# Nitrogen pools in soil covered by biological soil crusts of different successional stages in a temperate desert in Central Asia

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## ABSTRACT

Biological soil crusts (BSCs) are a primary source of nitrogen (N) in deserts through N-fixation. N-fixation rates may be determined by the species present within BSCs, and environmental factors like temperature and moisture, which vary seasonally. These same factors may also govern dynamics of within-soil N transformations. Few studies have explored the dynamics of different N forms in response to seasonal microclimate variations in BSCs, especially across both the growing season and the snow-covered season (winter). In this study, monthly changes in multiple soil N pools across a full year and beneath three soil cover types – bare soil, cyanobacteria BSC, and lichen BSC – were assessed across a full year in the Gurbantunggut Desert, Central Asia. We focused on multiple organic and inorganic N pools including: total N, alkali-hydrolyzable N, DON, inorganic N ($NH_4^+$-N, $NO_3^-$-N), free amino acids, and microbial biomass N. We found that different N forms had divergent trends during the year, peaked in different months, and showed non-synchronous responses related to seasonal temperature and moisture patterns. Most N forms were most abundant in lichen BSC > cyanobacteria BSC > bare soil, although significant differences were only observed in a few months. In the growing season, available N forms such as soil DON and inorganic N were related to both water and temperature. In winter, available N was strongly related to temperature variability prior to the sampling dates. The high $NH_4^+$-N/$NO_3^-$-N in the early growing season suggest that N fixation or N mineralization were highest at this time. Our results indicate non-synchronous availability of different N forms, and elevated N availability beneath lichen BSCs, which may maintain the diverse N uptake requirements for different plant species.

## 1. Introduction

After water, nitrogen (N) is generally the major factor limiting primary production in desert ecosystems (Gebauer and Ehleringer, 2000; Hooper and Johnson, 1999; Noy-Meir, 1973), so that understanding the factors controlling N availability is critical for management of dryland ecosystems (Peterjohn and Schlesinger, 1990). Soil N availability is generally low in desert ecosystems, decreases with increasing aridity (Delgado-Baquerizo et al., 2013b), and soil N cycling often shows a pulse pattern in response to precipitation events (Austin et al., 2004; Collins et al., 2008). Soil N transformations are for the most part microbially-mediated processes, and are influenced by a large suite of factors, such as soil microclimate and physicochemical properties, substrate quantity and quality, and microbial community composition (Marusenko et al., 2013; Schimel and Bennett, 2004; Sinsabaugh et al., 2015; Wang et al., 2016), with moisture and temperature being

principal among these factors in desert ecosystems (e.g., McCalley and Sparks, 2008; van Gestel et al., 2016). Therefore, the interactive effects of water and temperature on soil N dynamics may regulate N availability for uptake by microbes and plants, both of which may exhibit preferential uptake for different forms of N during different seasons (Aanderud and Bledsoe, 2009; Gherardi et al., 2013). Many temperate deserts, such as our study system in the Gurbantunggut desert, are covered by stable snowpack in winter (Zhou et al., 2018), resulting in more stable soil temperature and higher moisture when compared to the warm season, and potentially different relationships between soil microclimate and N cycling during winter and the growing seasons.

Biological soil crusts (BSCs) – complexes of cyanobacteria, lichen and moss that aggregate surficial mineral soil – form hotspots of N transformation in desert ecosystems (Evans and Johansen, 1999). In deserts, BSCs coverage of the soil surface can reach 80% in some sites, and BSCs have been shown to enhance soil stability, nutrient cycling

and water retention (Belnap and Lang, 2003; Belnap et al., 2016). Importantly, many BSC organisms fix atmospheric $N_2$ into bioavailable forms, and may create a mantle of fertility in desert ecosystems (Belnap, 2002; Garcia-Pichel et al., 2003). A recent global estimate suggests that cryptogamic covers, including BSCs in arid lands, may supply nearly half of the fixed N in natural ecosystem globally (Elbert et al., 2012). In addition to enhancing the input of N into ecosystems, BSCs may also serve as patches of accelerated N cycling. The relatively rich microbial community in BSC patches can exhibit high rates of mineralization, nitrification and denitrification (Abed et al., 2010; Brankatschk et al., 2013). It has also been suggested, although remains to be demonstrated conclusively, that BSCs with fungal partners may possibly directly transfer N to plants (Bates et al., 2012; Green et al., 2008). High N loss, via emission of $N_2O$, NO, HONO, are usually observed in BSCs (Weber et al., 2015). Some researchers also reported that BSCs can inhibit nitrification, with lower $NO_3^-$-N than other microsites (Castillo-Monroy et al., 2010).

BSCs can be categorized into different successional stages, with bare soil progressing to the early successional stages dominated by cyanobacteria, while bryophytes and lichen increase in abundance in later successional stages (Lan et al., 2013). Dominant phototrophic organisms, biomass and ecological functions vary predictably among these different successional stages (Lan et al., 2012; Miralles et al., 2012; Tucker et al., 2019). In addition, later successional BSCs exhibit higher rates of N fixation and transformation (Brankatschk et al., 2013) and higher abundance of N cycle corresponding functional genes (Brankatschk et al., 2013; Housman et al., 2006), and some BSC lichen exhibit particularly high rates of N fixation (Torres-Cruz et al. 2018). Thus, moss and lichen BSCs may be associated with higher levels of overall soil N, and different ratios of the various soil N forms, because of their effects on the major N turnover processes.

