structure and diversity. Our overall hypotheses are that an increase of geodiversity will 1) improve the physiological conditions of *N. mucronata* shrubs and 2) enhance plant diversity.

## Materials And Methods

### *Regional settings*

The study was conducted between February 2016 and May 2017 in a fenced area of the Sayeret Shaked Park (~20 ha). The park is located in the semi-arid north-western Negev of Israel (31°17'N, 34°37'E; 200 m.a.s.l.), where annual average rainfall is ~165 and standard deviation of 58 mm/year [19]. The site's soil is aeolian loess, with sandy loamy to loamy sand texture [35]. The park is covered with dwarf shrubs (0.1–0.6 m tall) such as *Atractylis serratuloides* Cass., *Thymelaea hirsuta* (L.) Endl., and the dominant *N. mucronata* shrubs. The site has a large number of annuals, geophyte (e.g., *Asphodelus ramosus* L.) and hemicryptophyte species, as well as a rich community of biological crusts [34,36–39].

Three low-geodiversity hillslopes, with a thick (> 1 m) and non-stony soil layer (homogeneous: HM; Fig. 1 A), and three high-geodiversity hillslopes, with a thin (~ 0.1 m) stony soil layer (heterogeneous: HT; Fig. 1 B) were selected for the study. Distance between two adjacent hillslopes was at least 100 m. On each of these hillslopes, a 400 m<sup>2</sup> (20 x 20 m) plot was established for data collection. To study the effect of geodiversity on plant community, we assessed the plant diversity at a once-a-month frequency over the growing season (November through June) of two sequential years (2016–2017). In each of these years, the last cycle of data collection took place when the annual plants were dried out, and at the point where the *N. mucronata*'s 'winter leaves' [40] have disappeared.

Figure 1 A view of a homogeneous (a) and a heterogeneous (b) hillslopes. In the homogeneous hillslopes, the white spots are piles of snails in the vicinity of dead shrubs. The piles indicate the location of dead shrubs. At the same time, most of the shrubs in the heterogeneous hillslope are alive, and survived the prolonged drought of 2008-2009.

## ***Vegetation survey***

The *N. mucronata* was the only perennial plant present in both HT and HM hillslope, making it the best-fit model species to assess the year-round differences in plant viability. In each plot (n=6) we studied three individual shrubs, to a total of nine individuals per hillslopes type. In order to monitor the shrub's morphological changes during the year, we measured the maximum length of green branches. Also, we measured the plant's size by measuring the maximum length from a green part to another on a north-south and east-west axes, as well as the shrub height. We multiplied the three axes to calculate the maximum plant size. In addition to these nine *N. mucronata* plants, we sampled leaves (winter leaves only) from other nine randomly selected *N. mucronata* plants to estimate their physiological condition, through measuring the relative water content (RWC), membrane stability (EC), carbon-nitrogen ratio (C:N), and chlorophyll content.

## ***Plant diversity***

To measure plant diversity, we identified all the plants to the species level along 3-m transects (one transect per plot), counted the number of individuals per species, and recorded the total cover per species. The monitoring of transects was conducted at a once-a-month frequency throughout the growing season (Feb–June 2016 and Feb–May 2017: a total of 11 sampling cycles). Due to overlapping plants, vegetation's total cover could exceed 100%. We classified all plant species into three life forms: annual, perennial, and hemicryptophyte. The use of any plants in this study was in accord with national guidelines. The formal identification of the plant material was performed by Prof. Rachmilevitch. We did not use voucher specimen.

In order to determine the plant diversity in the different hillslope, we calculate species richness (n) as the number of species present at the site, and species abundance as the total number of plants present at the site (N). In order to determine the diversity in the communities, we calculate the Shannon Diversity Index and Shannon Evenness Index and the Simpson Index, [41,42]

## ***Biochemical analysis***

### ***Relative water content (RWC)***

We added 3–5 gr of young leaves of each individual to a 50ml vial with a wet tissue to maintain humidity. The leaves were weighted for fresh weight using Sartorius AG Göttingen CP225D, Germany. The samples were submerged in de-ionized water for 24hr and then weighted for turgor weight. Additionally, the samples were dried at 65°C for 24hr in the oven for dry weight.

