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Combining different species in restoration is not always the right decision: monocultures can provide higher ecological functions than intercropping in a desert ecosystem

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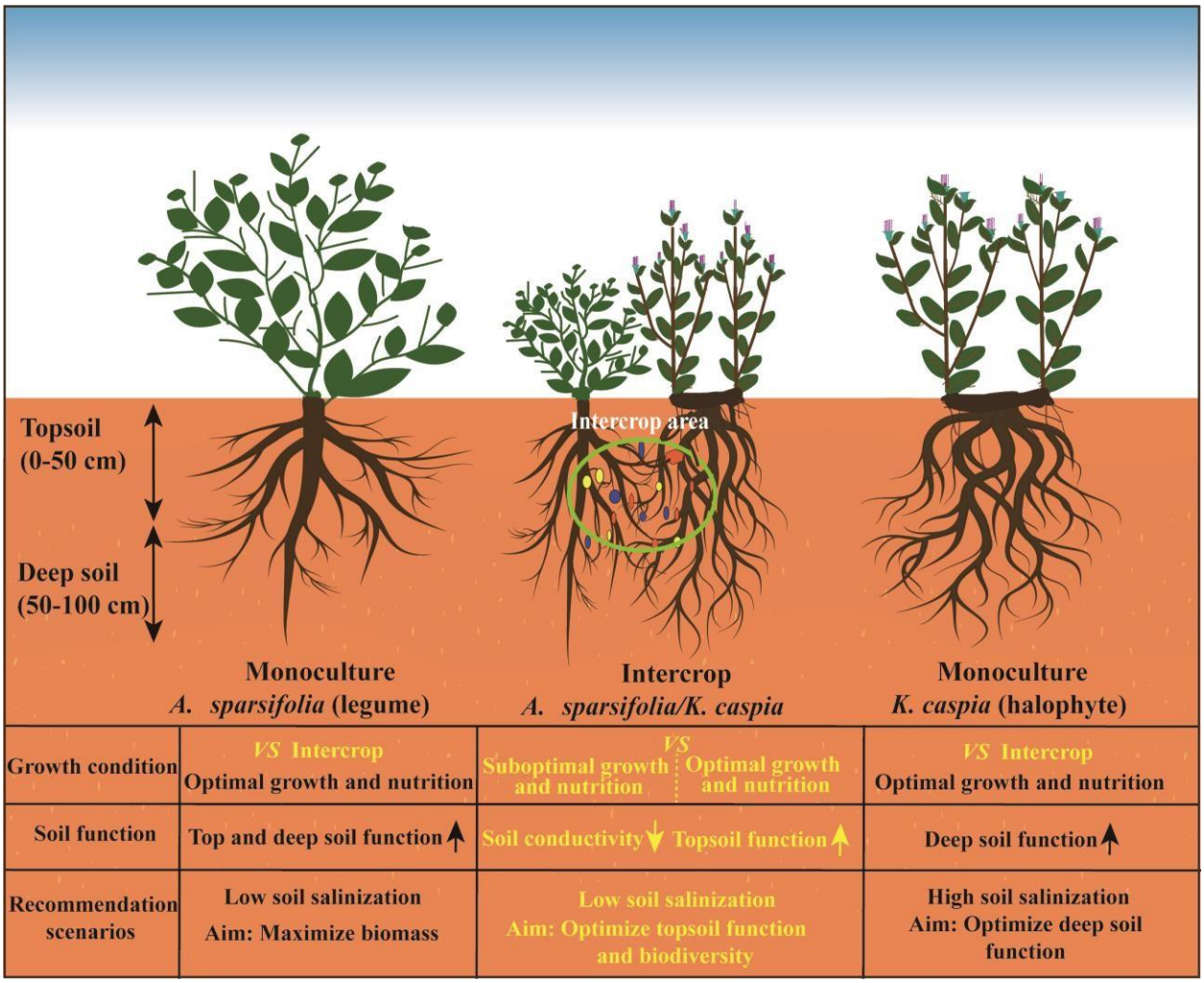
Graphical Abstract



Highlights

- Intercropping affects phreatophytic legumes and halophytes differently.
- Legume monoculture yields high biomass and ecological functions.
- Intercropping lowers soil conductivity and enhances topsoil functions.
- Monoculture of halophytes improves deep soil functions.
- Species selection should be optimized based on desired outcomes.

Combining different species in restoration is not always the right decision: monocultures can provide higher ecological functions than intercropping in a desert ecosystem

Abstract

Vegetation restoration in deserts is challenging due to these ecosystems' inherent fragility and harsh environmental conditions. One approach for active restoration involves planting native species, which can accelerate the recovery of ecosystem functions. To ensure the effectiveness of this process, carefully selecting species for planting is crucial. Generally, it is expected that a more diverse mix of species in the plantation will lead to the recovery of a greater number of ecosystem functions, especially when the selected species have complementary niche traits that facilitate maximum cooperation and minimize competition among them. In this study, we evaluated the planting of two native species from the hyper-desert of Taklamakan, China, which exhibit marked morpho-physiological differences: a phreatophytic legume (*Alhagi sparsifolia*) and a halophytic non-legume (*Karelinia caspia*). These species were grown in both monoculture and intercrop communities. Monoculture of the legume resulted in the highest biomass accumulation. Intercropping improved several ecosystem functions in the 50cm-upper soil, particularly those related to phosphorus (P), carbon (C), and sulfur (S) concentrations, as well as soil enzyme activities. However, it also increased soil sodium (Na^+) concentration and pH. Halophyte monocultures enhanced ecological functions associated with nitrogen concentrations in the upper soil and with P, S, C, and cation concentrations (K^+, Ca^{2+}, Mg^{2+}, Cu^{2+}, Fe^{2+}, Zn^{2+}, Co^{2+}, Ni^{2+}), along with enzyme activities in the deep soil. It also maximized Na^+ accumulation in plant biomass. In summary, we recommend legume monoculture when the primary goal is to optimize biomass accumulation. Conversely, halophyte monoculture is advisable when the objective is to extract sodium from the soil or enhance ecosystem functions in the deep soil. Intercropping the two species is recommended to maximize the ecosystem functions of the upper soil, provided there is no salinization risk. When planning restoration efforts in desert regions, it is essential to understand the impact of each species on ecosystem function and how complementary species behave when intercropped. However, these interactions are likely species- and system- specific, highlighting the need for more work to optimize solutions for different arid ecosystems.

Key words: Desert ecosystems, intercropping systems, ecological functions, restoration practices

1. Introduction

Drylands, which encompass almost 41% of the Earth's surface and are home to 38% of the global population, hold significant socio-economic and scientific importance (Tariq et al., 2022c; Zhang et al., 2022). Nonetheless, compared to other ecosystems, these regions have received less attention regarding management and sustainability efforts (Spinoni et al., 2021; Zhang et al., 2023; Tariq et al., 2024). Drylands face vulnerability from climate change and human activities, impacting their structure, phenology, productivity, growth, diversity, and coverage (Wei et al., 2021; Lian et al., 2021). Therefore, it is imperative to enhance research practices for sustainable management, enhance productivity, and preserve diversity in these ecosystems to prepare for future climate challenges.

Desertification poses a significant global threat in arid and semi-arid regions, leading to ecological and socio-economic issues. It results in soil and nutrient degradation, reducing land productivity and ecosystem service provision (He and Dijkstra, 2014; Sardans et al., 2017a; Sardans et al., 2017b). This, in turn, impacts desert plant species' composition, survival, and productivity (Sardans et al., 2021). Nutrients and carbon (C) play essential roles in soil biology, correlating positively with plant nutrient supply, water-holding capacity, and resistance to soil compaction and erosion (Cong et al., 2014). Consequently, understanding the plant-soil nutrient status is crucial for desertification control and effective management of regional water resources and soil in arid lands (Zhang et al., 2020; Gao et al., 2022ab; Tariq et al., 2022a). The arid desert environment's low soil moisture content significantly hinders nutrient mobility, uptake, and C sequestration, limiting net primary productivity (Lal, 2019). Furthermore, desert regions contend with salinity issues due to elevated sodium (Na) and electrical conductivity (EC), which impede plant productivity by hindering water and nutrient uptake (Tariq et al., 2022c). Unsustainable agriculture, inadequate management, overexploitation, frequent wildfires, and climate fluctuations further contribute to the substantial degradation of desert ecosystems (Feng and Fu, 2017). Hence, active restoration practices are indispensable for promoting recovery and restoring ecological functions in desert regions (Galaviz et al., 2018).

Intercropping, a sustainable agricultural practice widely employed in developing countries, enhances crop productivity. Complementarity and facilitation processes among intercropped species primarily contribute to improved soil fertility, soil enzyme activity, nutrient and C accumulation, and biomass production (Solanki et al., 2019). Intercropping with a mixture of leguminous and non-leguminous crops is favored sustainable agriculture as it reduces competition for the same niche and provides diverse strategies for acquiring nitrogen (Zang et al., 2018; Wang et al., 2019). Previous studies have indicated that intercropping efficiently utilizes soil nutrients compared to monoculture plant communities, resulting in higher biomass yield, improved nitrogen recovery, and fewer adverse environmental effects (Luo et al., 2016). While intercropping has been extensively studied, most of the existing knowledge, particularly regarding plant-soil nutrient cycling, pertains to agroecosystems. There remains limited understanding of the combined effects of different indigenous plant species, particularly leguminous and non-leguminous, on nutrient cycling and ecological restoration in desert ecosystems.

Different coexisting plant species in a specific region can experience varying degrees of competition among themselves and facilitate each other through niche complementation (Li et al., 2007). For example, one species may fix atmospheric nitrogen (N) or release enzymes like phosphatases in the soil, benefiting other speciesin nutrient uptake (Xue et al., 2016). In desert ecosystems, phreatophytes are vital role in lifting groundwater to upper soil horizons, facilitating neighboring species with shallow root systems (Tariq et al., 2022b). Planting species with complementary root systems can reduce competition and enhance resource acquisition.

Ecosystem multifunctionality (EMF) has gained attention in recent years as it refers to the ability of ecosystems to perform multiple functions such as soil nutrient storage and cycling, C sequestration, and more efficient resource utilization (Meyer et al., 2018; Migliavacca et al., 2021). EMF encompasses a range of biological, geochemical, and physical processes (Manning et al., 2018). When multifunctionality metrics focus solely on ecosystem functions (rather than ecosystem services), they measure an ecosystem's overall performance and are termed EMF. When restoring an ecosystem, the highest EMF is sought after, as functions restored through active restoration should catalyze the recovery of other functions. Therefore, planting multiple species in degraded ecosystems is desirable as greater biodiversity is likely to be more resilient in the face of environmental change and provide higher ecosystem functionality (Chase et al., 2020). In this context, meadows restored through reseeding in communities with higher biodiversity displayed elevated EMF levels (Tian et al., 2023).

