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# *Artemisia sieberi* dominated landscapes of Northeastern Iran host great diversity in lichen and annual plant species

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## ARTICLE INFO

## ABSTRACT

In this study, we aim to evaluate the diversity of vascular plants and lichens coexisting in *Artemisia sieberi* dominated landscapes of northern Iran. Specifically, we wanted to unveil to what extent *Artemisia* plant cover and soil features affected species diversity and composition of annuals and lichens growing beneath them, and if annual plants and lichen species were associated at fine spatial scales. The study area was located in *Artemisia* steppes in North-Eastern Iran. Therefore, four localities dominated by *Artemisia sieberi* in Golestan National Park and Alagol wetland were selected. We quantified plant and lichen species cover in 5 plots in each location, including 25 subplots and five soil samples to characterize edaphic heterogeneity. Data were analyzed using GLM, NMDS, PERMANOVA, and Mantel Tests. We recorded 19 lichen species, three moss species, and 21 annual plant species in the four localities. Alagol and Alikhani had the most similar lichen compositions and Almeh showed great differences with other sites. However, Bagh and Almeh had the most similar and the most different annual species composition comparing the rest locations, respectively. Location explained 50% and 30% of the variance in lichens and annuals species composition, respectively. Soil chemical properties had no significant influences on lichens and annuals parameters except for Mg content in lichen evenness and clay content on total plant cover. We found a highly significant relationship between the lichen composition and annual plant species composition on fine scale (Mantel r: 0.13; p = 0.0003). The cover of *Artemisia* explained significant but tiny fractions of lichen species composition (1%) and annual plant species composition (2%) at subplot level. *Artemisia* steppes of northeastern Iran are not homogeneous habitats and shelter high diversity in lichen and annual plant species. Site location conditions may explain the differences among lichens and annuals compositions.

## 1. Introduction

Several large vegetated areas around the world have one dominating species that covers a wide range of environmental conditions, such as *Pinus sylvestris* in Europe and North Asia (Kelly and Connolly, 2000). In North America, *Artemisia tridentata* dominated landscapes (Hazlett and Hoffman, 1975), whereas different *Artemisia* species cover vast areas in the Middle East and Central Asia (Kapustina et al., 2000). *Artemisia* shrublands are particularly important in the Middle East, where they provide one of the most noticeable landscapes in a variety of climates (Jalili et al., 2013). Plant patches dominated by *Artemisia* interspersed within open areas with tiny perennials, annuals, and well-developed Biological Soil Crusts (BSCs, hereinafter) dominated by lichens and mosses constitute a biphasic structure in these types of shrublands (Abedi et al., 2007). Although Iran shelters large areas of *Artemisia* steppes mainly dominated mostly by *A. sieberi* (over 34 million ha *sensu* Jalili, 2015), these communities have received very little attention in terms of the biological diversity associated with these monospecific formations. In particular, important components of the community, such as lichens and annual plants that coexist in the understory of *Artemisia* shrubs in Iran, are poorly understood. It is well-known that plant diversity is primarily determined by climate and edaphic features

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(Lopez-Angulo et al., 2020), and dominant species in the community may have complex effects on understory species, which can affect the species composition of other members of the community, such as annual plants or lichens (Luzuriaga et al., 2012; Espinosa et al., 2014). Although the effect of *Artemisia* plants on understory species, development is debatable, some studies have demonstrated that the allelopathic effects of *Artemisia* may limit the successful establishment of understory species in laboratory and field conditions (Escudero et al., 2000; Jessing et al., 2014; Pueyo et al., 2016; Arroyo et al., 2017, 2018). However, Artemisia shrubs have been shown to have moderate nursing effects on perennial grasses in stressful conditions in Northeast Iran (Jankju, 2013; Bahalkeh et al., 2021), probably because Artemisia shrubs can mitigate unfavorable conditions by creating fertility islands and protecting plants from grazing (Callaway and Pugnaire, 1999; Ahmadian et al., 2018c; Ahmadian et al., 2019).Biological soil crusts (BSCs) are assemblages of organisms composed mainly of cyanobacteria, bryophytes, and lichens which are found throughout the world's drylands (Belnap and Lange, 2003). BSCs are critical drivers of ecosystem function, such as carbon, nitrogen, and water cycling, limiting soil evapotranspiration, and enhancing resource availability beneath them (Delgado-Baquerizo et al., 2013; Berdugo et al., 2014). BSCs and vascular plants have a complicated interaction (Luzuriaga et al., 2012; Zhang et al., 2016). Some studies suggest that BSCs act as environmental biotic filters during the formation of soil seed banks (Peralta et al., 2016), or may limit or have neutral effects on seed germination and seedling establishment (Escudero et al., 2007; Ahmadian et al., 2018a, 2018b; Ahmadian et al., 2022; Peralta et al., 2019). Other research (Ghiloufi et al., 2017) found that BSCs improved native vascular plant species germination and establishment, which varied depending on water availability (Ahmadian et al., 2019). The reduction in soil evapotranspiration beneath BSCs, which buffer dry conditions, may be linked to the favorable effects of BSC on plant growth (Peralta et al., 2019). In this context, it is critical to reveal the diversity of Artemisia-dominated shrublands in Iran and assess how soil characteristics and Artemisia plant cover affect the diversity of other coexisting biological guilds such as lichens and annual plant species. Furthermore, understanding the relationship between plants and lichens at fine spatial scales is critical. This is especially important in drylands, where BSCs dominated by lichens play an important role in ecosystem functioning (Belnap and Lange, 2003; Abedi et al., 2007). This knowledge would be useful for proper ecosystem management, establishing conservation priorities, and maximizing ecosystem services in these widely distributed habitats. We expect that the *Artemisia*-dominated systems of northeastern Iran shelter diverse lichen and annuals species assemblages. Therefore, in this study, we aim to evaluate the following specific questions:

1) How diverse are the vascular plants and lichens that coexist in northern Iran environments dominated by *Artemisia sieberi*?
2) Did environmental variables associated to location such as climate, soil features and *Artemisia* plant cover affect species diversity and composition of annuals and lichens growing beneath them?
3) Do the effects observed on lichen and annual communities depend on the study's spatial scale?
4) How *Artemisia* and location influence on annual plants and lichen species association at fine spatial scales?