## ***C:N ratio***

Few leaves from each shrub were collected for total organic carbon ( $C_{org}$ ) and total nitrogen content ( $N_{tot}$ ) analysis, dried at 65°C for 12h and manually ground by mortar and pestle. Of these samples, 20 mg were put in a C-N analyzer (CHNS elemental analyzer, Thermo Scientific, USA).

## ***Membrane stability index (MSI)***

From each plant, 20–30 leaves were collected and placed in 50 ml vials filled with 20 ml of double distilled water (DDW). The electrolyte's electric conductivity (EC) was measured with a probe (EUTECH Instruments, CON 510, Singapore), as initial leakage ( $C_i$ ). The samples were then placed on a shaker for 12 h at 200 rpm and the EC was measured again as  $C_r$ . The samples were then autoclaved to blast cell membrane, and the maximum conductivity ( $C_m$ ) was measured. Membrane stability index (MSI) was calculated according to Equation 1:

*Equation 1:*

$$MSI = 100 * \frac{C_f - C_i}{C_m - C_i}$$

## ***Chlorophyll content***

10 leaves of *N. mucronata* were collected and add into a 2 ml Eppendorf with 1ml of Dimethyl sulfoxide (DMSO), covered with aluminum foils. In the lab, all vials were kept in a 65 ° C incubator for 72 h and then centrifuged for 14000 rpm at 20°C for 10 min. 200 ml of the supernatant was added to a 96 wells plate and the absorption was read with Epoch™ spectrophotometer (BioTek Instruments, Inc., Vermont, USA). Chlorophyll *a* (*Chl a*), contents was calculated using Equation 2 [43]:

*Equation 2:*

$$\begin{aligned} \text{Chl } a &= 13.7 * A_{656} - 5.7 * A_{650} \\ \text{Chl } b &= -7.6 * A_{656} + 25.8 * A_{650} \end{aligned}$$

## Results

The two years of sampling were characterized by two different rain regimes (Fig. 2B), where 2016 was substantially wet compared to 2017 (223 and 96 mm, respectively: Fig. 2B, Mann-Whitney Ranks Sum Test  $p < 0.001$ ). Data of total solar radiation (Fig. 2A) indicates that 2016 was colder than 2017 (22.6 and 25.1 MJ/ m<sup>2</sup> year of Solar Radiation respectively, Mann-Whitney Ranks Sum Test  $p = 0.033$ ). This resulted in increase of soil temperature in 2016 at both 25 and 50 cm soil depths (Fig. 2C), as well as the reduction of soil moisture at both depths (Fig. 2D).

We did not find significant differences in physiological measurements of *N. mucronata* plants between the two hillslope types throughout the two years of sampling (SI). For the phenological measurements, the estimated mean *N. mucronata* size was greater in HM hillslopes than that in HT hillslopes ( $p < 0.0001$ )

Nevertheless, once we plotted the data for different years (2016 vs 2017), we found a significant difference for most of the parameters between the two years, and especially regarding the C:N ratio and RWC. In 2016, *N. mucronata* had a higher C:N ratio (HT, Dunn's Method: DiffRanks 15.896,  $Q = 2.687$ ,  $p < 0.05$ , HM Dunn's Method: DiffRanks 45.000,  $Q = 8.152$ ,  $p < 0.05$ , Fig. 3A) and higher RWC (HT Holm-Sidak method: DiffMeans 55.499,  $t = 12.130$ ,  $p < 0.001$ , HM Dunn's Method: DiffRanks 46.000,  $Q = 8.254$ ,  $p < 0.05$ , Fig. 3B) than these in 2017. For the C:N ratio, this trend was similar for HT and HM hillslopes (a decrease of 26% and 28% from 2016 to 2017 in HT and HM, respectively). At the same time, the decrease in RWC was much smaller in HT hillslopes (5%) than that in HM hillslopes (11%).