Soil microbial diversity is crucial for maintaining ecosystem multifunctionality by supporting processes such as litter decomposition and organic matter mineralization. These processes facilitate the transfer of matter and energy between above- and below-ground biological communities and are critical for ecosystem functioning (Delgado-Baquerizo et al., 2016). Research has demonstrated that biodiversity enhances multifunctionality in dryland environments (Maestre et al., 2012). However, limited literature exists regarding desert ecosystems with lowspecies diversity. Therefore, evaluating soil EMF performance is vital to enhance our comprehension of the effectsof desert plant intercropping on nutrient cycling, C sequestration, and soil health.

Alhagi sparsifolia, a leguminous species, is a practical ecological engineer in combating desertification in Central and Eastern Asia, primarily found in Xinjiang, Gansu, Qinghai provinces, and Inner Mongolia in China. It is a phreatophyte, with a high root:crown ratio, small or distorted branches and a root systems which directly reaches downward to a depth of several meters (possibly over 10 m) to reach groundwater (Gui et al, 2013). However, the root elongation decreases when soil water content (SWC) rises, and the water table is shallow, thus developing lateral roots and tillers, leading to increased aboveground coverage (Zeng et al., 2012; Gui et al., 2013; Tariq et al., 2024). *A. sparsifolia* serves various ecological functions, including lifting groundwater and nutrients to upper soil horizons through its deep root system and facilitating resource acquisition by neighboring plant species (Tariq et al., 2022c). Conversely, *Karelinia caspia*, a non-leguminous halophyte species, possesses a relatively shallower root system than *A. sparsifolia* and grows across Central Asia, Russia, and Northwest China. It employs distinct strategies to tolerate drought and salinity, contributing significantly to desertification mitigation (Gao et al., 2022b).

Besides ecological importance, these species are also used as forage for livestock in some regions and provide economic benefits to residents (Li et al., 2021; Wet et al., 2021; Tariq et al., 2022b). Combining an N-fixing phreatophyte like *A. sparsifolia* with a salinity-tolerant species like *K. caspia*, which has differing root architecture, can yield complementary results through niche differentiation and resource complementarity (Barry et al., 2019). In natural ecosystems, the root system of intercrop appears as *K. caspia* root system entangling *A. sparsifolia*, which may be attributed to *A. sparsifolia*'s ability to lift water from deeper soil or groundwater. Tariq et al. (2022b) suggested that intercropping these two species may not facilitate phosphorus (P) mineralization but provides low EC,improved water uptake, and enhanced microbial N-use efficiency, offering long-term advantages. Enhancing soil nutritional conditions and mitigating soil salinization can effectively bolster the resistance and resilience of native shrub communities in desert ecosystems against increasing aridity. Therefore, this study addresses critical questions:
1) Can intercropping enhance the N nutrition of the studied species? 2) Will soil EC be lower in intercrop systems than monocultures, and can intercropping alleviate soil salinization in the longer term? 3) Does intercropping enhance ecological functions and soil EMF in the desert ecosystem relative to monocultures? This research will provide vital information to guide restoration practices in desert ecosystems using indigenous vegetation to combat degradation.

2. Materials and Methods

2.1 Study Sites and Experimental Design

The research was conducted at the Cele National Station of Observation and Research for Desert-Grassland Ecosystems (80°43'45" E, 37°00'57" N) on the southern edge of the Taklamakan Desert in China's Xinjiang Province. This region experiences a hyper-arid climate characterized by an average annual precipitation of 35 mm, an average yearly potential evaporation of 2600 mm, and a mean annual temperature of 11.9°C (Gui et al., 2013).

From July 2017 to September 2018, we established and cultivated monocultures of *A. sparsifolia* and *K. caspia*, as well as intercropped plots under field conditions. *A. sparsifolia* plants were grown from seeds, whereas *K. caspia* was established from tubers. *A. sparsifolia* reproduces sexually via seeds, while *K. caspia* reproduces asexually from tubers due to the low germination rate of their seeds. To accommodate the differences in growth rates associated with these two reproductive modes, we planted *K. caspia* tubers one year after planting *A. sparsifolia* seedlings. Specifically, we collected *A. sparsifolia* seeds from the natural desert area located 1 km away from the experimental plots and sowed them in seedling cups. Once the seedlings had reached a similar size, we transplanted them into the experimental plots. The *K. caspia* plants were cultivated in the plots from tuberous roots excavated from the nearby desert area in March 2018.

Using a block design, we organized these two species into three community structures: monocultures of *A. sparsifolia* and *K. caspia* and an intercropped system (see Figure S1). Each community structure was replicated five times. The plots were 4 meters in length and 2 meters in width. The distance between individual plants in each plot was maintained at 0.5 meters, while the separation between two plots was set at 1 meter. During the establishment

stage, we buried plastic sheets up to 1.5m depth around each plot to avoid any possible below-ground influence of plants. All plots received consistent field management and sufficient irrigation during the growing season (from April to September) before 2020. This was done to ensure plant establishment. After establishment, all plants grew under natural conditions (i.e., rain-fed only), except for weed removal.

2.2 Plant and soil sampling

In August 2022, we collected leaves, stems, and root samples from three plots randomly taken from the five replications by selecting plants representative of the average plant size of each treatment, approximately 90 cm in height (Table 1). Within each plot, we sampled three individual plants and mixed equal weight of each organ for making composite samples, gathering three samples of each plant part (leaves, stem, and roots) for each plant species (*A. sparsifolia* and *K. caspia*) for each community (monoculture and intercrop), resulting in 3 organs × 2 species × 2 communities × 3 replicates; n=36. We cut the stems using scissors and manually separated the leaves from the branches. We removed the top 50 cm of soil to expose the roots and collected root samples. To prepare composite samples for chemical analysis, we included equal weights of each plant from each plot.

To collect soil samples, we first removed the litter layer and then utilized a soil auger to randomly collect three bulk soil core samples from both the upper soil (0–50 cm) and deep soil (50–100 cm) horizons in each plot, hereafter referred to as topsoil and deep soil, respectively. This process yielded 18 soil samples (3 treatments × 3 replicates × 2 soil horizons) collected from monoculture and intercrop settings. We carefully stored the plant and soil samples in separate ziplock bags and transported them to the laboratory, maintaining a low temperature (4-8°C). Samples were in the field for no longer than one hour.

The fresh leaf, stem, and root samples were divided into two subsamples: one was stored at -80°C to determine non-structural carbohydrates, and the other was dried at 60°C to determine other plant traits. We sieved the fresh soil using 2-mm screens to remove stones and roots. Subsequently, we further divided it into three subsamples for the assessment of enzyme activities: microbial biomass C (MBC), N (MBN), and P (MBP), soil properties, and soil moisture content.

2.3 Plant traits determination

After undergoing digestion in concentrated sulfuric acid (H_2SO_4), the concentrations of N and P in the leaf, stem, and root were determined using a Kjeldahl Nitrogen Analyzer (K1160, Jinan Hanon Instruments Co. Ltd., China) and an inductively coupled plasma optical emission spectrometer (iCAP 6300, Thermo Elemental, USA), respectively. The concentrations of potassium (K^+), calcium (Ca^{2+}), sulfur (S), magnesium (Mg^{2+}), copper (Cu^{2+}), zinc (Zn^{2+}), cobalt (Co^{2+}), nickel (Ni^{2+}), iron (Fe^{2+}), and sodium (Na^+) in the samples of leaf, stem, and root material were assessed after soaking overnight in nitric acid (HNO_3) and HF–HNO_3–H_2O_2. An inductively coupled plasma optical emission spectrometer (iCAP 6300, Thermo Elemental, USA) was used to test the samples. Nitrate (NO_3^-) was determined from 0.2g of frozen plant material from each part using 5 mL of deionized water. Ammonium (NH_4^+)

concentration was determined from 0.2 g of frozen leaf material that was homogenized in 2 mL of 10% HCl, with the supernatants being analyzed using a quantitative colorimetric method (Tang, 1999). The concentrations of soluble sugar and sucrose in 2 g samples of each plant part were determined by the anthrone and 3,5-dinitrosalicylic acid methods (Zhang et al., 2003) using a glucose solution as a standard. The starch concentration was determined by the anthrone-H_2SO_4 method (Liu et al., 2014).

Before harvesting, we measured the height of plants grown in monoculture and intercropping. We collected all the shoots (leaves and stems) from each plant to calculate the aboveground biomass of the plots. Using the shoot concentrations of N, P, and K^+, we calculated the total amount of these chemicals stored in the aboveground biomass by multiplying the concentration by the biomass of each plant.

2.4 Soil bio-physicochemical properties

The soil pH was determined using a Delta pH meter in a soil-to-water ratio of 1:2.5. Soil relative water content (SRWC) was determined as the difference between water weights at sampling with oven-dry soil weight (weight of water at sampling), divided the difference between water-saturated soil weight minus oven dry soil weight (total amount of water that the soil can retain). For the measurement of electrical conductivity (EC), a soil-to-water ratio of 1:5 (w/v) was used along with an EC meter (DDSJ-319L, INESA Scientific Instrument Co. Ltd., China). The concentration of soil microbial biomass C (MBC), N (MBN), and P (MBP) was determined using the chloroform fumigation-extraction method as described by Turner et al. (2014). Soil total N (TN) concentrations were determined using micro-Kjeldahl digestion (KDN-102C, Shanghai, China), whereas soil total P (TP) concentrations were determined using molybdenum blue colorimetric analysis with a visible spectrophotometer (UV-1200, Shanghai, China), after Na_2CO_3 oxidation. Soil total K^+ (TK) concentrations were determined using a flame photometer (FP6400A, Shanghai, China) after Na_2CO_3 oxidation, as described by Yang et al. (2008). Soil-available phosphorus (AP) was extracted using 0.5 mol/L Na_2CO_3 solution at pH 8.5. The concentration was determined in the same way as for total phosphorus (TP). Soil-available potassium (AK) concentrations were determined from extracts of 1 mol/L ammonium acetate (NH_4Ac) solution at pH 7.0 using flame photometry (FP640: INASA).

Concentrations of trace elements including Ca^{2+}, S, Mg^{2+}, Cu^{2+}, Zn^{2+}, Co^{2+}, Ni^{2+}, Fe^{2+}, and Na^+ were determined using Inductively Coupled Plasma Mass Spectrometry (ICP-MS) (PerkinElmer, SCIEX ELAN-9000; PerkinElmer SCIEX, Concord, ON, Canada) from the clear solutions.

According to the methods developed by Jones and Willett (2006), chemical extracts were used to measure the concentrations of total dissolved N (TDN), ammonium-N (NH^+-N), and nitrate-N (NO^--N) in soil samples. Fresh, field-moist soil samples (not sieved) were extracted with 2 M KCl. The TDN, NH +-N, and NO –N concentrations were determined using a Quickchem Automated Ion Analyzer (Lachat Instruments, WI, USA). The dissolved organic N (DON) was calculated by subtracting the NH +-N and NO −-N concentrations from the TDN concentration. Soil-dissolved organic carbon (DOC) was determined using a TOC/TDN analyzer (Shimadzu 5000, Japan). Soil moisture was determined by drying for 48 hours at 105°C. The concentration of soil alkali-hydrolyzable

N (AH-N) was determined using the method of Roberts et al. (2011). In this method, 5-gram soil samples were distilled with 2 mol L^{-1} NaOH for five hours and then with 10 mol L^{-1} NaOH for 7 minutes. Boric acid (40 g L^{-1}) was used to absorb the liberated NH_3. The soil alkali-hydrolyzable N concentration was quantified by conductometric titration.