The dynamics of different soil N pools are crucial for understanding soil N availability in relation to BSCs, yet these dynamics remain poorly documented. The total N pool is composed of both organic and inorganic forms of N. The organic pool can be found in either dissolved or solid phases, and is composed primarily of free amino acides, microbial biomass N, and proteins, among their organic molecules, and is less readily available than the inorganic pool for direct uptake by soil organisms (Schimel and Bennett, 2004). Dissolved organic N represents the pool of soluble N, of which the low molecular weight components are the N source for microorganisms and can be utilized directly by many plants (Näsholm et al., 2009). The ammonium and nitrate composing most of inorganic N pool are products of either mineralization of the organic pool, N-fixation, or transformations within the inorganic pool, such as nitrification and these forms are readily available for uptake by plants and microorganisms (Schimel and Bennett, 2004). For understanding N availability to plants and soil microorganisms, the potentially mineralizable pool may be more informative than the instantaneous pools of any particular form; akali-hyrolyzable N, which includes inorganic N and some hydrolysable organic N (such as amino oacids, ammonium acylate, and hydrolysable proteins), is an indicator of potentially mineralizable soil N and soil N supplying capacity (Roberts et al., 2009; Chen et al. 2016). Thus, evaluating multiple N pools simultaneously can shed light on patterns of soil N cycling and availability that no pool considered in isolation will adequately reflect.

Research suggests that soil N pools associated with BSCs may be highly vulnerable to altered precipitation and warming (Reed et al., 2012). The development of BSCs can mediate the effects of environmental changes on microbial processes. For example, BSC-forming mosses mitigated the impact of aridity on the community composition soil bacteria and fungi (Delgado-Baquerizo et al., 2018). BSCs increased the resistance of soil nitrogen dynamics to temperature change in a semi-arid ecosystem (Delgado-Baquerizo et al., 2013a). In addition, late successional BSC types can increase surface soil temperature by as much as 10 °C by decreasing the surface albedo relative to bare soil (Couradeau et al., 2016). Thus, not only the responses of N availability

to environmental changes, but also differences in the sensitivity among BSC types of these responses need to be considered.

The ecology of BSCs and soil microbes involved in soil N cycling, along with the dramatic differences in the soil environment between the growing season and winter in temperate deserts, suggest substantial inter-seasonal differences in soil N cycling among BSC types. While much work has been done on N cycling in dryland ecosystems, as well as on the contribution of BSCs to the N cycle in dryland soils, the relative abundance of different forms of N between seasons across BSC cover types remain largely unknown, and in this study we address that knowledge gap.

This study was conducted in the Gurbantunggut desert, a seasonally snow-covered temperate desert of Central Asia, where BSCs are commonly distributed (Zhang et al., 2010). Our objectives were to 1) evaluate differences in N availability and dynamics between different BSC types (bare soil, cyanobacteria BSC and lichen BSC), and 2) explore the relationship between N dynamics in BSCs and seasonally varying environmental factors. We hypothesized that 1) the seasonal changes in soil moisture and soil temperature are the dominant factors regulating the available N supply, respectively, in the growing season and winter because the growing season is generally very dry, while the winter is extremely cold, 2) late successional BSCs will enhance soil N availability and maintain more stable soil N levels during seasonal transitions (i.e., they will exhibit higher resistance to environmental change across seasons) due to their long term persistence, and 3) different N forms would show non-synchronous responses to seasonal environmental changes because the transformations are being mediated by different processes.

## 2. Materials and methods

### 2.1. Study area

The study was conducted at the south edge of the Gurbantunggut Desert, Central Asia (44°87′N, 87°82′ E). The Gurbantunggut Desert is the second largest desert in China, with the area $4.88 \times 10^4$ km². The soil at the site is a loamy sand, composed of 73%-82.6% sand, 5.2–14.d % silt (0.005–0.063 mm), and 0.6–1.8% clay (< 0.005 mm) (Chen et al., 2007). The region has a temperate continental climate with mean annual temperature of ~8.1 °C, where the maximum air temperature exceeds 40 °C in summer and minimum temperature are lower than −30 °C in winter. The mean annual precipitation is 70 to 150 mm, most of which occurs from April to July. For the purposes of this paper, "winter" is considered late November through mid-March, when an average of 20 cm snow covers the surface of the desert. The growing season for annual plants lasts from spring through fall, and for the purposes of this paper is defined as late March through mid-November. The dominant shrub species are *Haloxylon ammendendron* and *H. pericum*, which cover 20–30% of the surface area, while well-developed BSCs cover about 40% of the area, where patches of cyanobacteria, lichen and moss BSC are found in interspace between the shrubs.

### 2.2. Sampling method

The study was conducted within a long term study site (1 km × 1 km) at the Fukang desert Ecology Research Station, Chinese Academy of Sciences. Five 10 × 10 m plots were located within the long term study site, as five replicates in our study. Replicate plots were separated from one another by > 15 m. From April 2013 until March 2014, samples were collected once a month, mostly near the end of the month. Within each plot, three types of BSCs were sampled: bare soil, cyanobacteria dominated BSCs (lichen and moss coverage < 20%), and lichen dominated crusts (lichen BSC > 20% but moss coverage < 20%). BSCs were categorized consistently with Lan et al. (2013). Bare soil patches occurred where vehicular disturbance or other activities had disrupted the BSC layer. The cyanobacteria and lichen BSC were

naturally developed and without disturbance. The three types represent regular successional stages of BSCs from initial stages to late successional stages, and ecosystem function has been shown to vary across BSC successional stage (Housman et al., 2006). In each plot on each sampling date, two core samples (5 cm diameter) of each BSC type were obtained from 0 to 5 cm soil depth and homogenized in a plastic bag. From the composite sample, one sub-sample was air dried for analysis of soil physicochemical characteristics, including total N and alkali-hydrolyzable N. The remainder of the soil was placed in an ice-box with ice and transfered to a 4 °C refrigerator for growing season samples, or −20 °C freezer for winter samples, for analysis of soil dissolved N and microbial N within 48 h.