## Plant diversity

We found that differences in plant diversity can be explained by hillslope type (Analysis of similarity:  $R = 0.36$ ,  $p = 0.0001$ ) (Fig. 4A and B). In addition, we measured the effect of sampling year (Fig. 5A, B, C and D), which was also significant, though the value explained was lower than the hillslope type ( $R = 0.11$ ,  $p = 0.002$ ). Moreover, we found a significant difference in life form composition, considering all species found, between the hillslopes (Pearson chi-square: Chi Square: 56.7,  $df = 2$ ,  $p < 0.0001$ ). HT plots had a higher mean value of perennial (39% in HT compared to 3% in HM) as well as higher mean value of hemicryptophyte plants (13% in HT compared to 7.5% in HM). At the same time, the mean value of annuals was significantly higher in HM (90% in HM compared to 48% in HT).

The accumulated cover of four species contributed to 52.8% of the differences between the two hillslope types. These species included *Stipa capensis* Thunb.(19.6%), *N. mucronata* (18.8%), *Anabasis articulata* (Forssk.) Moq. (8.6%), and *Onobrychista crista-gali* (L.) Lam. (5.8%) (Similarity percentage analysis, SI 2). The main differences were caused by two perennial plants that were absent from the HM transects: *N. mucronata* and *A. articulata*. Additionally, once we plotted the annuals' diversity data per year (Fig. 5A-D), we found that the annual community structure in the HT hillslopes during the shift from 2016 to 2017 became more even, with a more uniform abundance of species (Fig. 5A and B). An opposite trend was found for the HM hillslopes, where an increase in abundance of dominant species was observed (Fig. 5C and D).

Species richness and abundance are reported in Table 1. Species richness was similar in HT and HM hillslopes (31 and 30 species, respectively). Once comparing 2016 to 2017 year – with equal species richness in both of the hillslope types but different structures and abundance in 2016 – HT hillslopes faced an increase in 2017, while HM hillslopes faced a decrease.

To gain more insights about the community structure, we calculated the Shannon Diversity Index and Simpson Diversity Index (Table 1). Overall, HT hillslope had a higher diversity (Shannon Diversity Index in HT was 3.5% higher than that in HM). Further, once we calculated the yearly data, we found that in 2017 the drop of diversity in HM hillslopes was significant, whilst a significant increase was observed for HT hillslopes. Moreover, in 2017, the Shannon Evenness Index showed an increase in HT hillslopes and a decrease in HM hillslopes. This suggests that in HM hillslopes, the functional group encompass few dominant species with high abundance and few sparser species with low abundance. In HT hillslopes, the community structure was more even.

Table 1

Mean species richness and species abundance in the Heterogeneous (HT) and homogeneous (HM) hillslopes in 2016 and 2017 years.

Plot	Species Richness (n)	Species Abundance (N)	Shannon Diversity's index (H)	Simpson Diversity's Index (D)	Shannon Evenness Index (E)
HT	31	122	1.71 ± 0.01	2.59 ± 0.01	0.50
HM	30	121	1.65 ± 0.01	2.59 ± 0.01	0.49
HT (2016)	19	141	1.43 ± 0.02	2.23 ± 0.02	0.49
HT (2017)	22	102	2.02 ± 0.02	4.01 ± 0.01	0.65
HM (2016)	19	71	1.83 ± 0.02	3.78 ± 0.01	0.62
HM (2017)	17	51	0.90 ± 0.01	1.47 ± 0.04	0.32

## Discussion

Geodiversity components such as geomorphology, topography, geology, and hydrology are associated with energy, nutrients, which regulate biodiversity [44,45]. Nevertheless, only recently, the impact of geodiversity on biodiversity has gained attention [46–51]. Considering global climatic change, it was proposed that high-geodiversity land units are potentially more capable to support biodiversity because of their intrinsic resilience [52–55]. A recent study highlighted the need in gaining more empirical data to support the geodiversity-biodiversity relations in different climate zones [21].