To measure the soil organic C (SOC), we used the dichromate oxidation method, as described by Mebius in 1960. We also determined the easily oxidizable organic C (EOC) using the method described by Xu et al. (2021). For the EOC determination, we added 2 g of soil into a 50 ml centrifuge tube, added 25 ml of 0.333 M $KMnO_4$ solution, and shook it for one hour at 180 r min^{-1}. We then centrifuged the solution for 5 min at 5000 r min^{-1} and diluted 1 ml of the supernatant by 250 times. Finally, we determined the absorbance at 565 nm.

2.5 Determination of soil enzymes

The activity of soil N-acetyl-β-glucosaminidase (NAG) was determined by measuring the rate of release of 4-methylumbelli-ferone (MU) from the MU-labeled fluorescent substrate (4-MU-N-acetyl-β-glucosaminidase) (Marx et al., 2001) and expressed as nmol MU g soil $^{-1}$ h^{-1}. Dehydrogenase and polyphenol oxidase activities were measured in the soil and expressed in units of enzyme activity (U) according to the description by Guan et al. (1986). One unit of dehydrogenase or polyphenol oxidase was defined as the amount of enzyme that catalyzed the formation of 1 μg of 1,3,5-triphenyl formazan (TTF) and 1 mg of gallic acid per gram of soil per minute (1 U = 1 TTF μg/(g·h) for dehydrogenase and 1 U = 1 gallic acid mg/(g·h) for polyphenol oxidase, respectively). Urease (EC 3.5.1.5) activity was determined by following the protocol outlined by Alef and Nannipieri (1995) based on incubating substrate samples with urea solution. Alkaline phosphatase (ALP) and β-glucosidase activity were determined according to the methods outlined by Tabata-bai and Bremner (1969) and Eivazi and Tabatabai (1988), respectively. Peroxidase activity (EC 1.11.1.7) was measured using 3,3′,5,5′ tetramethylbenzidine (TMB) as a substrate (Johnsen and Jacobsen, 2008). Protease assays were carried out to determine the amount of tyrosine released when the soil was incubated with sodium caseinate and 0.1 M Tris (hydroxymethyl) amino methane buffer (pH 8.1) at 50 °C for 2 hours. The method used was described by Zubair et al. (2021). The reaction was stopped by adding trichloroacetic acid (TCA) solution, and the amount of tyrosine released was determined using the Folin–Ciocalteu reagent. Protease activity was expressed as μg tyrosine g−1 soil h^{-1}. Sucrase activity was determined by measuring the glucose concentration after incubating with sucrose as a substrate for 24 hours at 37 °C (Guan, 1986). Amylase activity was determined by measuring the amount of glucose produced during hydrolysis and by colorimetry, according to Zhou (1987).

2.6 Statistical analysis

Plant height and dry matter were analyzed by general linear mixed models (GLMM), with community and species as fixed factors and block as a random factor. Concentrations of N, P, K^+, Ca^{2+}, NO_3^-, NH_4^+, soluble sugars, starch, and Na^+ concentration were analyzed separately for each organ (leaf, stem, and root) by GLMM with community and species as fixed factors and block as a random factor. Shoot concentrations of N, P, and K^+ were analyzed by GLMM with community and species as fixed factors and block as a random factor. The VarIdent function was used to consider the different variances between species. In all cases, means were compared by the Bonferroni test ($p<0.05$).

The relationship between EC and nutrients was performed by Principal Component Analysis (PCA) with the variables EC, pH, SOC, NO_3^-, available-P, S, and the concentration of macro and micronutrients in the topsoil and deep soil of the monocultures and the intercrop. The cations included were Na^+, Mg^{2+}, Ca^{2+}, and available-K^+, Fe^{2+}, Cu^{2+}, Co^{2+}, Zn^{2+}, and Ni^+. Additionally, we performed a PCA to analyze the relationship of EC with soil microbial data including enzyme activities, including the following variables: protease, peroxidase, urease, S- amylase, M-amylase, sucrose, APase, glucosidase, DHase, NAGase, PPOase, MBN, MBP, MBC, and EC. Further, we analyzed the relationship of EC with pH, N, and C soil forms, including the following variables: DTN, DON, DOC, pH, SRWC, AH-N, SOC, EO-OC, and EC. In all PCAs, variables were standardized, and Euclidean distance was used.

The variables that better explain EC were chosen by forward stepwise regression, with a p-value to include and remove lower than 0.05. The 27 variables included were DTN, DON, protease, urease, NAGase, NO_3-N, DOC, glucosidase, peroxidase, PPOase, DHase, M-amylase, S-amylase, sucrase, SRWC, EO-OC, TN, TP, SOC, AH-N, APase, AvP, S, pH, MBC, MBN, MBP. All the cation concentrations were excluded, as they directly affect EC.

Soil EC, urease, AH-N, and DOC were analyzed by GLMM considering soil depth (top or deep soil) and the community (*A. sparsifolia*, *K. caspia*, or intercrop) as fixed effects and block as random effects. The interaction soil depth * community was included, and the means of each combination were compared by Bonferroni post-hoc test ($p<0.05$).

To calculate soil ecological multifunctionality (EMF), we divided the variables into groups related to N, P, C, and S, enzyme activities, and cations. We calculated EMF separately for the top and deep soil, as the effects differed in each layer. Each EMF was calculated as the mean of the standardized variables for each plot. N-EMF included DTN, DON, NAG, urease, NO3 − -N, NH4+-N, TN, AH-N, and MBN. P-EMF included PPOase, TP, Apase, AvP, and MBP. ENZ-EMF included protease, urease, glucosidase, peroxidase, PPOase, DHase, M-amylase, S- amylase, NAG, and APase. CAT-EMF included Ca^{2+}, Mg^{2+}, Cu^{2+}, Fe^{2+}, Zn^{2+}, Co^{2+}, and Ni^{2+}. CS-EMF included C and S. We considered three single functions as they are relevant to understanding the effect of the intercrop, and lower values of these variables are better for plants in this desert ecosystem: EC, pH, and Na. All the EMF and EC, pH, and Na^+ were analyzed by PCA, one for the topsoil and the other for the deep soil. Variables were standardized, and Euclidean distance was used. We also performed an analysis of variance (ANOVA) to compare each EMF, considering each monocrop and intercrop as the main factor. Means were compared by Bonferroni post-hoc test ($p<0.05$).

3. Results

3.1 Aboveground biomass

The aboveground dry mass of *A. sparsifolia* was greater in monoculture than in intercrop, primarily due to higher leaf and stem dry mass. *K. caspia* exhibited a similar aboveground dry mass in both communities (Table 1), although it had a lower leaf dry mass. It's important to note that *A. sparsifolia* plant height was slightly greater in theintercrop than in monoculture, while the opposite trend was observed in *K. caspia*.

3.2 Concentrations of N, P, K^+, and Ca^{2+} in plant organs

N and K^+ concentrations in leaves, stems, and roots were higher in *A. sparsifolia* in monoculture than in intercrop, but P and Ca^{2+}

concentrations were greater in the intercrop than in the monoculture. Conversely, *K. caspia* exhibited higher N and K^{2+} concentrations in leaves, stems, and roots in the intercrop compared to the monoculture, while P and Ca^{2+} concentrations were lower. In general, when one species showed lower concentrations in the intercrop compared to the monoculture, the other species exhibited increased concentrations in the intercrop (Figure 1).

3.3 Concentration of nitrate, ammonium, soluble sugars, and starch in plant organs

Leaf concentrations of NO3− and NH4+ were higher in A. sparsifolia in monoculture than in intercrop, while soluble sugar concentrations were lower in monoculture than in intercrop. In contrast, roots had higher concentrations of soluble sugars and starch in the intercrop than in A. sparsifolia monoculture (Fig. 2). In K. caspia, NO3− and NH4+ concentrations in leaves, stems, and roots were lower in the intercrop compared to monoculture. However, soluble sugars and starch concentrations in leaves and stems were higher, while those in roots were lower in the intercrop (Fig. 2).

3.4 Plant-soil nutrient relationship

The content of N, P, and K^+ in shoots (leaves and stems) of both species (i.e., concentration multiplied by dry mass) did not directly correlate with soil nutrient concentration (Figure 3). The soil nutrient content differed between the intercrop and the monocultures. *A. sparsifolia* had higher N, P, and K^+ content in the monoculture than in the intercrop despite the higher concentration of these nutrients in the intercrop's topsoil. However, the content of N, P, and K^+ in the deep soil was higher in the intercrop than in the monoculture of *A. sparsifolia.* The lower nutrient content in *A. sparsifolia* is associated with lower nutrient concentration in the tissues and reduced dry mass accumulation. For *K. caspia*, N content in plant tissues was higher in the intercrop than in monoculture, consistent with the increase in topsoil N concentration. However, P and K^+ content in *K. caspia* tissues did not show a straightforward relationship with soil nutrient concentration.

3.5 Cations exchange and electric conductivity in monocrop and intercrop soils

EC exhibited the opposite pattern of cations, as observed in the PCA (Fig. 4). EC negatively correlated with SOC, pH, Fe2+, Na+, available-K+, Ca2+, and Mg2+ concentrations. Micronutrients such as Ni2+, Zn2+, Co2+, and Cu2+ concentrations explained the most variability along the second axis (Table S2). Consequently, the topsoil of the intercrop had the lowest EC and the highest cation concentrations. In contrast, the topsoil of K. caspia monoculture had the highest EC and the lowest cation concentrations. A. sparsifolia had similar EC and cation concentrations in the topsoil and deep soil. In contrast, K. caspia and intercrop topsoil differed from the deep soil, with opposing trends in each community. The intercrop had the highest SOC in the top and deep soil, while K. caspia monoculture had the lowest SOC in the topsoil and A. sparsifolia had the lowest SOC in the deep soil (Fig. 4); Protease and DTN showed a positive correlation with EC, while most variables related with N and the soil enzymes exhibited a negative correlation or no significant correlation with EC (Figs. S2 and S3).

3.6 Urease, DOC, and AH-N in monocrop

Among the 27 variables analyzed, the three variables that best explained EC were urease (positively correlated) and DOC and AH-N (negatively correlated) (EC = 479 + 210 urease – 2 DOC - 29 AH-N; R2 adj 0.86; $p < 0.0001$) (Table S3). Thus, lower EC values were found in plots with lower urease activity and higher DOC and/or AH-N. We present the results of each of those three variables to compare communities. Urease concentration was the highest in K. caspia monoculture and the lowest in A. sparsifolia monoculture, with the deep soil exhibiting a higher concentration than the topsoil (Fig. 5). DOC and AH-N were higher in the intercrop than in the monocultures (Fig. 5).

3.7 Plant-soil Na + relationship in monocrop and intercrop

Intercropping had higher concentrations of sodium in both the top and deep soils than monocultures. However, the relationship between soil sodium concentration and plant tissue concentration varied: A. sparsifolia had higher sodium concentrations in leaves, stems, and roots in the intercropping than in the monoculture, while the opposite trend was observed with K. caspia (Fig. 6).