## 2. Materials and methods

### 2.1. Study area

*Artemisia sieberi* Besser is a dwarf shrub that covers almost 20.7 million hectares, mostly in the arid and semi-arid steppes of central and northeastern Iran (Jalili, 2015; Memariani et al., 2016). These habitats are composed of vegetation patches dominated by *Artemisia sieberi*, with other perennials like *Stipa caucasica* Schmalh., *Poa bulbosa* L., and dwarf shrubs like *Acanthophyllum pungens* (Bunge) Boiss. Patches grow sparsely

in a matrix of bare soil that is usually covered with BSCs, mainly composed of lichens, such as *Psora decipiens, Gyalolechia fulgens, Endocarpon pusillum, Diploschistes diacapsis*, mosses (*Tortella tortuosa)*, and cyanobacteria (*Microcoleus vaginatus*; Table 1).

We selected four representative locations dominated by *Artemisia sieberi* shrubs: Almeh valley (37° 21′ 8.4″ N; 56° 12′ 48.6″ E), Bagh valley (37° 21′ 51.9″ N; 56° 15′ 12.3″ E) and Alikhani (37° 29′ 10.9″ N; 56° 7′ 42.3″ E) were located in the Golestan national park beyond the Hyrcanian forest, where precipitations strongly reduced and Alagol (37° 20′ 31.1″ N; 54° 34′ 12.1″ E) is located in Turkmen Sahra, influenced by Karakum desert in Turkmenistan, which promoted low precipitations similar to those in Golestan. Percentage cover of the *Artemisia* shrub ranged on average from 17.6%±3.0 (Alagol) to 25.5%± 8.8 (Bagh valley). Almeh valley is alluvial and contain the upstream deposits of stones, pebbles, clay with slopes below 5%, but Bagh valley contain the upstream tiny sediments with slopes below 2% (Bahalkeh et al., 2021), Alikhani consists of a gentle hilly landscape. Alagol includes small loess hills around the Alagol wetlands (Kakeh et al., 2018). To make annual plant inventories comparable, sampling was done in the four locations during the phenological peak of the annual species. Soil chemical composition significantly differed among the four study locations (Appendix C). Average altitude ranged from 30 m.a.s.l. (Alagol) to 1330 m.a.s.l. (Almeh valley), and rainfall and mean annual temperatures from 141.7 mm and 13.0 °C (Bagh valley) to 250 mm and 13.1 °C (Alagol). Almeh valley and Alikhani also had 161 mm and 230 mm, respectively. Precipitation in the study year was above average annual precipitation in all locations (Alagol (261 mm), Bagh valley (162 mm), Almeh valley (176 mm), and Alikhani (250 mm). All study sites have moderate grazing by wildlife and domestic livestock.

### 2.2. Vegetation and lichen sampling

In April 2016, we haphazardly established five plots (50 cm × 50 cm) per location, consisting of 25 subplots (10 cm × 10 cm) to control for very fine-scale heterogeneity in composition. We estimated the percentage cover of annual plant species, mosses, lichens, and bare soil in each subplot. Lichen identification was confirmed by specialists of the Iranian Scientific and Industrial Research Organization (Cryptomorphous Iran, ICH).

### 2.3. Soil analyses

We collected a soil sample in open areas adjacent to each sampling plot (i.e. five soil samples per locality), using a 15 cm diameter and 10 cm deep core. After air-drying, the samples were sieved through a 2-mm sieve. Soil texture was determined by the Bouyoucos hydrometer method (Bouyoucos, 1962). Soil pH was determined using an Orion Ionalyzer Model 901 pH meter, electrical conductivity (EC) using an Orion Ionalyzer Model 901 EC meter in a 1:2.5, soil: water solution. Soil organic C was determined using the Walkey-Black technique (Allison, 1965). The total N content was measured using a semi Micro-Kjeldahl technique (Bremner and Mulvaney, 1982). Available P was determined with a spectrophotometer and the Olsen method (Homer and Pratt, 1961), and available K, Ca, and Mg (by ammonium acetate extraction at pH 9) were determined with an atomic absorption spectrophotometer (Bower et al., 1952).

### 2.4. Taxonomic diversity indices

To estimate lichen and annual plant community diversities, we calculated the inverse Simpson index (1/D) using each species cover percentage per plot and subplot (Jost, 2006):