### 2.3. Dissolved N extraction and analysis

Inorganic N, free amino acids, and DON were extracted using 2 M KCl solution (Evans and Belnap, 1999). A fresh soil sample (10 g) was mixed with 50 mL KCl, and shaken at a speed of 240 rev/min for 1 h (Jones and Willett, 2006). The extract liquid was filtered and stored at −20 °C prior to analysis. Inorganic N ($NH_4^+$-N and $NO_3^-$-N) was analyzed by colorimetric determination of the nitrate and ammonium content of the filtered extracts on a Continuous Flow Injection Analysis (SEAL Analytical GmbH, Norderstedt, Germany). Dissolved total N was analyzed using the $K_2S_2O_8$ oxidation method, in which the extract was first oxidized to $NO_3^-$-N in an autoclave at 121 °C for 30 min, using 0.15 M NaOH and 3% $K_2S_2O_8$ was used for oxidizer according to the literature (Yang et al., 2007). The absorbance was then recorded at 220 nm and 275 nm, and the dissolved total N was calculated (Yang et al., 2007). DON was then calculated as the differences between dissolved total N and inorganic N. Free amino acids were measured based on the method of Moore and Stein (1948), where a soil extract was mixed with ninhydrin, sealed and put in water bath at 95 °C for 25 min, after which 10% ethanol was added and absorbance was determined at 570 nm.

Microbial biomass N (MBN) was measured using chloroform fumigation and $K_2SO_4$-extraction technique (Nunan et al., 1998). A fresh soil sample (30 g) was put in a bottle, and the soil moisture was adjusted to 40% of the water holding capacity. The bottles were placed in dark and incubated for 10 days at 25 °C. The 10-day incubation was designed to indicate potential MBN at a standard temperature at each sampling date, and admittedly may have minimized month-to-month and intra-seasonal variation in our estimate of MBN. After 10 days, one sub-sample (10 g) was fumigated for 48 h in a desiccator containing alcohol-free $CHCl_3$ while another 10 g subsample was not fumigated. Each subsample was extracted by shaking in 40 mL of 0.5 M $K_2SO_4$ for 30 min and filtered through Whatman #42 filter paper (material: Cotton Linters; pore size:2.5 μm). The extract was spectrophotometrically measured at 280 nm after filtration and N concentration was calculated using the regression relationship between the increased absorbance and absorbance of known standards. MBN was calculated as the difference in N concentration between the fumigated and unfumigated samples.

Total N and alkali-hydrolyzable N was measured using the air-dried soil samples. Total N was measured by the $CuSO_4$-Se powder diffusion method (GB7848-87), and alkali- hydrolyzable N by the alkali hydrolyzation-diffusion method (Chen et al., 2007). All results are expressed on a dry soil basis.

### 2.4. Climate and soil microclimate

Air temperature and precipitation were recorded at 30 min intervals at the Fukang Station, which is 15 km from plots. Fukang Station and the plots are located at the same elevation, and they were tested to have similar air temperature and precipitation. Soil moisture and temperature were measured at 5 cm depth every 10 min using Soil-Four-Parameter-Automatic-Recorder Machines (Channel Corp., Beijing,

China) installed in the plots. Temperature and moisture of the 10 day period prior to the sampling date (including the mean values as well as the range calculated as the difference between maximum and minimum over the 10 days interval) was used for the correlation analysis between N dynamics and physical characteristics of interest. On each sampling date, soil gravimetric water content was measured for each sample.

### 2.5. Statistical and numerical analysis

Two-way repeated measures analysis of variances (ANOVA) was used to determine the effects of months, BSC types and their interactions on different soil N pools. Within each BSC type, one -way repeated measures ANOVA was performed to compare the differences among months. Within each month, one-way ANOVA was used to compare among BSC types. Non-metric multidimensional scaling (NMDS) was also performed for the further analysis of the relationship. To explore the dominant factors affecting soil N dynamics, redundancy analysis (RDA) was used to analyze the relationship between N dynamics and environmental factors in the growing season and the non-growing season. Before analysis, all the data were tested using to verify that they met assumptions for each statistical test. For the RDA, the hellinger transformation were applied to N pool data. All the analysis was conducted using R software (3.4.1, vegan package).

To evaluate the stability or resistance of soil N pools under different BSC types across seasonal changes, we calculated a resistance index for each pool across monthly transitions within a season. For the different N pools, this resistance index can indicate how dynamic that pool is across months within a season, and therefore what effect the BSC type has on stabilizing the soil N pool. This resistance index was calculated according to the equation proposed by (Orwin and Wardle, 2004). The equation is: $RS = 1 - \frac{2 \mid D0 \mid}{(C0 + \mid D0 \mid)}$, where D0 = C0-P0, RS = resistance index; and C0 in the current study is the specific N content in one month, and the P0 is the content in next month. Disturbance (D0) is considered here to be the period of environmental changes that soils were exposed to over the course of the month between sampling events. The method has been used to evaluate how BSCs affected the resistance of the soil to changes in soil temperature and moisture (Delgado-Baquerizo et al., 2013a). This index is standardized by the control, with RS bounded by −1 (least resistance) and +1 (maximal resistance). We calculated resistance indices of each N pool separately for the growing season and winter, under each BSC type.

## 3. Results

### 3.1. Seasonal patterns of climate and microclimate

Air and soil temperature showed similar trends from March 2013 to April 2014 (Fig. 1A and B). The temperature increased from the beginning of the early growing season (March) and peaked during July and August, then the temperature decreased and reached lowest at about mid-January. Air temperature ranged from −26.1 °C to 30.6 °C, while soil temperature ranged from −14.2 °C to 36.9 °C. Measurable precipitation occurred every month in the growing season, with large events in mid-April and late June. Soil moisture rapidly increased after rainfall events. The diurnal range of air temperature variation (maximum-minimum) in air temperature was relatively higher in the growing season compared to winter (Sup Fig. 1). 3.2. Monthly trends in N forms from different BSC types.