3.8 Ecological Multifunctionality in monoculture and intercrop

The topsoil of the intercrop exhibited high ecological multifunctionality (EMF) in functions related to P, C, and S, cations, and enzymes, which correlated negatively with EC. However, two negative functions (Na^+ and pH) were high in the intercrop (Figure 7 and Table S5). The EMF related to N did not show any significant correlation with EC or pH but was higher in the intercrop and *K. caspia* monoculture than in *A. sparsifolia* monoculture. Although pH and Na^+ concentrations were higher in the intercrop's deep soil, the EMF related to N was also higher. However, the EMF associated with C and S, cations, P, and enzymes was greater in *K. caspia* monoculture than in the intercrop, while *A. sparsifolia* monoculture exhibited medium or low EMFs in the topsoil and deep soil.

4. Discussion

Plant dry mass accumulation reflects the plant's ability to sequester carbon. Despite the taller plant height 59 397 in K. caspia monoculture was significantly higher than that in A. sparsifolia monoculture and intercrop. However, in intercropped plots, plants had lower shoot size than those in monoculture plots. In contrast, *K. caspia* was slightly shorter in the intercrop than in the monoculture, but shoot weights were similar in both communities. Moreover, in K. *caspia*, the intercrop facilitated N assimilation in leaves, leading to a decrease in inorganic N and lower C accumulation in roots. These results suggest that the presence of *K. caspia* negatively impacted *A. sparsifolia*. In general, when interspecific competition is relieved by pairing larger plants with smaller ones, one would expect better performance from the larger plants (Maclaren et al., 2023). In this case, however, an unexpected outcome occurred, suggesting that *K. caspia* influenced the soil conditions in a manner detrimental to *A. sparsifolia*. This mayinclude competing more effectively for nutrient uptake in the topsoil despite the presence of a nitrogen-fixing species that should have provided benefits (Tariq et al., 2022b; Gao et al., 2023). *K. caspia* can accumulate more nutrients in the intercrop soil due to its higher fine root activity and respiration rate than *A. sparsifolia* (Liu et al., 2016). The availability of nutrients such as P, Mo, Mn, and Fe is altered by pH (Marschner, 1995) and soil structure,water movement, and aeration (Arya et al., 1995). These changes in soil structure due to pH fluctuations can create stressful conditions for plants, affecting their root development, water uptake, and overall growth and survival. However, caution is needed, as other pairs of species may have had somewhat different outcomes, highlighting the need for consideration of species ecology and ecophysiology in developing these approaches (Yang et al., 2016; Nanand Guo, 2018).

In this site, intercropping had a negative impact on the phosphorus (P) and nitrogen (N) nutrition of *A. sparsifolia* (Tariq et al., 2022b). Four years later, the biogeochemical dynamics in the soil continued, and it was observed that the N, P, and potassium (K) nutrition of *A. sparsifolia* was still negatively affected in the intercrop. Additionally, $NO3^-$ and NH4 + accumulated in A. sparsifolia leaves, and soluble sugars and starch were lower in A. sparsifolia in the intercrop than in the monoculture. This implies that the N metabolism of *A. sparsifolia* leaves was reduced in the intercrop, leading to the accumulation of inorganic N and C primarily in the roots. Therefore, more N and C accumulation in *A. sparsifolia* root may result in higher SOC concentration in the intercrop than in the monoculture. In addition, the SOC concentration of *A. sparsifolia* monoculture was higher than that of *K. caspia* monoculture, which may be attributed to the higher litter decomposition rate associated with legumes than that of non-legume (Hassan et al., 2012; Liao et al., 2020). Furthermore, the concentration of all macro and micronutrient cations was higher in the intercrop than in the monocultures. Surprisingly, in *A. sparsifolia* plants, the smaller plant size and lower leaf and stem nutrient concentrations resulted in lower N, P, and K^+ contents aboveground in the intercrop than in the monoculture. Interestingly, the total N, available P, and K^+ in the soil of the intercrop soils was higher than in *A. sparsifolia* monoculture. It is evident that the higher nutrient concentration in the intercrop did not result in increased plant growth or higher nutrient accumulation. Therefore, the impairment in *A. sparsifolia*nutrition and growth could not be attributed to nutrient availability in the soil. We will develop an explanation of this result in the following sections.

The upper soil layer in the intercrop had lower EC than the soil in both monocultures. This result was unexpected, especially given the high concentration of cations in the intercrop. It might be related to the fact that *K. caspia* belongs to perennial halophytes (Guo et al., 2022). As the results of this study indicated, the EC of upper soil

in K. caspia monoculture was significantly higher than that in A. sparsifolia monoculture and intercrop. H However, compared to the soil condition of K. caspia monoculture, deep-rooted A. sparsifolia could lift more water from deeper soil or groundwater to the upper soil in intercrop, and this water would leach some salts from the upper soil to deep soil to a certain extent (Gao et al., 2023). In addition, among all the variables related to soil biological activity, urease, dissolved organic carbon (DOC), and ammonium nitrogen (AH-N) concentrations in this desert ecosystem were most closely related to EC. This underscores the importance of microbial activity in plant-soil interactions. Reduced EC in intercrop upper soil led to an increase in DOC and AH-N, which is attributed to the negative response of soil microbial activity and litter decomposition to soil EC (Kohl et al., 2023). AH-N is mainly linked to organic nitrogen, which is available for microbial mineralization (Dodor et al., 2022). Therefore, EC is higher when soil urease activity is high and mineralizable organic nitrogen and DOC are low. However, the most likely reason for the reduction in EC in the intercrop was not low urease activity but higher DOC and AH-N levels, which have a high capacity to adsorb cations, consequently reducing free cations in the soil solution (Jardine et al., 1989). Notably, urease activity was higher in K. caspia than in A. sparsifolia monoculture, with the intercrop showing intermediate values. Interestingly, the intercrop's upper soil layer had higher DOC and AH-N than any monoculture. Consequently, by increasing carbon in the upper layer, EC can be reduced due to the soil's enhanced capacity to adsorb cations. Moreover, in the intercrop, where soil pH was higher and EC was lower in the upper layer, soil ion exchange capacity would be occupied mainly by cations in a soil medium with low H+ concentration, thereby reducing potential EC. When evaluating the concentrations of all cations, the intercrop's upper soil layer had higher total cation amounts, but these cations were more fixed and less mobile. This observation aligns with previous research demonstrating the relationship between high pH and low EC due partly to soil colloid adsorption capacity and microbial cation consumption (Su et al., 2023). Consequently, the soil's cation exchange capacity allows for high cation concentrations despite low EC.

The higher concentration of cations does not account for the lower growth of A. sparsifolia in the intercrop compared to the monoculture. However, the increased availability of sodium (Na+) likely explains the drop in A. sparsifolia's nutrition and growth. A high concentration of Na+ in the soil leads to various soil effects, such as the loss of aggregation. In this hyper-arid area with nearly sandy soil, the impact of sodicity on soil aggregation is limited (Oster and Shainberg, 2001). In the intercrop, Na+ concentration in the soil was much higher than in any monoculture, resulting in significantly higher Na + accumulation in A. sparsifolia tissues in the intercrop compared to the monoculture, which can effectively account for lower plant growth and altered nutrition (Rubio et al., 2020). Surprisingly, K. caspia tissues had lower Na + concentration and soil content despite the higher soil Na+ concentration in the intercrop. Some halophytes can exclude Na+ at the root-soil interface and/or leaves to avoid high tissue concentrations when growing in saline soils (Munir et al., 2022; Kohl et al., 2023). Therefore, K. caspia excludes Na+ from the soil in the intercrop, where soil Na+ concentration is higher than in the monoculture, improving N and K+ concentrations in leaves, stems, and roots. Moreover, K. caspia showed higher soluble sugars and starch concentrations in leaves and stems, indicating better mineral nutrition and carbon assimilation in the intercrop than in the monoculture. Therefore, while the growth of K. caspia may not have been higher in the intercrop compared to the monoculture, its plant nutrition was enhanced.

Evidently, no direct positive relationships existed between nutrient availability, uptake, and plant growth. This experiment underscores the importance of adopting an integrative perspective when examining plant-soil systems. Ecological multifunctionality (EMF) is a valuable tool for analyzing these systems comprehensively and assessing the advantages of intercropping (Ma et al., 2022). However, there are trade-offs between the number of variables included in EMF analysis and their applicability to other ecosystems (Manning et al., 2018). Moreover, apparent differences in EMF were observed between the topsoil and deep soil layers. In general, the intercrop increased EMF in the topsoil, but *K. caspia* monoculture exhibited greater EMF regarding N in the topsoil and other nutrients in the deep soil. It is challenging to find a few variables that can describe plant-soil interactions (Zheng et al., 2023). Soil organic matter, total nitrogen, and microbial biomass are frequently used as indicators of soil degradation, as they are closely linked to ecological functions such as decomposition and mineralization (Ferreira et al., 2016). Consistently, in degraded soils, these chemical variables change more in the topsoil than in deeper soil layers. However, when comparing the intercrop and monocultures, these variables exhibited different change directions in the topsoil and deep soil. Therefore, evaluating various soil and plant variables at different soil depthsis essential to conclude the advantages of intercropping over monocultures in restoring ecological functions.

4.1 Implication of the results to desert ecosystem restoration

It is crucial to consider vital ecological functions, including water conservation, soil erosion control, wind and sand control, biodiversity maintenance, flood regulation, protection of designated areas, and connectivity (Liu et al., 2023). These ecological functions are related to food provision, refuges, soil stability, or nutrient biogeochemical cycling (Table S6). It is essential to prioritize plant biomass accumulation and nutritional quality to enhance the trophic network, as plants form the base of food webs (Tariq et al., 2024). Plant biomass is critical for desert ecosystem restoration because it catalyzes various ecological functions, including reducing sandstorms, providing food for animals and microbes, buffering harsh environmental conditions, and potentially lifting deep water (Fei et al., 2022). However, grazing can decrease plant biomass, reduce topsoil nitrogen concentration, and significantly impact nitrogen cycling in desert ecosystems (Li et al., 2022). Therefore, communities should be evaluated with the presence of animals, as preferential legume grazing can alter community composition. Thus, different species shouldbe selected based on the probable grazing pressure, and to increase the resilience of these communities to various forms of change.

To increase diversity of animals and plants, intercropping may be preferable due to the different canopy strata and taller plants. Furthermore, such communities generally have higher resilience to disease and climatic changes and thus may be more stable in the longer term. The presence of multiple canopy strata creates a range of microenvironments that accommodate more diverse flora and fauna, enhancing the survival of species in the harsh desert environment, especially during the early stages when they are more vulnerable to environmental stress (Copeland et al., 2023). However, if the objective is to retain nutrients and reduce leaching, in that case, *A.sparsifolia* monoculture is a better choice, given its higher retention of N, P, and K+ in biomass than in the intercrop.