Recent studies from the semi-arid north-western Negev suggested that hillslope-scale geodiversity improves the source-sink relations [15] and positively affect soil quality and geo-ecosystem functions. Specifically, it was reported that the hillslopes had 22% greater mean hygroscopic moisture [56] than that in HM hillslopes. The comparatively favorable conditions in the HT hillslopes were proposed to be the key of survival of *N. mucronata* plants during the mass mortality that occurred during different drought events started in 1999 [18].

However, the favorable soil conditions in HT hillslopes were not straightforward translated into a better physiological state of plants (SI 1). Contradictory, we found that shrubs in HM hillslopes have a significantly greater size than those in HT hillslopes for any of the two studied years (SI 1). Despite that, during 2017, the shrubs in HM hillslopes faced stronger water stress compared to these in HT hillslopes (Fig. 3B). The positive effect of increased geodiversity on hygroscopic moisture [56], and the overall higher soil-water content in HT hillslopes [57], might explain the reduced water stress for shrubs in HT hillslopes [18,58].

The shrub patch is the driver of the cyclic succession of plants community [32,59–61]. According to the biodiversity cyclic hypothesis [32], once the patch is consolidated, the dissimilarity in community structure between the shrubby patches and interpatch spaces increases. Therefore, shrublands patchiness is critical for sustaining spatial heterogeneity [62]. In our study region, the HT hillslopes have higher patchiness, mainly due to higher geodiversity that supports shrub durability to droughts. The perennials in HM were 2% of the community structure, whilst being 38% in HT (Fig. 4A and B). Specifically, in HM we found two shrubby species (*Pituranthos tortnokus* and *N. mucronata*), and a total of 3 individuals, while in the HT we found six shrubby species (*N. mucronata*, *A. articulata*, *Dianthus monadelphus subsp. judaicus*, *Salvia lanigera* Poir., *Helianthemum stipulatum* (Forssk.) C. Chr. and *Helianthemum lippii* (L.) Dum. Courset) and a total of 47 individuals. The annual plant community in HM encompassed of 25 species and 110 individuals, while in the HT it encompassed 20 species and 58 individuals. In both HM and HT, five species encompassed 50% of the total abundance. The dominant annual species is *S. capensis* in both hillslope types. In HM, the annuals contributed 90% of the total community structure, while in HT they contributed 48% (Fig. 4A and B).

The annual community structure faced a shift from the wetter 2016 to the dryer 2017 in both hillslopes (Fig. 5A-D). In HT hillslopes, the annuals community become more even, having fewer dominant species with high abundance (Fig. 5A and B). At the same time, in HM hillslopes, the annuals' community

structure became less even (Fig. 5C and D). In our diversity analysis, we showed that in the drier year, plant diversity increased in HT hillslopes (Table 1) and decreased in HM hillslopes. Different simulation studies, where plant communities underwent abiotic stresses related to climate changes – such as higher temperature or lower precipitations – showed similar results [63,64]. It was shown that community response to changes is rapid (two seasons), and that stresses can change patterns of plant dominance and evenness [63,64]. Changes in dominance in community composition can have consequences for species coexistence and ecosystem functions [65]. In our study, we show that the effect of geodiversity on community structure and species richness is greater in the drier year than that in a wetter year.

The motivation of this study was to understand how different geodiversity features, expressed by the degree of stoniness and soil thickness, affect the physiological state of *N. mucronata* and the plant life form variability. In conclusion, our data show that in a semi-arid regions, hillslopes with higher geodiversity better buffer the effect of drier years, and supported a more diverse plant community compared to lower geodiversity hillslopes. Additional studies should be conducted in other drylands of the world in order to verify the mechanisms through which geodiversity regulates the structure and composition of vegetation community.