The three cover types showed similar temporal patterns in total N, which varied significantly across months in bare soil and lichen BSC (P < 0.05) (Fig. 2A). Significantly higher total N in lichen BSC compared to the other two types was observed in July, August, October, December, and February, and the highest total N in lichen BSC occurred in July. Alkali-hydrolyzable N showed trends similar to total N along across months and among BSCs (Fig. 2B). Alkali-hydrolyzable N was
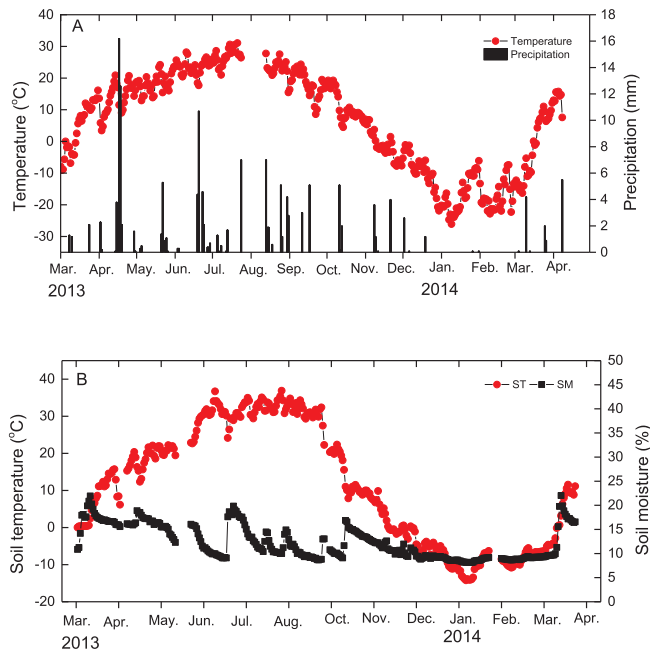
**Fig. 1.** Air and soil temperature from May 2013 to April 2014. A) Daily total precipitation (mm) and mean daily air temperature (°C). B) Soil temperature and soil volumetric moisture at depths of 5 cm near the plots.

significantly lower in bare soil than in lichen BSC in January, February, June and July.

Soil DON showed strong temporal dynamics, with significant differences across months in all three BSCs (P < 0.01) (Fig. 2C). Soil DON fluctuated between months during growing season. In the winter, DON increased from November to January or February of the next year, and then decreased to March. DON was highest in cyanobacteria BSC in August (P < 0.05), but was highest in lichen BSC in November and March (P < 0.05). Soil inorganic N also varied significantly across months (P < 0.01), although the trend was quite different from DON (Fig. 2D). Peaks of inorganic N were found in June and October, while inorganic N was low during winter. Significant differences in inorganic N among three BSCs were only found in April and June, when lichen BSC had relatively higher inorganic N contents.

Potential microbial biomass N (MBN) of bare soil and lichen BSC differed significantly among months (P < 0.01) (Fig. 2E). Within the growing season, MBN increased from May through November, and then decreased in winter. Significant differences in MBN were also found among the three BSC types, with MBN being highest in lichen BSC > cyanobacteria BSC > bare soil in most months. Free amino acids also differed significantly among months for the three BSC types (Fig. 2F). Free amino acids fluctuated in the first half of the growing season, and then increased from August to December (November for bare soil). However, no significant differences in free amino acids were observed among BSC types.

$NH_4^+$-N varied significantly across months (P < 0.01), showed two peaks (June and October) in the growing season, and was lowest in the mid-winter (Fig. 3A). $NO_3^-$-N of the three BSCs peaked in October (Fig. 3B). $NO_3^-$-N varied more across months in cyanobacteria and lichen BSC (P < 0.01) than in bare soil (P < 0.05), however, significant differences among three BSCs were only found in July. The ratio $NH_4^+$-N/$NO_3^-$-N of all BSCs was > 1 from March to June, ~ 1 from July to November, and < 1 in December and January (Fig. 3C), but only cyanobacteria BSC showed significant differences in the ratio of $NH_4^+$-N/$NO_3^-$-N across months. No significant differences in the ratios were observed among BSC types. DON accounted for 86.4%, 85.6 and 85.4% of the dissolved total N pool respectively for bare soil, cyanobacteria and lichen BSC (Sup Fig. 2). The growing season generally
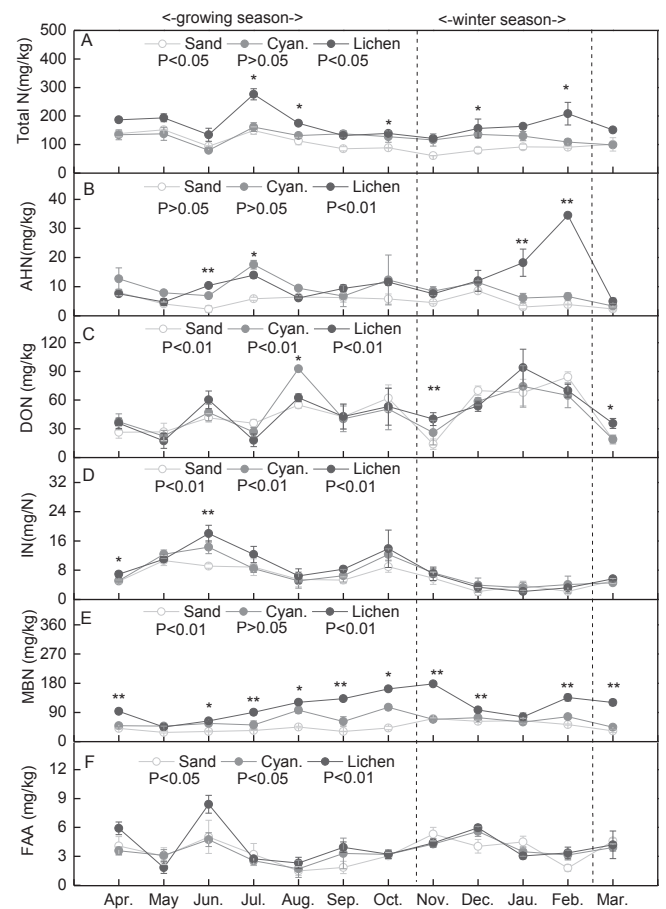