When improving the ecological functions of the soil is the goal, the intercrop is a better choice, as most EMFs SOC were higher in the intercrop's topsoil. However, if the enhancement of deep soil EMF is needed, *K. caspia* monoculture stimulates deep soil EMF more than the intercrop.

In addition, *K. caspia* monoculture has low pH and SOC content, so its use in restoration should consider the current soil conditions and the risk of soil salinization. Furthermore, pH and SOC affect community biodiversity in the Taklamakan desert (Shi et al., 2022), so long-term assessments of monocultures and intercropping are essential since ecological functions are closely linked to successional changes (Zheng et al., 2023). Therefore, when restoring desert ecosystems, it is crucial to assess the specific goals and prioritize the ecological functions that need to be restored. The choice between monoculture and intercropping depends on these specific objectives and the current soil conditions in the restoration area.

Conclusions

The intercropping of the halophyte *K. caspia* and the legume *A. sparsifolia* had varying effects on their nutrition and growth. The intercrop led to an increase in sodium concentration in both the soil and *A. sparsifolia* tissues, which might explain the suboptimal growth and nutrition of the legume. However, the halophyte was able totolerate the salinity and benefited from the nutrients released by the legume. The intercrop had a positive impact on various ecological functions related to most nutrients in the topsoil. However, in the deep soil, only the functions related to nitrogen were enhanced in the intercrop, while all other favorable functions were more prominent in the *K.caspia* monoculture.

This experiment underscores the significance of conducting comprehensive evaluations of the effects of monocultures and intercrops, considering multiple functions, including the deep soil. When implementing an active restoration program, it is vital to consider these findings when selecting the appropriate plant species for restoration, taking into account the chemical condition of degraded soil and the specific ecosystem functions that need to be prioritized for restoration. Moreover, there is a dire need to evaluate long-term effects of the introduced species on the desert ecosystem, exploring additional plant species combinations, and investigating the impact of restoration efforts on local wildlife. To obtain more concrete and practically applicable recommendations for ecologicalrestoration, new long-term experiments testing a more extensive range of environments and a larger number of species are necessary. Whilst it is clear that intercropping and the planting of multiple species with different traits can help in restoration as well as more sustainable agriculture, the impacts of these species also varies across different timescales. Further work is needed to better understand these nuances, and refine our approaches to restoration and agriculture within arid ecosystems.

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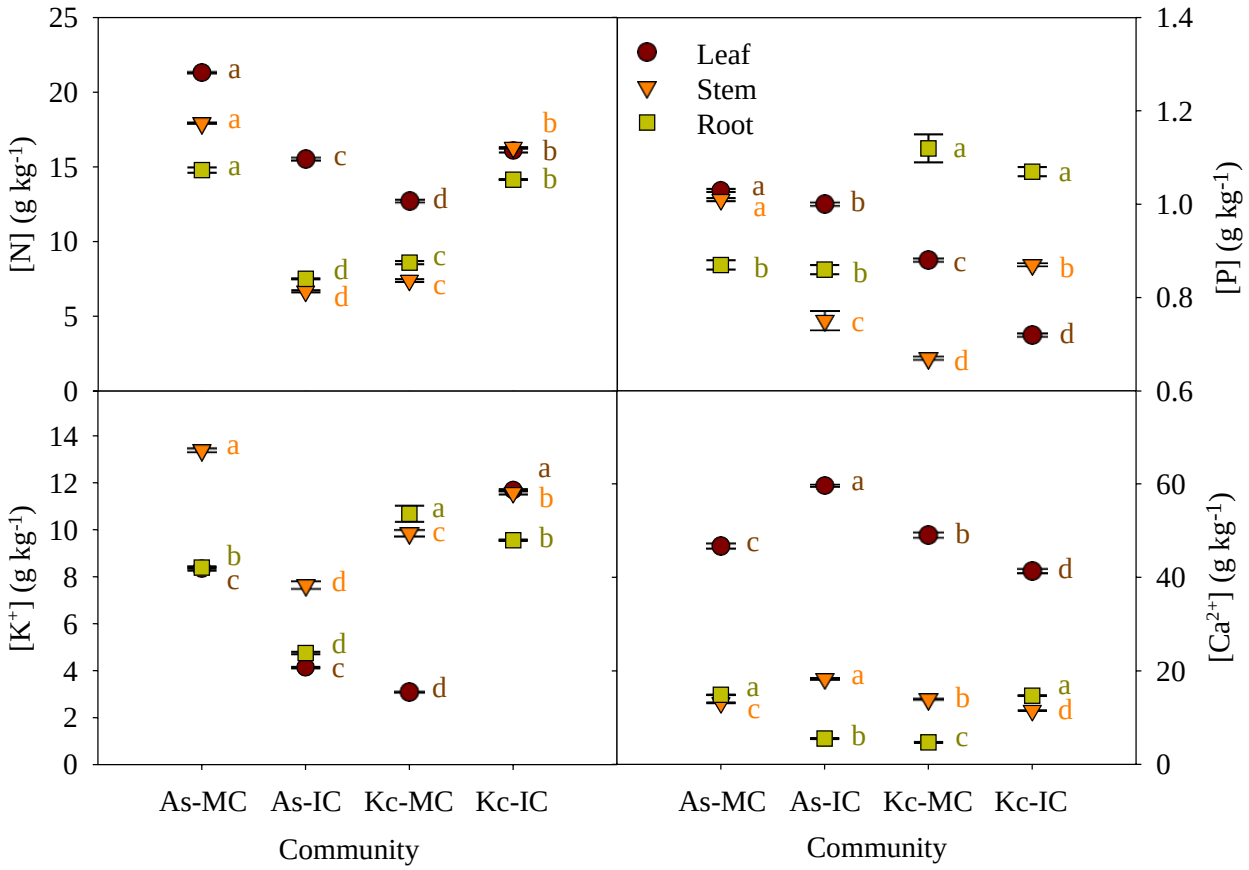

Figure 1: Concentration of N, P, K^+ and Ca^{2+} in leaves, stems and roots of *Alhagi sparsifolia* (As) and *Karelinia caspia* (Kc) in monoculture (MC) and intercrop (IC). Different letters indicate significant differences between species and communities for each organ. Bars in the symbols indicate standard errors. P-values for each organ and nutrient are reported in Table S1.

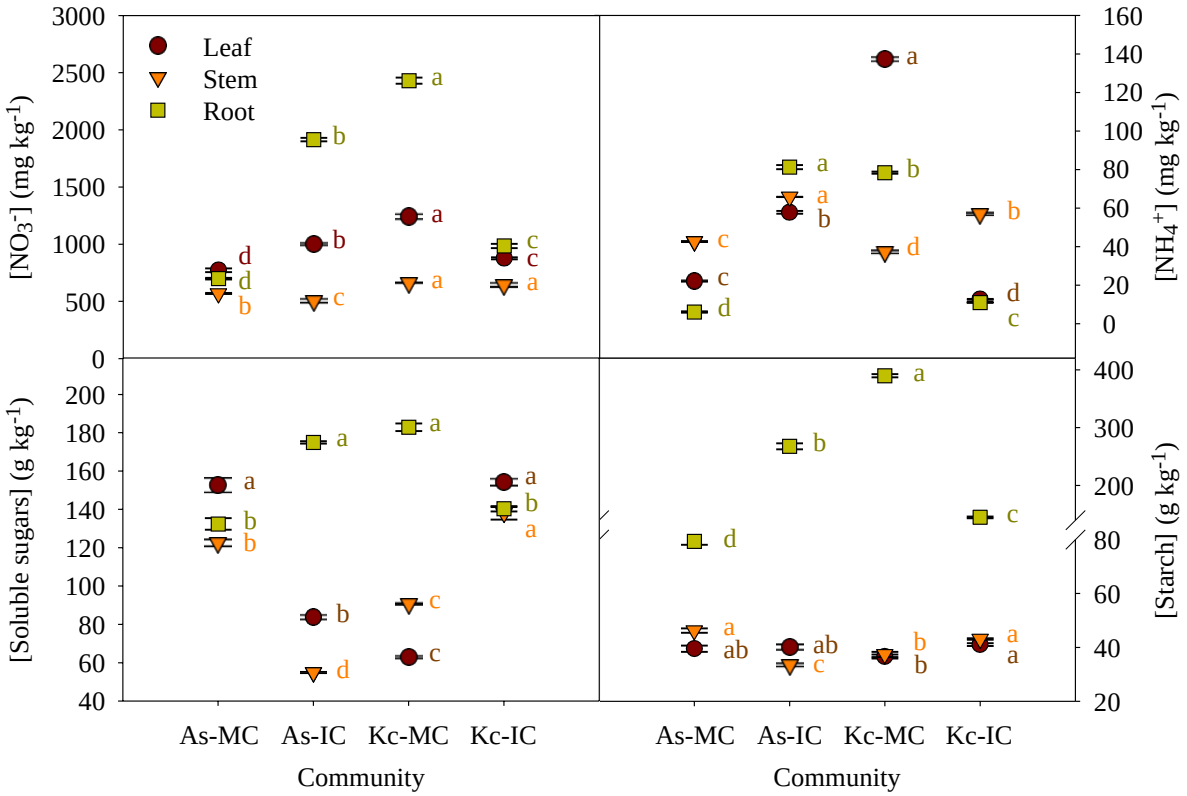

Figure 2. Concentration of nitrate (NO_3^-), ammonium (NH_4^+), soluble sugars and starch in leaves, stems and roots of *Alhagi sparsifolia* (As) and *Karelinia caspia* (Kc) in monoculture (MC) and intercrop (IC). Different letters indicate significant differences between species and communities for each organ. Bars in the symbols indicate standard errors. P- values for each organ and concentration are reported in Table S1.