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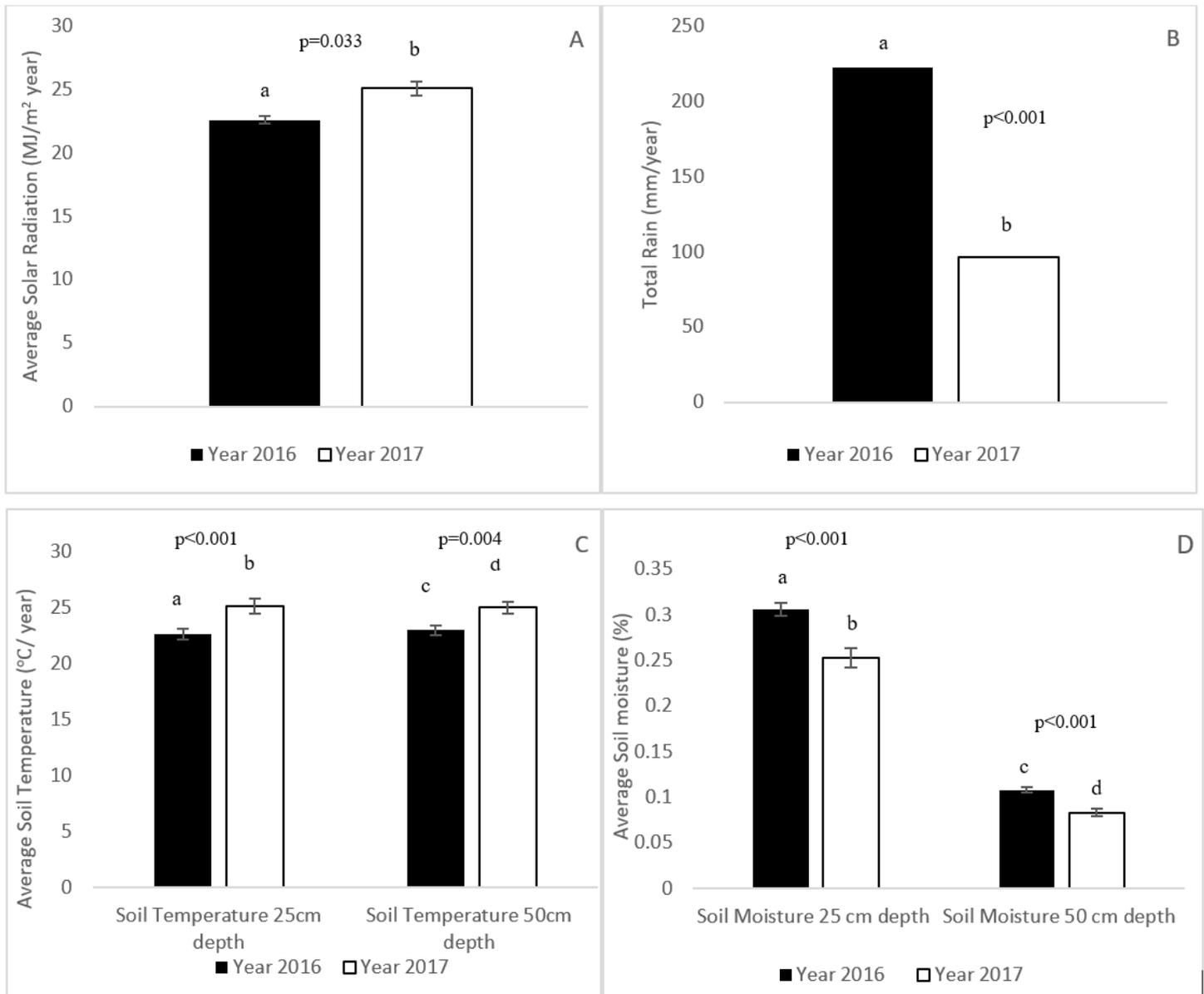
## Figures



**Figure 1**

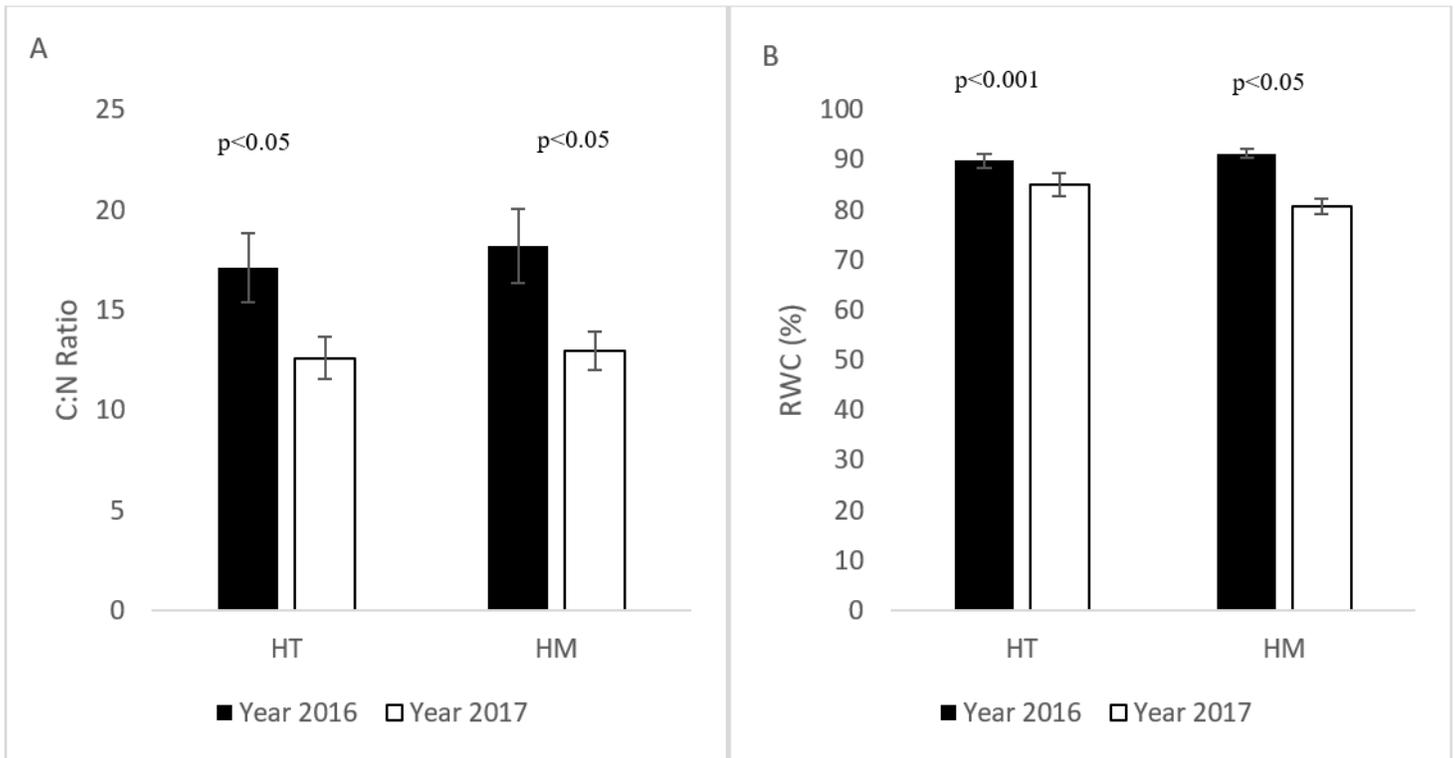
A view of a homogeneous (a) and a heterogeneous (b) hillslopes. In the homogeneous hillslopes, the white spots are piles of snails in the vicinity of dead shrubs. The piles indicate the location of dead

shrubs. At the same time, most of the shrubs in the heterogeneous hillslope are alive, and survived the prolonged drought of 2008-2009.



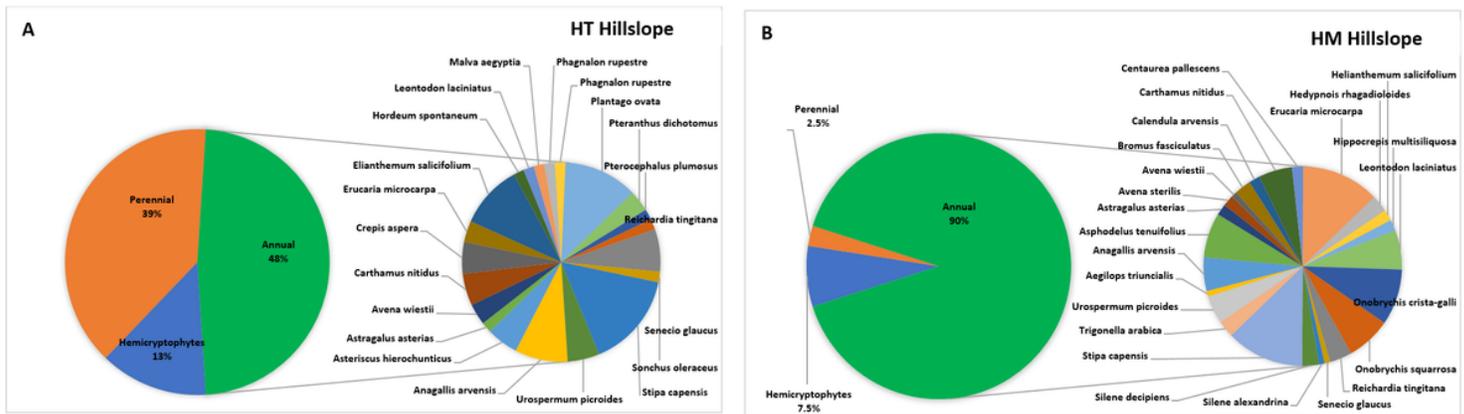
**Figure 2**

Total solar radiation (A), total rain (B), average soil Temperature (°C), and average soil moisture (D), for 2016 and 2017.



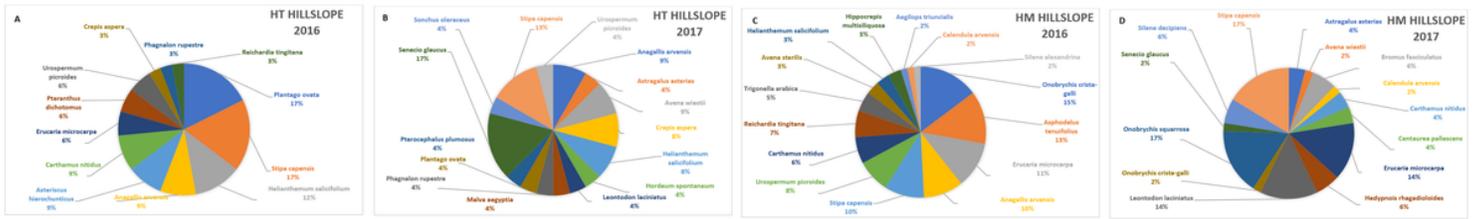
**Figure 3**

Mean C:N ratio (A) and Relative Water Content (RWC: B) in *N. mucronata* leaves at the heterogeneous and homogeneous hillslopes, for 2016 and 2017.



**Figure 4**

Life form composition in heterogeneous (HT: A) and homogeneous (HM: B) hillslopes. Differentiation among perennial (red), hemicryptophyte (blue), and annuals (green) is presented in the left circles, and species-level differentiation of annuals is presented in the right circles.



**Figure 5**

Annual community structure in the heterogeneous hillslopes in 2016 (A) and 2017 (B), and in the homogeneous hillslopes in 2016 (C) and 2017 (D).

## Supplementary Files

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