**Fig. 2.** . Total N (A), alkali-hydrolyzable N(AHN,B), dissolved organic N(DON, C), inorganic N (IN, D), microbial biomass N(MBN, E), free amino acids (FAA, F) in three BSC types across months. * indicates the significant differences among BSC types (P < 0.05), and ** P < 0.01. The P value under legends indicates the differences among months. Cyan. = cyanobacteria BSC. Error bar indicates standard error.
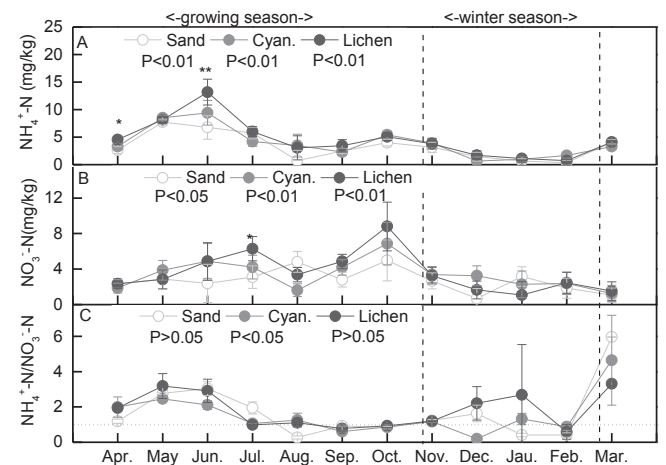


**Fig. 3.** $NH_4^+$-N (A), $NO_3^-$-N (B) and $NH_4^+$-N/$NO_3^-$-N (C) in three BSC types across months. * indicates the significant differences among BSC types (P < 0.05), and ** P < 0.01. The P value under legends indicates the differences among months. Cyan. = cyanobacteria BSC. Error bar indicates standard error.

**Table 1**
Summary results of two way-repeated measures ANOVA for effects of biological soil crust (BSCs) types, month, and their interactions on different N forms.

| | df | TN | AHN | DTN | NO$_3^-$-N | NH$_4^+$-N | IN | DON | FAA | MBN | DON/DTN | FAA/DON | NH$_4^+$-N/NO$_3^-$-N | DON/TN | AHN/TN | IN/TN |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BSC type | 2 | 26.79** | 27.68** | 0.94 | 2.11 | 6.29** | 5.47** | 0.34 | 2.58 | 101.64** | 0.25 | 2.62 | 0.28 | 6.78** | 3.07 | 2.07 |
| month | 11 | 3.85** | 3.80** | 21.07** | 7.61** | 44.43** | 22.88** | 25.66** | 9.42** | 10.25** | 24.03** | 5.88** | 3.50** | 9.32** | 1.72* | 12.66** |
| month × BSC type | 22 | 0.92 | 5.78** | 1.23 | 1.09 | 0.08* | 0.94 | 1.22 | 1.51 | 3.56** | 0.97 | 2.03* | 0.83 | 1.12 | 2.77 | 1.05 |

AHN = Alkali-hydrolyzable N, DTN = Dissolved total N, IN = inorganic N, DON = Dissolved organic N, FAA = Free amino acids, MBN = microbial biomass N, TN = total N.

had relatively higher inorganic N proportions than winter.

### 3.2. Overall effects of months and BSC types on soil N

All soil N forms and their ratios showed significant differences across months (P < 0.01) (Table 1). Significant differences in total N, alkali-hydrolyzable N, NH$_4^+$-N, inorganic N, MBN and ratio DON/total N were found among BSC types. There was a significant effect of the interaction between month and BSC on NH$_4^+$-N, microbial biomass N, alkali-hydrolyzable N and the ratio of free amino acids: DON (Table 1).

### 3.3. Correlation between different N forms and environmental conditions

NMDS showed strong differentiation of the N indices (Sup Fig. 3) between the growing season and winter season. Inorganic N was positively related to the growing season, while the DON and dissolve total N were more related to the winter. To better understand the dominant environmental factors driving differences in the N pool in different seasons, RDA was conducted on N forms and physical environmental conditions for both growing season (Fig. 4A) and winter (Fig. 4B). The DON in growing season was positively correlated with soil gravimetrical moisture (SGM), while the inorganic N or NH4 + -N was more negatively affected by differences average difference in air temperature of each day (DT). In winter, DON and dissolved total N were more positively correlated to the differences in air temperature (Dat). Mean air temperature and precipitation affected MBN most in winter.

Similar results were also shown by a correlation analysis of environmental factors and contents of specific N forms (Sup Fig. 4). Generally, soil N was less correlated with environmental factors in the growing season than in the winter. Total N and alkali-hydrolyzable N were both relatively insensitive to environmental factors. DON and dissolved total N were negatively related to soil temperature variability and soil moisture in the growing season, and strongly negatively correlated with all indices of temperature and moisture, with the exception of Dat, in the winter. MBN showed weak but contrasting relation to soil microclimate in the growing season (negative) and winter (mostly positive). FAA show similar patterns with microclimate factors between seasons. NO$_3^-$-N is mostly negatively related to microclimate indices in the growing season, but positively in the winter. NH$_4^+$-N and inorganic N are strongly, and mostly negatively responsive to soil microclimate indices in the winter, but not very correlated with them in the growing season.

### 3.4. Resistance of different N forms to change across months

The resistance index (RS) of different N forms showed distinct patterns among BSC types (Table 2). In the growing season, RS was highest in bare soil for alkali-hydrolyzable N, DON, microbial biomass N, NO$_3^-$-N, inorganic N, while RS was highest in cyanobacteria BSC for total N, free amino acids and NH$_4^+$-N. Lichen BSC generally showed lowest RS to environmental changes in growing season. However, in the winter, cyanobacteria and lichen BSC had relatively higher resistance than bare soil in most case, such as total N, DON, dissolved total N, free amino acids, NO$_3^-$-N, and inorganic N.