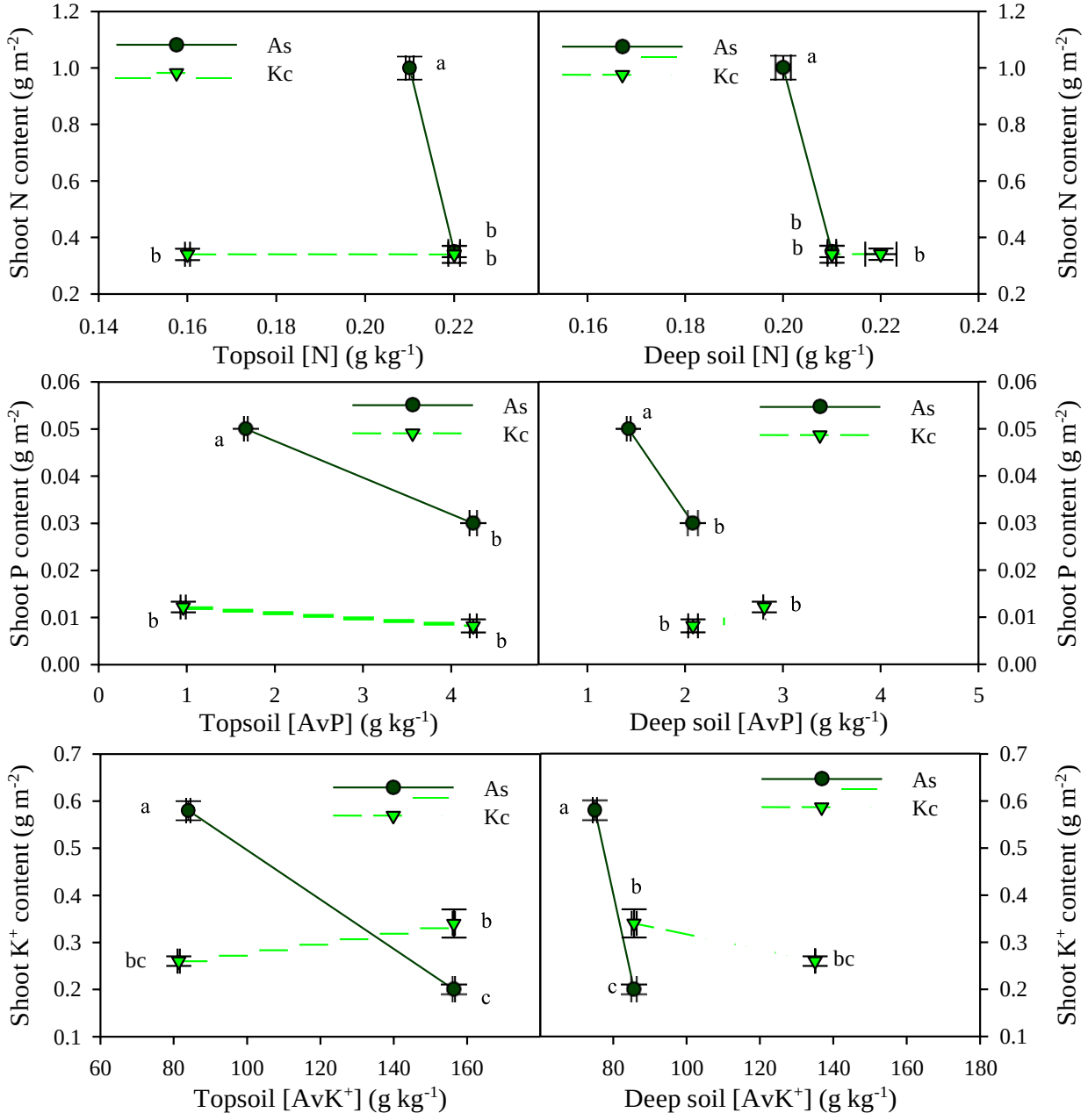

Figure 3: Plant-soil nutrient relationship: N, P and K^+ content (g m^{-2}) in shoots (leaves + stems) of *Alhagi sparsifolia* (As) and *Karelinia caspia* (Kc) in monoculture and intercrop in relation with the concentration of N, P and K^+ in the topsoil and deep soil. Different letters indicate significant differences in nutrient contents ($p<0.05$).

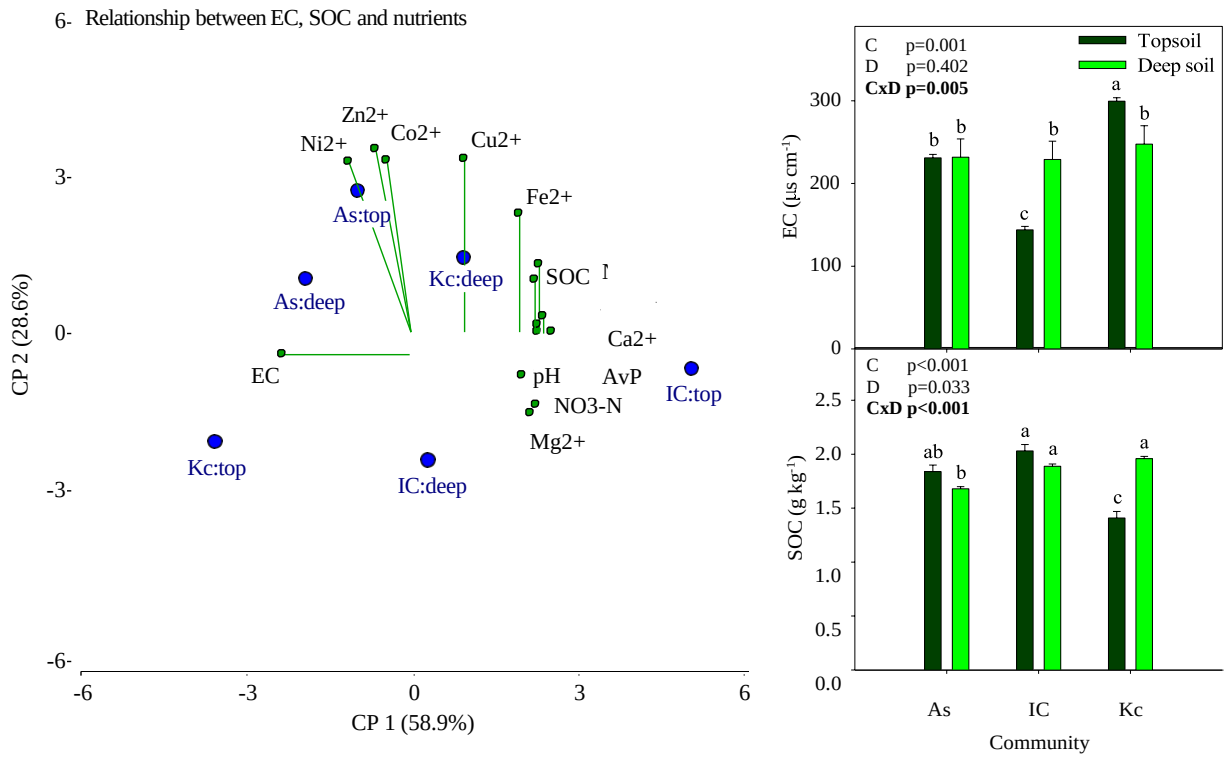

Figure 4: On the left, principal component analysis (PCA) considering EC, SOC, all the cations analyzed, available P (AvP), nitrate (NO3-N) and S. Autovectors are reports in Table S2. On the right, soil electric conductivity (EC) (µs cm^{-1}) and soil organic carbon (SOC) (g kg^{-1}) measured in the topsoil (0-50cm) and in the deep soil (50-100 cm) in themonocultures of *Alhagi sparsifolia* (As) and *Karelinia caspia* (Kc) and in the intercrop of both species (IC). The p-values ofthe ANOVA are shown in the insert, C: community, D: soil depth, CxD: interaction between community and soil depth. Differences considered significant (p<0.05) are in bold. Different letters above the bars indicate significant differences.

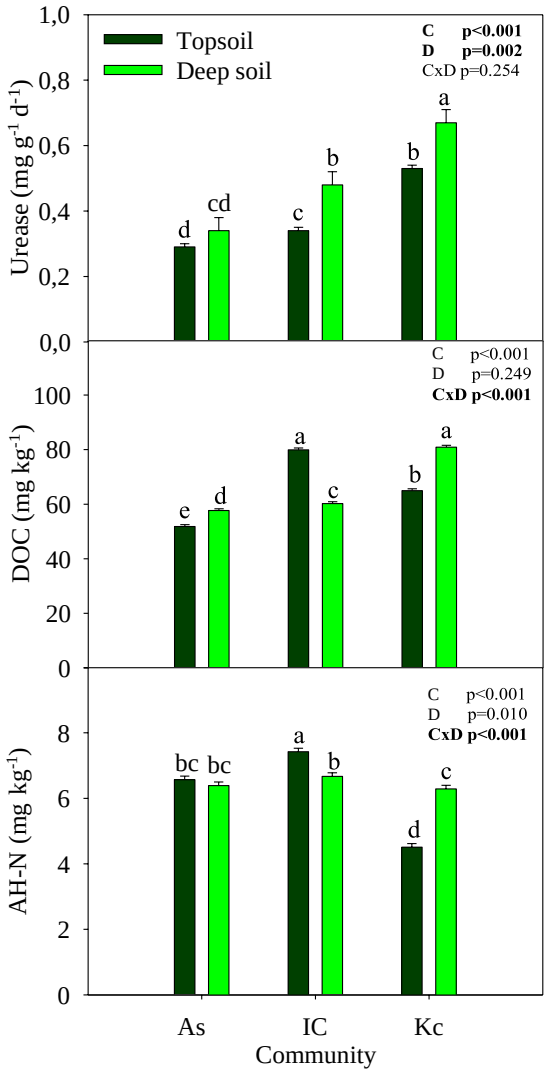

Figure 5: Urease, dissolved organic carbon (DOC), and alkaline hydrolyzable N (AH-N) concentrations in the topsoil (0-50cm) and in the deep soil (50-100 cm) in the monocultures of *Alhagi sparsifolia* (As) and *Karelinia caspia* (Kc) and in the intercrop of both species (IC). The p-values of the ANOVA are shown in the insert, C: community, D: soil depth, CxD: interaction between community and soil depth. Differences considered significant (p<0.05) are in bold. Different letters above the bars indicate significant differences.