$$\frac{1}{D} = \frac{1}{\left(\sum pi^2\right)}$$

**Table 1**
Frequency of lichen and plant species occurrences in the four study locations (n = 125 per location).

| Frequencies | | | | Family | Abbreviation | Species |
|---|---|---|---|---|---|---|
| Alagol | Alikhani | Bagh valley | Almeh valley | | | |
| | | | | | | **Lichens** |
| 53 | 0 | 0 | 0 | Acarosporaceae | Acarea | *Acarospora reagens* Zahlbr. |
| 19 | 0 | 0 | 18 | Teloschistaceae | Calthu | *Caloplaca raesaenenii* Bredkina (syn. *C. thuringiaca* Søchting & Stordeur) |
| 0 | 0 | 0 | 7 | Candelariaceae | Canvit | *Candelariella vitellina* (Hoffm.) Müll. Arg. |
| 0 | 0 | 0 | 3 | Megasporaceae | Cirelm | *Circinaria elmorei* (E. D. Rudolph) Owe-Larsson, A. Nordin & M. Sohrabi. |
| 1 | 0 | 29 | 1 | Megasporaceae | Cirhis | *Circinaria hispida* (Mereschk.) A. Nordin, S.Savic. |
| 0 | 0 | 13 | 0 | Megasporaceae | Cirros | *Circinaria rostamii* Sohrabi. |
| 7 | 0 | 68 | 45 | Megasporaceae | Cirman | *Circinaria mansourii* (Sohrabi) Sohrabi. |
| 45 | 12 | 79 | 85 | Collemataceae | Colten | *Collema tenax* (Sw.) Ach. |
| 85 | 54 | 0 | 0 | Graphidaceae | Dipdia | *Diploschistes diacapsis* (Ach.) Lumbsch. |
| 58 | 83 | 29 | 10 | Verrucariaceae | Endpus | *Endocarpon pusillum* Hedw. |
| 27 | 12 | 0 | 0 | Teloschistaceae | Gyades | *Gyalolechia desertorum (Tomin)* Søchting, Frödén & Arup. |
| 79 | 0 | 82 | 2 | Teloschistaceae | Gyaful | *Gyalolechia fulgens* (Sw.) Søchting, Frödén & Arup. |
| 52 | 29 | 0 | 0 | Teloschistaceae | Gyasub | *Gyalolechia subbracteata* (Nyl.) Søchting, Frödén & Arup. |
| 53 | 0 | 0 | 0 | Squamarinaceae | Squlen | *Squamarina lentigera* (Weber) Poelt. |
| 0 | 31 | 24 | 10 | Lichinaceae | Pecter | *Peccania terricola* H. Magn. |
| 19 | 18 | 14 | 44 | Psoraceae | Psodec | *Psora decipiens* (Hedw.) Hoffm. |
| 0 | 3 | 0 | 0 | Psoraceae | Psosav | *Psora saviczii* (Tomin) Follmann & A. Crespo |
| 2 | 0 | 54 | 6 | Ramalinaceae | Tonsed | *Toninia sedifolia* (Scop.) Timdal |
| 0 | 0 | 0 | 1 | Physciaceae | Rinspp | *Rinodina* sp. |
| | | | | | | **Mosses** |
| 106 | 0 | 14 | 0 | Pottiaceae | Tortor | *Tortella tortuosa* |
| 0 | 90 | 0 | 0 | Pottiaceae | Synspp | *Syntrichia* sp. |
| 0 | 0 | 0 | 69 | Pottiaceae | Alospp | *Aloina* sp. |
| | | | | | | **Cyanobacteria** |
| 0 | 0 | 0 | 28 | Microcoleaceae | Micvag | *Microcoleus vaginatus* Gomont ex Gomont |
| | | | | | | **Annual plants** |
| 0 | 5 | 25 | 1 | Brassicaceae | Alydes | *Alyssum desertorum* Stapf |
| 0 | 0 | 2 | 0 | Primulaceae | Andmax | *Androsace maxima* L. |
| 0 | 4 | 0 | 0 | Boraginaceae | Arndec | *Arnebia decumbens* (Vent.) Coss. & Kralik |
| 0 | 0 | 8 | 0 | Poaceae | Brotec | *Bromus tectorum* L. |
| 0 | 0 | 0 | 1 | Ranunculaceae | Cerfal | *Ceratocephala falcata* (L.) Pers. |
| 0 | 0 | 0 | 6 | Poaceae | Eretri | *Eremopyrum triticeum* (Gaertn.) Nevski |
| 0 | 0 | 4 | 0 | Geraniaceae | Erocic | *Erodium cicutarium* (L.) L'Hér. |
| 12 | 1 | 0 | 0 | Cistaceae | Helsal | *Helianthemum salicifolium* (L.) Mill. |
| 0 | 0 | 2 | 0 | Poaceae | Henper | *Henrardia persica* (Boiss.) C.E.Hubb. |
| 0 | 0 | 7 | 0 | Caryophyllaceae | Holglu | *Holosteum glutinosum* (M.Bieb.) Fisch. & C.A.Mey. |
| 0 | 7 | 0 | 0 | Asteraceae | Koelin | *Koelpinia linearis* Pall. |
| 0 | 0 | 3 | 0 | Boraginaceae | Lapsin | *Lappula sinaica* (DC.) Asch. & Schweinf. |
| 5 | 0 | 0 | 1 | Brassicaceae | Lepfil | *Leptaleum filifolium* (Willd.) DC. |
| 0 | 0 | 13 | 0 | Poaceae | Lolsub | *Loliolum subulatum* (Banks & Sol.) Eig |
| 0 | 0 | 4 | 0 | Papaveraceae | Papacu | *Papaver aculeatum* Thunb. |
| 16 | 0 | 0 | 0 | Plantaginaceae | Plaspp | *Plantago* sp. |
| 0 | 0 | 1 | 0 | Papaveraceae | Roehyb | *Roemeria hybrida* (L.) DC. |
| 0 | 4 | 0 | 0 | Dipsacaceae | Scarot | *Scabiosa rotata* M. Bieb. |
| 0 | 1 | 0 | 0 | Asteraceae | Scaspp | *Scariola* sp. |
| 0 | 2 | 0 | 0 | Poaceae | Taecap | *Taeniatherum caput-medusae* (L.) Nevski |
| 0 | 0 | 7 | 0 | Labiatae | Zizten | *Ziziphora tenuior* L. |
| | | | | | | **Perennial plants** |
| 0 | 2 | 0 | 0 | Caryophyllaceae | Acapun | *Acanthophyllum pungens* (Bunge) Boiss. |
| 0 | 0 | 0 | 1 | Liliaceae | Allrub | *Allium rubellum* M.Bieb. |
| 69 | 59 | 58 | 64 | Asteraceae | Artsie | *Artemisia sieberi* Besser |
| 4 | 0 | 0 | 0 | Fabaceae | Astspp | *Astragalus* sp. |
| 1 | 0 | 0 | 1 | Chenopodiaceae | Gagsp | *Gagea* sp. |
| 4 | 0 | 0 | 1 | Geraniaceae | Gerkot | *Geranium kotschyi* Boiss. |
| 0 | 1 | 0 | 0 | Rutaceae | Hapobt | *Haplophyllum obtusifolium* Ledeb. |
| 0 | 0 | 7 | 0 | Fabaceae | Hedmic | *Hedysarum micropterum* Boiss. |
| 22 | 0 | 68 | 5 | Poaceae | Poabul | *Poa bulbosa* L. |
| 0 | 0 | 0 | 1 | Chenopodiaceae | Salauc | *Salsola aucheri* (Moq.) Bunge ex Iljin |
| 0 | 0 | 8 | 4 | Poaceae | Sticau | *Stipa caucasica* Schmalh. |
| 0 | 0 | 0 | 1 | Asteraceae | Traspp | *Tragopogon* spp |

Where $p_i$ is the proportion of species i in each sampling unit.