## 4. Discussion

### 4.1. Effects of BSCs successional stages on N availability

Overall, BSC type had highly significant effects on soil N availability. In general, soil available N was highest in lichen BSC > cyanobacteria BSC > bare soil. However, the effects of BSC type on N availability depended on seasons and specific N forms. Total N, alkali-hydrolyzable N, and microbial biomass N strongly increased with BSC successional stage. These results are consistent with other studies on BSCs, and are consistent with basic ecology of BSC organisms
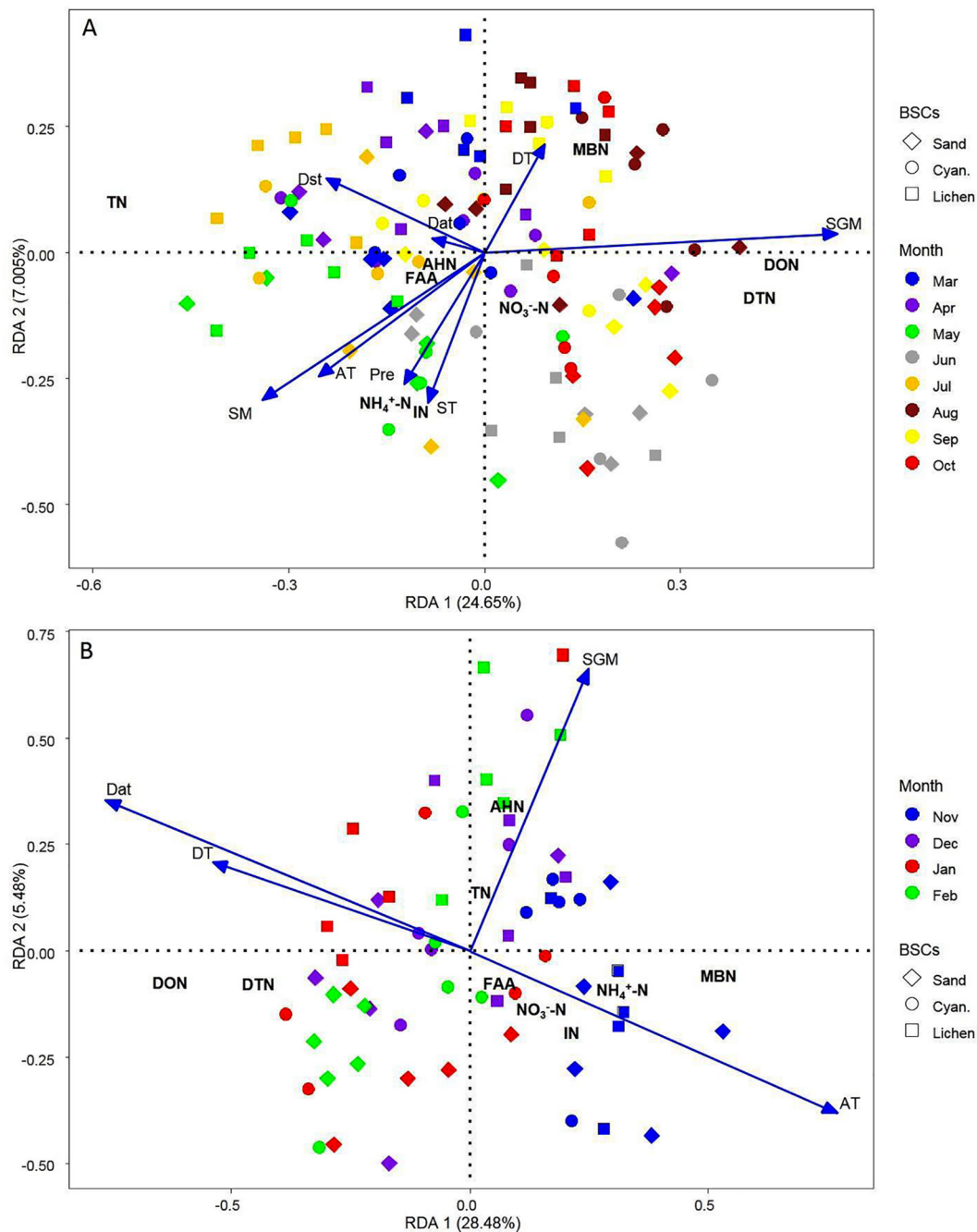
**Fig. 4.** RDA ordination triplots in two dimensions for the samples in growing season (A) and winter (B). The different symbols means different BSC types (Sand, bare soil; Cyan., cyanobacteria BSC; L, Lichen, lichen BSC). The bold letters indicate different N forms. AHN = Alkali-hydrolyzable N; DTN = Dissolved total N; IN = inorganic N; DON = Dissolved organic N; FAA = Free amino acids; MBN = microbial biomass N; TN = total N. Arrows indicate physical characteristics of interest. SGM = soil gravimetric moisture of the soil sample; Following indices are obtained over the 10 day interval prior to soil sampling. SM = soil moisture; DT = average difference in air temperature of each day; AT = average temperature; Pre = precipitation; Dat = differences in air temperature of maximum and minimum value; Dst = difference in soil moisture of maximum and minimum value. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Brankatschk et al., 2013; Chamizo et al., 2012; Delgado-Baquerizo et al., 2013a). Previous research has demonstrated that inputs, within-soil transformations, and gaseous losses of soil N vary among different BSC types (Barger et al., 2016). In terms of inputs of N from the atmosphere to the soil, different BSC types have different N fixation potential. The heterotrophic soil stage (i.e, bare mobile sand without BSCs) shows very limited N-fixation, while the abundance and activity of N-fixing cyanobacteria increases in the later successional BSCs (e.g., Lan et al., 2013).