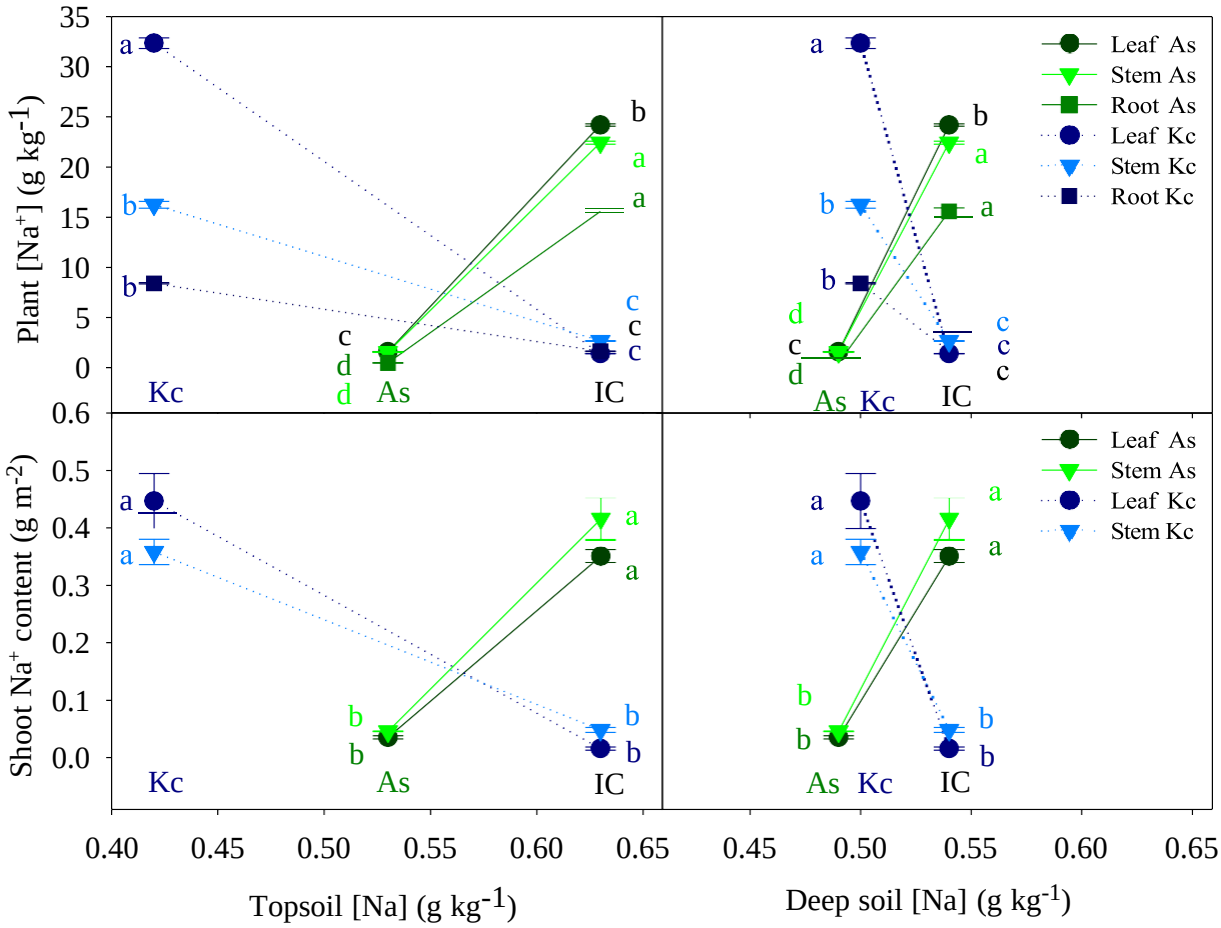

Figure 6: Leaf, stem and root Na concentration and stem and leaf Na^+ content in relation with the Na^+ concentration in the topsoil (0-50cm) and in the deep soil (50-100 cm) in monocultures of *Alhagi sparsifolia* (As) and *Karelinia caspia* (Kc) and in the intercrop of both species (IC).

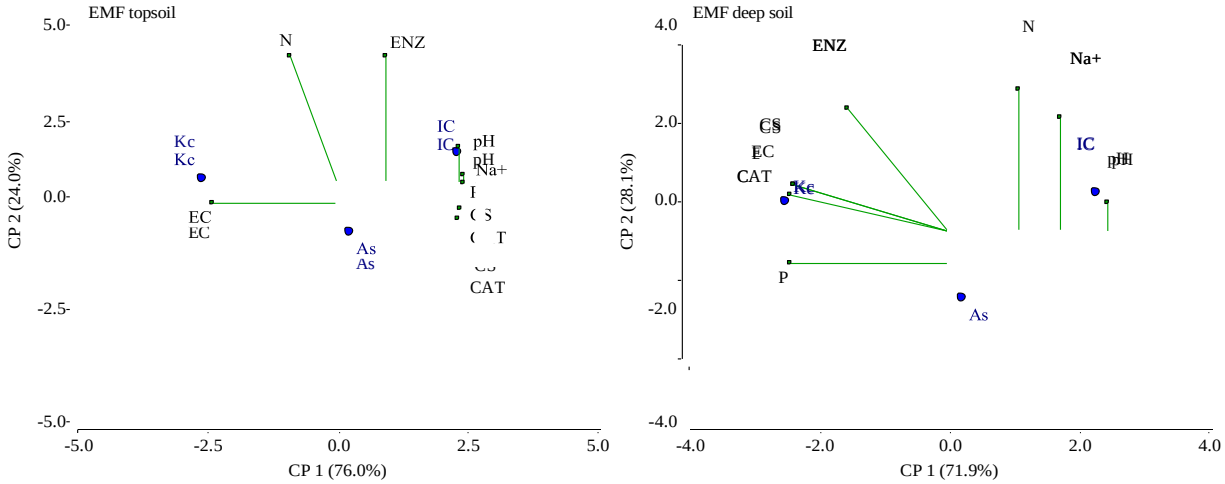

Figure 7: Soil ecological multifunctionality (EMF) in the top soil and deep soil of *Alhagi sparsifolia* monocultures (As), *Karelinia caspia* monoculture (Kc) and in the intercrop of both species (IC). EMF was calculated for N (DTN, DON, NAG, urease, NO_3^--N, NH_4^+-N, TN, AH-N, MBN), P (PPOase, TP, Apase, AvP, MBP), enzymes (ENZ: protease, urease, glucosidase, peroxidase, PPOase, DHase, M-amylase, S-amylase, NAG, APase), cations (CAT: K^+, Ca^{2+}, Mg^{2+}, Cu^{2+}, Fe^{2+}, Zn^{2+}, Co^{2+}, Ni^{2+}) and carbon and sulphur concentrations (CS). Three single functions were included: EC, pH and Na^+. Autovectors are reported in Table S4.

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Table 1: Plant height (H), leaf dry mass (Leaf DM), stem dry mass (Stem DM) and aboveground dry mass (AGDM) in *Alhagi sparsifolia* (As) and *Karelinia caspia* (Kc) planted in monoculture (MC) or in intercrop (IC). Means, standard errors (SE), and the p-values of the GLM for species (Sp), community (C) and the interaction Sp*C are reported. Different lowercase letters indicate significant different means among community species x community cases and differentcapital letters means differences between species (p<0.05).

C	Sp	H (cm)			Leaf DM (g/plant)			Stem DM (g/plant)			AGDM (g)		
		Mean	SE		Mean	SE		Mean	SE		Mean	SE	
MC	As	86	6	ab	74	6	A a	98	2	a	172	5	a
IC	As	96	4	a	48	2	b	62	6	b	110	6	b
MC	Kc	88	1	ab	46	4	B a	73	4	b	119	7	b
IC	Kc	79	4	b	38	6	b	60	5	b	98	8	b
p-value	Sp	0.968			**0.014**			0.001			0.001		
	C	0.107			**0.008**			0.016			0.003		
	Sp*C	**0.048**			0.125			**0.025**			**0.023**		

Supplementary materials

Table S1. Means, standard errors, and p-values of the GLMM with species (Sp: *Alhagi sparsifolia* (As) or *Karelinia caspia* (KC)) and community (C: monoculture (MC) or intercrop (IC)) as fix factors and the interaction Sp*C.

	Leaf		Stem		Root			Leaf	Stem	Root
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**			**p-value**	
N (g/kg)										
As-MC	21.32	0.05	17.9	0.04	14.79	0.18	**Sp**	<0.0001	0.0001	<0.0001
As-IC	15.55	0.09	6.68	0.07	7.51	0.03	**C**	<0.0001	0.081	0.0001
Kc-MC	12.70	9.00E-02	7.40	0.09	8.59	0.11	**Sp*C**	**<0.0001**	**<0.0001**	**<0.0001**
Kc-IC	16.10	0.13	16.3	0.03	14.15	0.03				
P (g/kg)										
As-MC	1.03	3.30E-03	1.01	3.30E-03	0.87	0.01	**Sp**	<0.0001	0.1772	0.0084
As-IC	1.00	3.30E-03	0.75	0.02	0.86	0.01	**C**	<0.0001	**<0.0001**	<0.0001
Kc-MC	0.88	3.30E-03	0.67	3.30E-03	1.12	0.03	**Sp*C**	**<0.0001**	0.228	**<0.0001**
Kc-IC	0.72	3.30E-03	0.87	3.30E-03	1.07	0.01				
K^+ (g/kg)										
As-MC	8.33	0.07	13.36	0.08	8.39	0.05	**Sp**	<0.0001	<0.0001	<0.0001
As-IC	4.13	0.03	7.61	0.15	4.75	0.05	**C**	<0.0001	<0.0001	0.0837
Kc-MC	3.08	2.00E-02	9.85	0.13	10.68	0.36	**Sp*C**	**<0.0001**	**0.0001**	**<0.0001**
Kc-IC	11.69	0.04	11.57	0.07	9.55	0.03				
Ca^{2+} (g/kg)										
As-MC	46.68	0.51	13.17	0.07	14.87	0.04	**Sp**	0.0003	0.0039	<0.0001
As-IC	59.61	0.24	18.28	0.2	5.51	0.1	**C**	<0.0001	0.0002	<0.0001
Kc-MC	49	0.53	13.92	0.12	4.7	0.1	**Sp*C**	**<0.0001**	**<0.0001**	**<0.0001**
Kc-IC	41.31	0.42	11.5	0.05	14.69	0.07				
NH_4^+ (mg/kg)								leaf	stem	root
As-MC	22.14	0.29	42.67	0.25	6.11	0.34	**Sp**	<0.0001	0.0002	<0.0001
As-IC	57.85	0.74	65.85	0.1	81.29	1.06	**C**	<0.0001	0.1402	<0.0001
Kc-MC	137.12	0.99	37.23	0.7	78.41	0.53	**Sp*C**	<0.0001	<0.0001	0.0056
Kc-IC	12.71	0.18	56.86	0.58	11.03	0.16				
NO_3^- (mg/kg)										
As-MC	773.53	15.74	569.77	4.56	699.48	7.51	**Sp**	0.0011	0.0003	0.0056
As-IC	999.09	9.67	504.47	15.05	1914.5	15.25	**C**	<0.0001	<0.0001	<0.0001
Kc-MC	1241.3	1.88E+01	660.5	2.19	2430.58	27.5	**Sp*C**	<0.0001	<0.0001	0.0708
Kc-IC	877.81	8.43	641.84	15.78	985.53	18.53				
Soluble Sugars (g/kg)										
As-MC	152.44	3.58	122.38	1.6	132.35	3.04	**Sp**	0.0006	0.9868	0.0006
As-IC	83.5	1.1	54.82	0.37	174.94	0.64	**C**	0.0017	0.0037	<0.0001
Kc-MC	62.68	0.61	90.54	0.41	182.84	1.97	**Sp*C**	<0.0001	<0.0001	<0.0001
Kc-IC	153.99	1.68	137.92	3.29	140.31	1.35				
Starch (g/kg)										
As-MC	39.49	1.17	46.2	0.81	79.29	1.23	**Sp**	0.0194	<0.0001	0.001
As-IC	40.21	0.95	33.42	0.53	267.69	5.22	**C**	0.2791	<0.0001	0.5564
Kc-MC	36.62	0.75	37.39	0.96	389.72	2.76	**Sp*C**	0.0694	<0.0001	<0.0001
Kc-IC	41.03	0.52	43.09	0.28	144.8	1.45				

Table S2: Autovectors of the PCA in Figure 4.

	Autovectors	
Variables	e1	e2
Ca^{2+}	0.30	0.01
Mg^{2+}	0.28	-0.20
Cu^{2+}	0.13	0.44
S	0.30	0.17
pH	0.26	-0.10
EC	-0.30	-0.05
Fe^{2+}	0.26	0.30
Na^{+}	0.31	0.04
Zn^{2+}	-0.08	0.46
Co^{2+}	-0.06	0.43
Ni^{2+}	-0.15	0.43
AvP	0.33	0.00
AvK^{+}	0.30	0.02
NO_3-N	0.29	-0.18
SOC	0.29	0.13

Table S3: Selection of soil chemical variables (excluding cations) that are most related with electric conductivity (EC).