This index has also been called the 'effective number of species' (MacArthur, 1965) and represents the number of species that a community would have if species were distributed equally. Species richness represents the number of different species that occur in each plot. Evenness was calculated as the inverse Simpson index divided by species richness in each sampling unit (Jost, 2006).

## 2.5. Statistical analyses

All statistical analyses were performed in R (version 2.4–6). Species accumulation curves were performed with the "*Specaccum*" function and the estimators with the "*specpool*" function of the "*vegan*" package in R. We performed GLMs to evaluate the effect of soil properties and *Artemisia* plant cover on species richness, diversity, evenness, and cover of the lichen and annual plant assemblages at plot and subplot levels. To avoid covariance among predictors, we only used variables that were not significantly correlated among them. Therefore, the Poisson link

function was used for richness and Gaussian link function for the rest dependent variables (Appendix D).

We performed a Principal Components Analysis with all the soil physicochemical variables measured at each site after scaling all variables and using the *rda* function in the vegan package version 2.4–6 (Oksanen et al., 2007). We used the first PCA axis (PC1soil, hereinafter) as a covariable in multivariate ordination analyses of lichen and annual species assemblages at plot and subplot scales. PC1soil axis is positively correlated to Ca and K edaphic content and higher values of pH, negatively associated with Mg and N edaphic content (Appendix E). PERMANOVA based on Bray-Curtis distances (Legendre and Legendre, 1998) and type III Sum of Squares were performed to assess species composition differences using *adonis* function in vegan package (Oksanen et al., 2007). Species that appeared in less than 5 % of the plots were removed to avoid statistical biases due to rare species, and cover data were square root-transformed. We performed two PERMANOVAs at the plot scale (50 cm x 50 cm) to evaluate lichen and annual plant species compositions, respectively. Both included PC1soil, *Artemisia* cover, and location as fixed factors. At the subplot scale (10 cm x 10 cm), we performed two nested PERMANOVAs using the "strata" function. Soil variables were sampled at the plot scale; thus, we did not include the PC1soil variable at the subplot scale since the plot was already nested within the location. In this case, we used as covariables the cover values of *Artemisia*, mosses, and bare soil that were registered in each subplot. Lichen cover was included as a covariable to model annual plant species composition. The significance of each PERMANOVA was tested using a Monte-Carlo test with 9999 permutations. Non-metric Multidimensional Scaling (NMDS) was performed using the *metaMDS* function in vegan package, to represent differences in lichen and annual plant species composition among locations. We used the *ordiellipse* function in vegan package to represent the ellipsoids with the standard deviation of the weighted centroids for each location. We performed standardized Mantel tests to evaluate the similarities between the lichen and annual plant species compositions at plot and subplot scales (Legendre and Legendre, 1998). At the subplot scale only samples where annuals and lichens occurred together were considered (n = 76). Species cover values were log-transformed, and Bray-Curtis distances were computed to build the distance matrices. For Mantel test, we used the "*ecodist*" package in R (Core Team, 2017).

## 3. Results

We recorded 19 lichens, 21 annual plants, 12 perennials and three moss species in the four study locations (Table 1). The species accumulation curves and Chao's estimates showed that in this study we accounted for more than 95% and more than 90% of the lichen and annual species respectively (Appendix A). At the plot level, there was no significant influence of soil chemical characteristics on lichen species richness, diversity, or total cover, however Mg content was relatively important in determining lichen evenness (Appendix D). Similarly, with the exception of clay content on total plant cover, these variables had no effect on annual plant richness, diversity, or cover at the plot level. Location at the plot scale had a considerable effect on lichen and annual species composition, explaining 50% and 30% of the species composition, respectively. Edaphic properties (PC1soil) had a marginal impact on lichen species composition (Table 2). Location explained the greatest proportion of the differences in the composition of annual and lichen communities at the subplot scale (Fig. 1, Table 3). The Artemisia cover explained significant but tiny fractions of lichen species composition (1%) and annual plant species composition (2%) (Table 3). The Alagol and Alikhani sites, that received the highest precipitation values in our study, had similar lichen species compositions, with Almeh having the most diverse lichen species composition (Fig. 1a). On the contrary, the annual species composition varied greatly between the four locations. Bagh valley plots had a quite similar species composition, and they were noticeably different from the other locations. Because the annual species

**Table 2**

Results of the PERMANOVA analyses at plot level (50 cm x 50 cm) for lichen and annual plant species compositions (n = 20). Type III sum of squares was performed. PC1soil: represents the values of the main PCA axis for edaphic variables (see Appendix E). The location represents the four sampling locations as a fixed factor. Df: degrees of freedom.

| | Df | F | $R^2$ | P |
|---|---|---|---|---|
| **Lichen species composition** | | | | |
| *Artemisia* cover | 1 | 0.4 | 0.008 | 0.86 |
| Location | 3 | 9.0 | 0.5 | **0.0001** |
| PC1soil | 1 | 2.1 | 0.04 | 0.08 |
| **Annual species composition** | | | | |
| *Artemisia* cover | 1 | 10.8 | 0.03 | 0.6 |
| Location | 3 | 2.6 | 0.31 | **0.0003** |
| PC1soil | 1 | 1.2 | 0.05 | 0.2 |

composition in Almeh was so variable, some plots resembled the species composition in the other locations. (See Fig. 1b.). Mantel tests at the plot scale (50 cm x 50 cm) showed that only 4 out of the 20 plots' composition of annual plants was spatially associated with lichen composition (Appendix F). Mantel tests at the subplot scale showed a weak but highly significant correlation between lichens and annuals (Mantel r: 0.13; p = 0.0003). Thus, a significant spatial association was detected between lichen and annual species compositions at fine spatial scales (10 cm x 10 cm).

## 4. Discussion

Our study reveals that the vast sagebrush landscapes of northeastern Iran are not homogeneous habitats. Still, they host distinct assemblages of lichens and annual species, so being more diverse systems than previously thought. There was no difference in species richness, diversity, or total cover, and soil properties did not exert any significant effects on annual and lichen communities among locations. However, the species assemblages of annuals and lichens were significantly different in the four locations, and it explained 31% and 50% of the variability for lichen and annual species composition, respectively (at plot scale). These results suggest that subtle differences among sites may drive significant diversity changes in a system dominated by a single species like the *Artemisia sieberi* shrublands of northern Iran.

Lichen and annual plant species compositions were strongly determined by locations, however, we should be aware that some degree of autocorrelation among plots in the same location is likely to occur. Lichen composition of Alagol and Alikhani contained several similar species such as *Collema tenax, Diploschistes diacapsis, Endocarpon pusillum, Gyalolechia desertorum, G. subbracteata* and *Psora decipiens*. Most likely, soils with silty clay loams favored colonization of these species (Soleimanzadeh et al., 2019; Kakeh et al., 2021). Silty clay soil together with the highest values of precipitation of the studied sites, may have caused larger similarities between these two sites in comparison to the others. However, annual plant species composition was relatively different between these two locations. Although the air humidity of Alagol wetland creates better conditions for annual establishment, Alagol was very poor in annual species, most likely due to the saline soils, which may have limited the plant species that were able to establish in these difficult conditions. Alikhani is located at the high altitude (1090 m), with intense freezing events in winter, that may have affected the soil seed bank able to germinate in the following season.

Almeh was the site with the greatest differences in lichen species composition and the greatest heterogeneity in annual species composition among plots (Fig. 1a). In this location, probably due to morning dews, mosses formed dense patches. The lichen community in this site was composed of *Caloplaca raesaenenii, Candelariella vitellina* and *Circinaria mansourii* growing on plant debris and mosses (Lumbsch et al., 2011; Søchting and Stordeur, 2001; Vondrak et al., 2012; Westberg and Sohrabi, 2012), and of *Circinaria elmorei* s.lat. and *C. hispida*, that grew
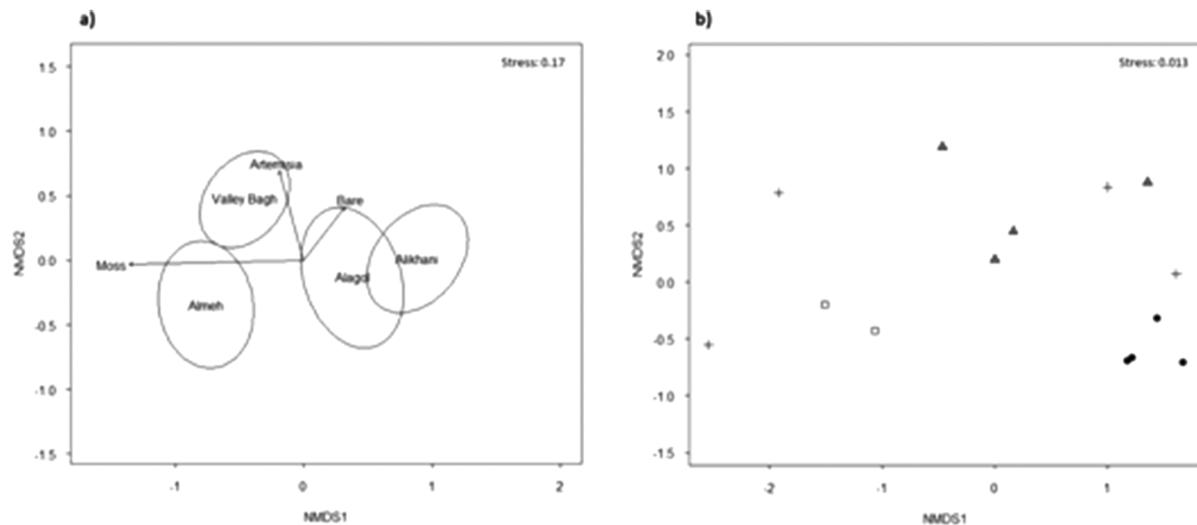
**Fig. 1.** (a) NMDS ordinations of lichen composition at subplot scale (10 cm x 10 cm). Each ellipsoid represents the standard deviation of the weighted centroids for each location with the function "ordiellipse" in vegan package. Significant environmental variables are represented (see Table 3). Vectors represent the directions in the ordination space towards which the environmental vectors change most rapidly and to which they have maximal correlations with the ordination configuration. *Artemisia*: % cover of *Artemisia sieberi*. Moss: % cover of moss; Bare: % cover of bare soil. (b) NMDS ordinations of annual plant species composition at plot scale (50 cm x 50 cm) where only locations had a significant effect (Table 2). Alagol: square; Alikhani: triangle; Almeh: cross; Valley Bagh: circle.

**Table 3**
Results of the PERMANOVA for lichen (n = 418) and annual plant species (n = 335) compositions at subplot scale (10 cm x 10 cm) in the four locations. Subplots that did not comprise lichens or annuals were excluded from the ordination analyses. DF: degrees of freedom.

| | DF | F | $R^2$ | P |
|---|---|---|---|---|
| **Lichen species composition** | | | | |
| Location | 3 | 73.6 | 0.3 | **0.0006** |
| *Artemisia* cover | 1 | 8.8 | 0.01 | **0.0001** |
| Moss_cover | 1 | 2.5 | 0.003 | **0.02** |
| Bare_Soil | 1 | 11.5 | 0.02 | **0.0001** |
| Residuals | 409 | | 0.58 | |
| Total | 417 | | 1 | |
| **Annual plant species composition** | | | | |
| Location | 2 | 13.9 | 0.24 | **0.0001** |
| *Artemisia* cover | 1 | 1.9 | 0.02 | **0.04** |
| Moss_cover | 1 | 1.0 | 0.01 | 0.4 |
| Bare_Soil | 1 | 2.0 | 0.02 | 0.08 |
| Lichen cover | 1 | 1.3 | 0.01 | 0.25 |
| Residuals | 88 | | | |
| Total | 90 | | | |

on pebbles or sandy soil under tiny shrubs (Hafellner et al., 2004, Sohrabi et al., 2013). This means that these species have different microhabitat requirements. However, for the annual plant community, dense moss patches hampered the germination of annual plants from the soils seed bank. In fact, annual plant communities in Almeh had the least species richness in our study and the lowest species richness per pot (1 or 2 species). This low richness combined with stochasticity may be the cause of the high variability in species composition observed.

Although precipitation was low in Bagh valley (141.7 mm) *Artemisia* covers the 25% of the area (significantly greater than in the rest locations), which are known to create milder micro -environmental conditions beneath them. The lichens *Circinaria hispida, Circinaria mansourii, Thalloidima sedifolium* and *Peccania terricola* are usually associated with *Artemisia* species in arid and semiarid regions (Sohrabi et al., 2013; Hafellner et al., 2004). Furthermore, *C. rostamii* is only known in Bagh Valley. On the other hand, in Bagh valley occurred the most species rich annual plant community (11 species), which suggests that the high cover of *Artemisia* and better soil quality may have favored annual plant establishment by means of lower evapotranspiration beneath their canopies.

Other studies found contrasting effects of *Artemisia* on neighbor species depending on environmental conditions. For example, Callaway et al. (1996), found that *Artemisia tridentata* had opposing effects on two species of *Pinus*, creating facilitative interactions with *P. monophyla* and competitive interactions with *P. ponderosa* in different ranges of the distribution of sagebush habitats of North America. In this line, Davies et al. (2007) found that *A. tridentata* ssp. *wyomingensis* (Beetle & A. Young) exerted different effects on the spatial distribution of herbaceous vegetation depending on local environmental conditions. Thus, the combination of species-specific effects of *Artemisia* on neighbors may result in the differences in lichen and annual species composition found from site to site. Bahalkeh et al. (2021) found contrasting effects of *A. sieberi* on neighbor plants, and Jankju (2013) found facilitative to neutral effects of *A. kopetdaghensis* depending on climatic conditions. These different interactions of *Artemisia* could be explained by several factors. *Artemisia* shrubs are known to increase nutrient availability (Burke et al., 1987; Davies et al., 2007) and temper soil temperature underneath shrubs (i.e., *A. tridentata* in Pierson and Wight, 1991; Chambers and Linnerooth, 2001; Davies et al., 2007 and *A. sieberi* in Ahmadian et al., 2019). In addition, competitive interactions may occur *via* direct competition for resources (Callaway et al., 1996; Jankju, 2013) or *via* release of allelopathic compounds (i.e., *Artemisia kopetdaghensis* in Jankju, 2013; *Artemisia herba-alba* in Pueyo et al., 2016).

At fine spatial scales (10 cm x 10 cm), where interactions with plants and lichens occur, we found a significant but small effect ($<$2%) of *Artemisia* cover on lichen and annual species composition. Furthermore, we found a remarkable association (13% of variability explained) between the spatial pattern of lichen species and annual plant species at this fine scale. These results highlight that the direct effect of the biotic components of the community on coexisting species is more likely to be detectable at fine spatial scales, but its influence may extend to larger spatial scales resulting in more diverse regional species pools (Espinosa et al., 2014). These results agree with other studies that detected facilitative effects of the lichen dominated BSCs on annual plants under highly stressful conditions and repulsion effects in milder environmental conditions in central Spain (Luzuriaga et al., 2012), and with studies that reported neutral to inhibitory effects of lichens on germination in northern Iran (Ahmadian et al., 2018a, 2022) and on plant performance (Havrilla et al., 2019). In conclusion, our study suggests that *Artemisia* steppes of northeastern Iran are not homogeneous habitats and that they

host high diversity in lichen and annual plant species. The effect of biotic components of the community such as perennial plants (i.e. *Artemisia*) of the relationship between lichens and annuals was more prone to be detected at fine spatial scales. Still, we suggest that the effects occurring at fine spatial scales can eventually be reflected in the differences in species compositions at larger spatial scales such as differences in species composition among locations. This study is a first attempt to assess the relationship between plants and lichens at the community level for this region of the world, and further studies would be needed to improve our knowledge about the general patterns of lichens and annuals responses to the dominant plant species effect and human land use of these landscapes.

## CRediT authorship contribution statement

**Negar Ahmadian:** Methodology, Data curation, Investigation. **Mehdi Abedi:** Supervision, Writing – original draft. **Adrian Escudero:** Supervision, Methodology, Writing – review & editing. **Mohammad Sohrabi:** Methodology, Data curation. **Arantzazu L. Luzuriaga:** Supervision, Writing – review & editing, Software.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A

Species accumulation curves for lichens (a) and annual species (b) in the study area. Central solid lines represent the mean values for the simulated species number after running 1000 bootstrap procedures. X axis represent the sampling effort in terms of number of subplots (10 cm x 10 cm). Gray areas represent the confidence intervals around mean values.
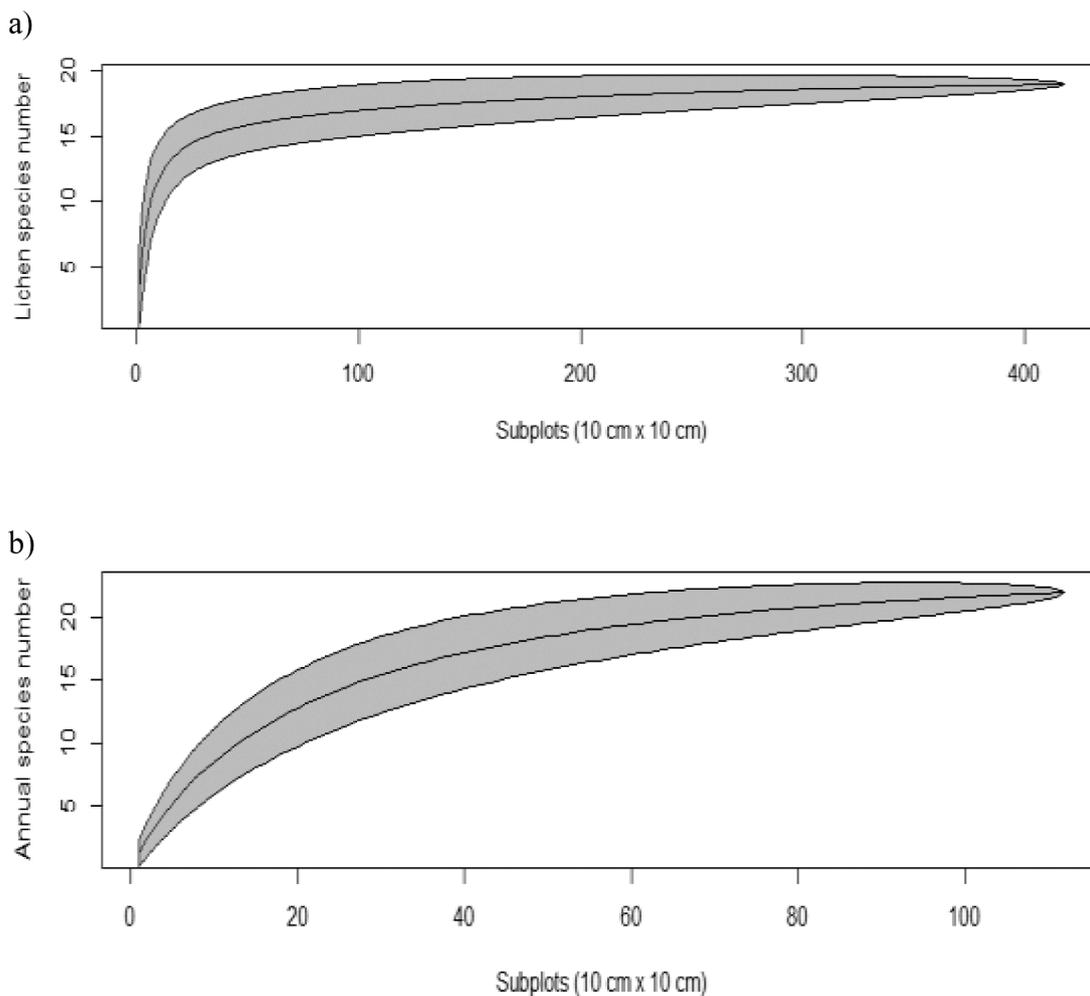
**Appendix B**

Results of the bootstrap procedures of Chao, Jacknife and Bootstrap in order to estimate the number of unseen species for the annual and lichen species pools. N: total observations. Obs: number of species observed in our study. SE: standard error.

|  | N | Obs | Chao (±SE) | Jacknife (±SE) | Bootstrap (±SE) |
|---|---|---|---|---|---|
| **Lichens** | 418 | 19 | 19.5 (±1.32) | 20 (±0.99) | 19.5 (±0.6) |
| **Annuals** | 112 | 21 | 23.1(±1.75) | 24.9(±1.7) | 23.75(±1.1) |

**Appendix C**

Soil parameters of the four study locations (mean ± SE, n = 5), and results of GLMs to test for differences in each soil parameter among locations. Gaussian family distribution was used (*: < 0.05, **: < 0.01, ***: < 0.001).

| Soil parameters | Bagh valley | Almeh valley | Alikhani | Alagol | F value |
|---|---|---|---|---|---|
| **EC (ds/m)** | 0.16 ± 0.01 | 0.15 ± 0.00 | 0.26 ± 0.04 | 1.06 ± 0.14 | 35.09 *** |
| **pH (1: 2.5 H$_2$O)** | 8.50 ± 0.02 | 8.34 ± 0.01 | 8.29 ± 0.04 | 7.85 ± 0.07 | 45.77 *** |
| **Organic Carbon (%)** | 0.29 ± 0.02 | 0.41 ± 0.04 | 0.76 ± 0.03 | 1.08 ± 0.03 | 226.69 *** |
| **Total Nitrogen (%)** | 0.06 ± 0.00 | 0.05 ± 0.01 | 0.09 ± 0.01 | 0.12 ± 0.01 | 15.15 *** |
| **C/N (%)** | 4.91 ± 0.46 | 8.45 ± 1.42 | 8.62 ± 0.77 | 9.37 ± 0.63 | 4.92 * |
| **Calcium carbonate (CaCO$_3$)** | 55.90 ± 2.58 | 25.40 ± 1.16 | 44.75 ± 0.79 | 18.00 ± 0.52 | 136.56 *** |
| **Available Phosphorus (mg kg$^{-1}$)** | 16.20 ± 0.97 | 16.12 ± 0.51 | 13.60 ± 0.87 | 5.70 ± 0.54 | 43.62 *** |
| **Calcium (mg kg$^{-1}$)** | 2441.60 ± 23.52 | 2271.20 ± 387.80 | 2619.20 ± 10.91 | 1641.60 ± 5.15 | 4.80 * |
| **Magnesium (mg kg$^{-1}$)** | 132.80 ± 4.27 | 148.00 ± 8.49 | 113.60 ± 7.76 | 198.40 ± 4.83 | 52.31 *** |
| **Available Potassium (mg kg$^{-1}$)** | 261.20 ± 3.92 | 227.80 ± 12.23 | 273.40 ± 4.61 | 251.80 ± 0.97 | 8.77 ** |
| **Clay (%)** | 12.60 ± 0.93 | 6.80 ± 1.20 | 20.00 ± 0.95 | 9.20 ± 0.20 | 401.57 *** |
| **Sand (%)** | 51.20 ± 2.27 | 75.20 ± 1.50 | 35.00 ± 1.73 | 45.80 ± 0.80 | 221.87 *** |
| **Silt (%)** | 36.20 ± 1.91 | 18.00 ± 0.89 | 45.00 ± 1.14 | 45.00 ± 0.63 | 105.54 *** |

**Appendix D**

Results of the GLMs with edaphic soil variables on lichen and plant species richness, diversity, evenness, and total cover at subplot level (n = 125 per location).

|  |  | Richness |  | Diversity |  | Evenness |  | Total Cover |  |
|---|---|---|---|---|---|---|---|---|---|
|  | Df | Chisq | P | F | P | F | P | F | P |
| **Lichen** |  |  |  |  |  |  |  |  |  |
| *Artemisia sieberi* | 1 | 0.48 | 0.48 | 0.31 | 0.59 | 0.02 | 0.88 | 0.78 | 0.40 |
| **pH** | 1 | 0.05 | 0.81 | 0.05 | 0.82 | 0.17 | 0.69 | 0.21 | 0.66 |
| **Total Nitrogen** | 1 | 0.07 | 0.79 | 1.04 | 0.33 | 1.18 | 0.30 | 1.71 | 0.22 |
| **C/N** | 1 | 0.58 | 0.44 | 0.02 | 0.89 | 0.47 | 0.51 | 0.13 | 0.72 |
| **Clay** | 1 | 0.33 | 0.56 | 3.20 | 0.10 | 3.39 | *0.09* | 0.29 | 0.61 |
| **Silt** | 1 | 0.10 | 0.75 | 0.67 | 0.43 | 3.63 | *0.08* | 0.29 | 0.60 |
| **Available Phosphorus** | 1 | 1.59 | 0.20 | 0.85 | 0.37 | 0.29 | 0.60 | 0.74 | 0.41 |
| **Calcium** | 1 | 1.22 | 0.26 | 0.05 | 0.82 | 1.42 | 0.26 | 0.18 | 0.67 |
| **Magnesium** | 1 | 0.26 | 0.60 | 1.90 | 0.20 | 5.91 | **0.03** | 0.12 | 0.73 |
| **Available Potassium** | 1 | 1.98 | 0.15 | 2.39 | 0.15 | 0.02 | 0.89 | 0.16 | 0.69 |
| **Annual plants** |  |  |  |  |  |  |  |  |  |
| **pH** | 1 | 0.10 | 0.74 | 0.21 | 0.65 | 1.97 | 0.19 | 3.07 | 0.11 |
| **Total Nitrogen** | 1 | 0.71 | 0.39 | 0.54 | 0.48 | 0.05 | 0.82 | 0.16 | 0.69 |
| **C/N** | 1 | 0.33 | 0.56 | 1.21 | 0.29 | 0.05 | 0.82 | 1.38 | 0.26 |
| **Clay** | 1 | 0.46 | 0.49 | 0.00 | 0.99 | 0.01 | 0.92 | 7.52 | **0.02** |
| **Silt** | 1 | 0.32 | 0.57 | 0.04 | 0.84 | 0.22 | 0.64 | 3.44 | *0.09* |
| **Available Phosphorus** | 1 | 0.12 | 0.73 | 0.06 | 0.81 | 0.00 | 0.98 | 0.10 | 0.76 |
| **Calcium** | 1 | 0.00 | 0.98 | 0.19 | 0.66 | 0.06 | 0.81 | 0.92 | 0.36 |
| **Magnesium** | 1 | 0.00 | 0.98 | 0.21 | 0.65 | 0.18 | 0.67 | 2.45 | 0.14 |
| **Available Potassium** | 1 | 0.38 | 0.53 | 0.30 | 0.59 | 0.14 | 0.71 | 0.10 | 0.76 |

**Appendix E**

Results of the Principal Components Analysis for the edaphic variables. Scores of the variables in the first three main axes are shown.

| Soil variables | PCA1 | PCA2 | PCA3 |
|---|---|---|---|
| **pH** | 0.47 | 0.05 | 0.02 |
| **Total Nitrogen** | -0.4 | 0.21 | 0.32 |
| **C/N** | -0.22 | -0.03 | -0.88 |
| **Clay** | 0.07 | 0.57 | -0.27 |
| **Silt** | -0.27 | 0.48 | 0.12 |
| **Available Phosphorus** | 0.46 | -0.02 | 0.07 |
| **Calcium** | 0.35 | 0.19 | -0.18 |
| **Magnesium** | -0.41 | -0.27 | -0.02 |
| **Available Potassium** | -0.06 | 0.53 | 0.05 |

## Appendix F

Results of the Mantel analyses for annual and lichen species compositions at the plot level (50 cm x 50 cm). R: Mantel coefficient of correlation.

| Location | Plot | R | p |
|---|---|---|---|
| Almeh valley | 1 | 0.07 | 0.26 |
| | 2 | 0.36 | **0.04** |
| | 3 | 0.08 | 0.16 |
| | 4 | -0.35 | 0.85 |
| | 5 | 0.02 | 0.44 |
| Bagh valley | 1 | -0.19 | 0.99 |
| | 2 | -0.15 | 0.87 |
| | 3 | 0.20 | **0.03** |
| | 4 | -0.09 | 0.82 |
| | 5 | 0.01 | 0.45 |
| Alikhani | 1 | 0.37 | 0.06 |
| | 2 | 0.73 | **0.02** |
| | 3 | 0.40 | 0.13 |
| | 4 | 0.71 | **0.04** |
| | 5 | 0.18 | 0.19 |
| Alagol | 1 | -0.10 | 0.77 |
| | 2 | -0.12 | 0.88 |
| | 3 | -0.12 | 0.88 |
| | 4 | 0.06 | 0.29 |
| | 5 | 0.17 | 0.08 |

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