Within-soil N transformations also may vary significantly among

BSC types, in ways that vary seasonally. For instance, BSCs have been shown to increase the net soil N transformation rates during the early growing season but reduce the inorganic N content during the peak growing season (Hu et al., 2015). Previous work has shown that BSCs increased the responsiveness of soil DON, $NH_4^+$-N and $NO_3^-$-N to wetting events compared to bare ground due to the distinct microbial communities (Morillas and Gallardo, 2015). Moreover, the BSC microsites may also have lower $NO_3^-$-N than plants sites, suggesting an inhibiting effects on net nitrification in semi-arid ecosystems (Castillo-Monroy et al., 2010). Well developed BSCs have been shown to enhance

**Table 2**
Changes in average resistance index for different N forms of biological soil crusts in growing season and winter.

|  |  | Total N | Alkali-hydrolyzable N | Dissolved organic N | Dissolved total N | Microbial biomass N | Free amino acids | $NO_3^-$-N | $NH_4^+$-N | Inorganic N | $NH_4^+$-N /$NO_3^-$-N |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Growing season | Sand | 0.64 | **0.51** | **0.50** | **0.51** | **0.60** | 0.31 | **0.44** | 0.03 | **0.43** | 0.11 |
|  | Cyanobacterial | **0.66** | 0.34 | 0.20 | 0.28 | 0.52 | **0.50** | 0.27 | **0.28** | 0.40 | 0.36 |
|  | Lichen | 0.57 | 0.31 | 0.16 | 0.26 | 0.56 | 0.29 | 0.38 | 0.21 | 0.32 | **0.37** |
| Winter | Sand | 0.69 | 0.36 | 0.27 | 0.34 | **0.65** | 0.45 | 0.09 | 0.40 | 0.31 | **0.50** |
|  | Cyanobacterial | **0.80** | **0.55** | 0.40 | 0.46 | **0.65** | **0.57** | **0.67** | 0.30 | **0.52** | 0.09 |
|  | Lichen | 0.70 | 0.28 | **0.46** | **0.50** | 0.49 | 0.53 | 0.23 | **0.47** | 0.38 | 0.35 |

Bold numbers indicate the maximum value among the three types of biological soil crust in each N form. A higher resistance index indicates more stability of the N pool across months within the season of interest.

gaseous losses of multiple forms of N. For example, nitric oxide fluxes increased with increasing N fixation potential of BSCs (dark > medium > light) in the summer months, while no differences in the spring and autumn were found (Barger et al., 2005; Barger et al., 2013; Meusel et al., 2018; Weber et al., 2015). Lichen uptake of $NO_3^-$-N can also increase the complexity of soil N dynamics (St Clair et al., 2002).

The observed resistance of N-cycling among different BSC types was divergent between seasons. N pools of lichen BSCs showed relatively higher resistance across months in the winter compared to cyanobacterial BSCs and bare soil. In contrast, during the growing season, N pools in bare soil exhibited higher resistance to changes between months than cyanobacteria and lichen BSCs. Thus, the results were only partially consistent with our hypothesis that late successional BSCs would exhibit higher resistance during seasonal changes. Our work shows that the patterns of N cycle resistances in BSC-dominated areas actually reverse between winter and the growing season, in contrast to previous work that found the N cycle is more resistant to changes in temperature in BSC-dominated than in bare ground areas, and that BSCs could help to minimize the impacts of climate change on soil N availability in some drylands (Delgado-Baquerizo et al., 2013a). This difference may indicate a different response between the two ecosystems, or may suggest that BSC effects on the soil N cycle are fundamentally different in the winter and growing season. Because much work on soil N dynamics in temperate deserts has focused on growing season process, this pattern may previously have gone undetected.

An important consideration when interpreting results of the current study is that non-significant differences in some N forms among BSC types in most months were also likely related to the sampling depth of the crusts. In another study, N content significantly increased in the crust and its underlying soil with crust development, especially in the first centimeter of soil underneath the crust (Chamizo et al., 2012), while the effect was diminished between 1 and 5 cm depth. Thus, the 0–5 cm sampling depths in our study may have somewhat masked the effects of BSCs. We therefore suggest that our results are fairly conservative estimates of BSC effects on surface soil N transformations.

### 4.2. Non-synchronous responses of different N forms

Different N forms peaked in different seasons, and showed a dissimilar trends across months, consistent with the third hypothesis that different N forms would show non-synchronous responses to seasonal environmental changes. Non-synchronous responses of different N forms can have large ecological effects in the desert ecosystems. While dryland soils are often N-limited (Schlesinger et al., 1996), it is possible that the peak of different forms in different seasons can reduce N limitation for plants and microbes, and thus maintain the temporal stability of the community structure. Similarly because different plant species preferentially uptake different forms of N (Harrison et al., 2007), the divergent peaks of N forms could be beneficial for specific plant species or lifeforms.

When evaluating non-synchronous changes in different forms of N over time, it is important to consider that all the N forms in this study

are linked through N transformation processes (Schimel and Bennett, 2004), such that N leaving one pool might subsequently be present in another pool. Thus, in addition to non-synchronous changes in different N forms being driven by abiotic factors or by biotic supply and demand, non-synchronous responses may be due to complex temporal dynamics of transfers between multiple pools. For example, because inorganic N was transformed or mineralized from organic N, lag effects and even opposite trends were found between the two indices. In winter, the sharp decreases in MBN likely contributed to the observed increase in DON. In addition, $NO_3^-$-N was nitrified from $NH_4^+$-N, which also contributed to non-synchronous effects in the current study.

The relatively higher ratio of $NH_4^+$-N to $NO_3^-$-N observed in early growing season indicates that mineralization (ammonification) dominated over nitrification. Additionally, the high $NH_4^+$-N may be attributed to high N fixation rate at this stage because of abundant soil moisture and appropriate temperature. In contrast, low NO3$^-$-N might occur due to increased denitrification during the freeze–thaw period (Gao et al., 2018), although denitrification rates have been reported to be low in some drylands (Johnson et al., 2005). In N limited ecosystems, strong competition between plants and microbes for mineral N reduces $NH_4^+$-N supply for nitrifiers, thus $NH_4^+$-N tends to be the dominant from of inorganic N, while as soil N increases, more $NH_4^+$-N is available for nitrifiers and the system shifts toward $NO_3^-$-N dominance (Schimel and Bennett, 2004). In the Gurbantunggut desert, annual plants germinate and grow rapidly during spring, with most annuals finishing their lifecycle by the end of May (Wang et al., 2006). By the end of May, the ratio of $NH_4^+$-N to $NO_3^-$-N switched to $NO_3^-$-N accumulation and predominance over $NH_4^+$-N (i.e., $NH_4^+$-N/$NO_3^-$-N < 1), suggesting increasing availability of soil N (Davidson et al., 2007).

In our study, DON was the dominant form of extractable N, and this proportion increased from growing season to winter. Similarly, DON was the dominant form and exhibited high temporal variability in BSCs in a semi-arid grassland in Spain (Delgado-Baquerizo et al., 2010). In contrast, these results were not consistent with Xiao et al. (2018), which found that the dynamics of soil inorganic N/DON ratio followed the same pattern as soil $NO_3^-$-N /$NH_4^+$-N ratio. Organic N uptake can contribute to plant nutrition in many ecosystems (Kranabetter et al., 2007; Weigelt et al., 2005). Thus, DON has great potential to supply N for vascular plants and microbes in the study area.

### 4.3. Soil microclimate factors regulating seasonal changes in N forms

Our results are partially consistent with our initial hypothesis that seasonal changes of soil moisture and temperature govern available N supply in growing season and winter, respectively. Soil gravimetrical moisture was closely related to the dynamics of DON, and, in winter, differences in air temperature greatly affected DON. Similarly, changes in inorganic N can be attributed to variation in soil water or temperature in the growing season. Seasonal changes in N availability driven by temperature and moisture are found in many other dryland ecosystems (Castillo-Monroy et al., 2010; Mazzarino et al., 1991), while

experimentally altered precipitation has been shown to significantly change the relative abundance of different N forms in BSC soils (Reed et al., 2012). In our study, different forms of available N sharply changed before and after rain in growing seasons, consistent with pulse dynamics of N supply in response to precipitation observed in other studies (Collins et al., 2008). Changes in transformation rates may lead to changes in contents of different N forms across months, such as seasonal variations in net N mineralization and nitrification rates (Hu et al., 2015).

Several mechanisms related to moisture and temperature may explain the fluctuations in N availability in our study. First, changes in inorganic and DON were strongly correlated with seasonal precipitation and soil moisture regimes. Precipitation pulses tend to cause direct loss of soil and ecosystem N via infiltration and runoff (Schimel et al., 1997), although some input in precipitation may also occur (Austin et al., 2004), and thus the seasonal trends in precipitation anticipate similar patterns in N. Further, microbial activity and plant demands generally increased after precipitation, especially in dryland (Sturges, 1986; Weber et al., 2015). N fixation, transformation, and transfer can be stimulated by soil moisture resulting in divergent changes in availability of different N forms. Moreover, moisture from dew has been shown to promote an increase in the decomposition of organic matter at microsites, which would tend to increase the concentration of DON (Delgado-Baquerizo et al., 2013c).

Second, air and soil temperatures had significant impacts on soil N availability. In previous work, although increased temperature did not have a detectable effects on soil microbial biomass and bacterial community composition of BSCs in response to simulated climate warming (Johnson et al., 2012), some N processes were controlled by temperature, such as N fixation (Hennecke and Shanmugam, 1979) and N ammonia oxidation (Zhou et al., 2016). Further, in laboratory incubations warming has been shown to increase net nitrification and N mineralization (Hu et al., 2014), and seasonal variation in climate significantly affected N transformation (Hu et al., 2015). The processes mentioned above likely affected N availability in our study as well. For example, air and soil temperature, combined with water, affected soil inorganic N. Interestingly, in this study the magnitude of the difference in temperature within a 10 day window prior to soil sampling was correlated with changes in DON availability, especially in winter. Microbial die-off in response to large temperature fluctuations may explain the increases in DON in winter in our experiments as has been seen in other studies (Hall et al., 2016). The soil temperature/soil moisture was measured at the depths of 5 cm, where the ranges between minimum and maximum temperature are more moderate than at the surface layer. Thus microbial populations are also likely more stable at 5 cm depth than at soil surface, where microbial population may exhibit more pronounced temporal fluctuations. In addition, freeze–thaw cycle during the winter period, may also increase N availability (Song et al., 2017). In our study, repeated freeze–thaw cycles occurred in November/December and again in March, and both periods appeared to be transition periods in temporal dynamics of multiple N forms.

## 5. Conclusion

In our study, availability of most forms of N increased along with the successional stages of BSCs (from bare soil to cyanobacteria BSC to lichen BSC), although significant differences were only observed in certain months. The total amount of available N in the soil, as well as the abundance of different forms of N, varied significantly across months over the course of a full year, and different forms of N showed non-synchronous trends across the months. DON accounted for most of the dissolved total N, and was higher in growing season than winter. Microclimate factors, including air and soil temperature, and soil moisture were significantly correlated with seasonal trends in different N pools, with temperature being relatively more important in the

winter than in the growing season. The seasonal cycles of many of soil N pools were consistent with known mechanisms of soil N transformations, in particular, higher $NH_4^+$-N/$NO_3^-$-N ratios were found in early growing season, suggesting a higher rates in N fixation and organic N mineralization than nitrification. We suggest that both the increased availability of soil N beneath later stage BSCs, and the non-synchronous availability of different forms of N, may play critical roles in maintaining the diversity and stability of plant community structure in desert ecosystems, and contribute to overall ecosystem function.

## 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.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2019.114166.

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