Variable	N	R^2	R^2 Adj	SCEp	AIC	BIC
EC	18	0.88	0.86	623.72	164	168.45

Independent var:EC	Est.	p-value
const	478.89	<0.0001
AH-N	-29.08	0.0005
urease	209.62	0.0005
DOC	-2.39	0.0007

Table S4: Autovectors of EFM in top soil and deep soil (Figure 7)

	Autovectors of topsoil		Autovectors of deep soil	
Variables	**e1**	**e2**	**e1**	**e2**
pH	0.39	0.19	0.41	0.12
EC	-0.40	-0.11	-0.40	0.20
Na^+	0.41	0.04	0.29	0.48
N	-0.15	0.67	0.18	0.60
P	0.41	-0.01	-0.41	-0.14
ENZ	0.16	0.67	-0.26	0.52
CAT	0.39	-0.20	-0.41	0.15
CS	0.40	-0.15	-0.40	0.20

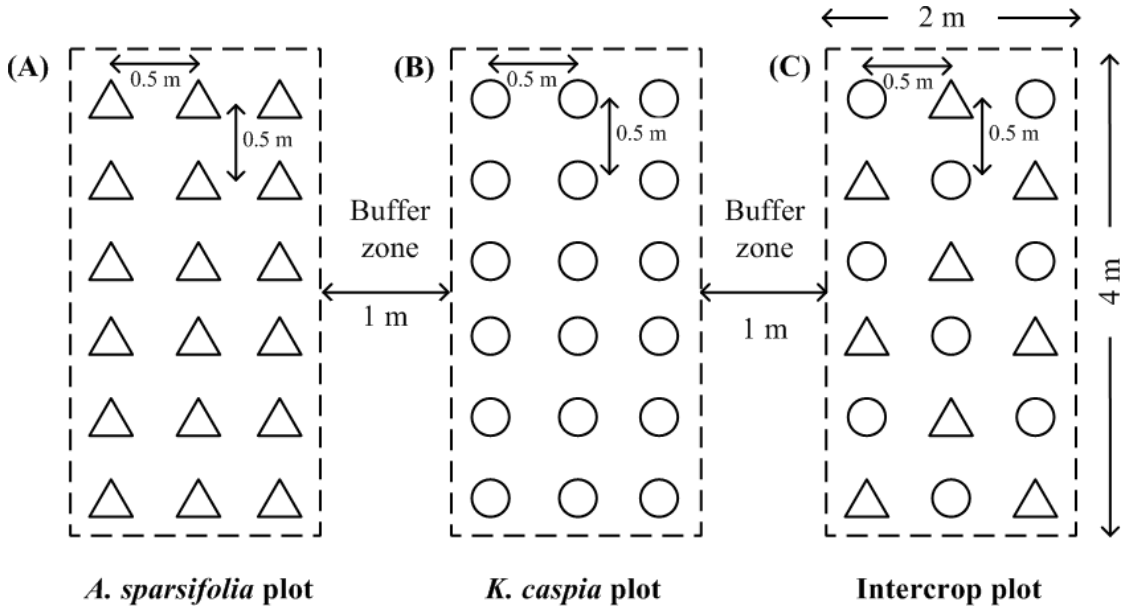
Table S5: Soil ecological multifunctionality (EMF) included in the PCA in Figure 7. *Alhagi sparsifolia* monoculture (As-MC), *Karelinia caspia* monoculture (Kc-MC) and the intercrop of both species (IC) were compared in the topsoil (top) and in the deep soil (deep). Mean and standard error (se) of each variable and the F and p-values of the ANOVA are shown. Different letters mean significant differences among communities for each EMF. The values in bold are the maximum EMF and the minimum single functions. In green we marked the worst values of single functions (the highest).

	As-MC			IC			Kc-MC				
	mean	se		mean	se		mean	se		F	p-value
Soil EMF (Higher better)											
N top	-0,3	0,1	b	0,1	0,0	a	**0,3**	**0,1**	**a**	21,9	0,0017
N deep	-0,5	0,2	c	**0,5**	**0,0**	**a**	0,0	0,1	b	29,1	0,0008
P top	0,1	0,1	b	**0,9**	**0,1**	**a**	-1,0	0,1	c	137,1	<0,0001
P deep	0,1	0,1	ab	-0,4	0,2	b	**0,4**	**0,0**	**a**	8,3	0,0186
CS top	0,3	0,1	b	**0,6**	**0,1**	**a**	-0,9	0,1	c	121,2	<0,0001
CS deep	-0,3	0,1	b	-0,5	0,1	b	**0,9**	**0,0**	**a**	71,5	0,0001
CAT top	**0,4**	**0,2**	**a**	0,3	0,2	a	-0,6	0,1	b	11	0,0099
CAT deep	-0,2	0,0	ab	-0,5	0,4	b	**0,7**	**0,1**	**a**	6,4	0,0325
ENZ top	-0,7	0,1	c	**0,7**	**0,0**	**a**	0,0	0,1	b	85,8	<0,0001
ENZ deep	-0,5	0,0	c	0,0	0,0	b	**0,5**	**0,1**	**a**	226,3	<0,0001
Single functions (Lower better)											
EC top	0,1	0,0	b	**-1,2**	**0,1**	**c**	1,1	0,0	a	362,1	<0,0001
EC deep	-0,1	0,3		-0,2	0,8		0,3	0,7		0,2	0,8174
pH top	-0,2	0,6		0,9	0,4		-0,7	0,4		3,2	0,112
pH deep	-0,1	0,9		0,6	0,2		-0,5	0,5		0,9	0,4464
Na^+ top	0,1	0,1	b	1,1	0,1	a	**-1,2**	**0,0**	**c**	267,1	<0,0001
Na^+ deep	**-0,8**	**0,1**	**b**	1,2	0,3	a	-0,4	0,4	b	14,8	0,0048

Table S6: Comparative synthesis of ecological functions in *Alhagi sparsifolia* monoculture (As-MC), *Karelinia caspia* monoculture (Kc-MC) and the intercrop of both species (IC). The ++, +, - signs represent the maximum, average and minimum values, respectively, while = represents no differences between communities of each function. We marked the community with the best level of each ecological function in bold green.

Ecological function	As-MC	IC	Kc-MC
Provision of refuges			
Canopy height	-	**+**	-
Number of strata	1	**2**	1
Provision of food for herbivores			
Biomass accumulation	**+**	-	-
Leaf N concentration	**++**	**+**	-
Leaf P concentration	**++**	+	-
Leaf K^+ concentration	+	-	**++**
Leaf Ca^{2+} concentration	+	**++**	-
Leaf soluble sugars concentration	**+**	-	**+**
Leaf starch concentration	=	=	=
Nutrient retention in aboveground plant biomass			
N	**++**	+	-
P	**+**	**+**	-
K^+	**+**	**+**	-
Na^+	-	**+**	**+**
Soil stability			
Soil EC topsoil	+	-	++
Soil EC deep soil	=	=	=
Soil Na^+ concentration topsoil	+	++	-
Soil Na^+ concentration deep soil	-	++	+
Soil EMF topsoil	+	**++**	-
Soil EMF deep soil	+	-	**++**

Fig. S1 Experimental design. Panels (A) and (B) show the monoculture plots of *A. sparsifolia* and *K. caspia*, respectively, and panel (C) shows their intercrop pattern. The triangle and circle represent the *A. sparsifolia* and *K. caspia*, respectively. These three plots were replicated five times, therefore we had 15 plots.



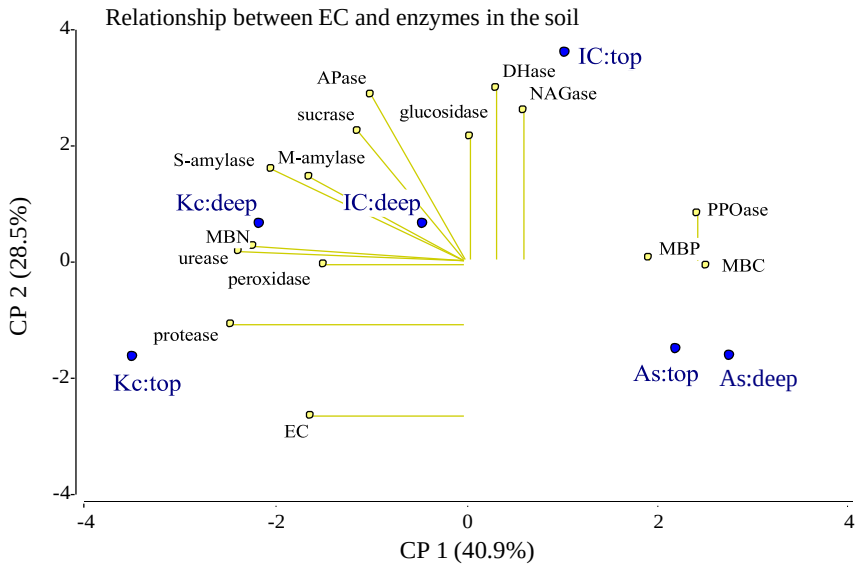


Figure S2: Relationship between electric conductivity (EC) and the enzymatic activity measured in the topsoil (upper 50 cm: 50cm) and in the deep soil (from 50 to 100 cm: 100cm) in the monocultures of *Alhagi sparsifolia* (As) and *Karelinia caspia* (Kc) and in the intercrop of both species (IC).

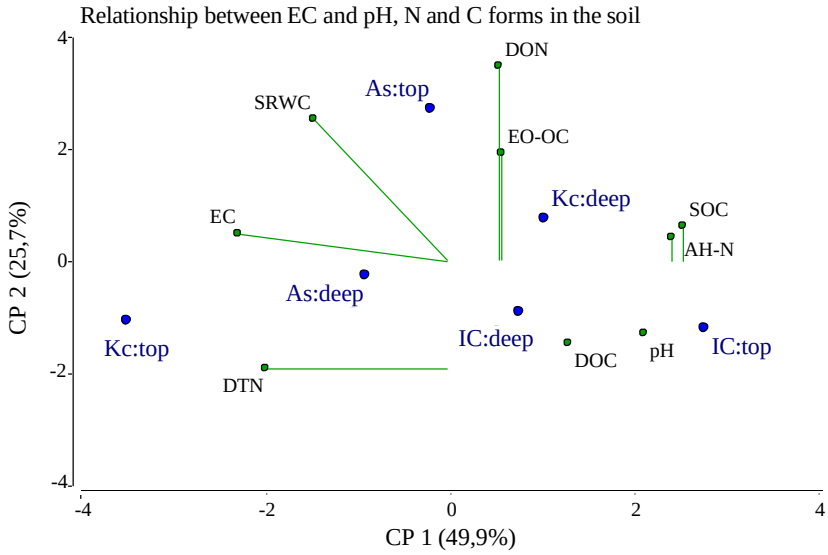


Figure S3: Relationship between electric conductivity (EC) and pH and N and C forms measured in the topsoil (upper 50 cm: 50cm) and in the deep soil (from 50 to100 cm: 100 cm) in the monocultures of *Alhagi sparsifolia* (As) and *Karelinia caspia* (Kc) and in the intercrop of both species (IC).

Declaration of interests

☒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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: