Relationship between ecological stoichiometry and plant community diversity in the upper reaches of Tarim River, northwestern China: Postprint

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Abstract

Changes in ecological stoichiometry reflect nitrogen (N), phosphorus (P) and both N and P limitations in a plant community, which in turn affect plant diversity of the community. However, the relationship between plant community diversity and ecological stoichiometry has not yet been fully researched in arid and semi-arid regions. Ecological stoichiometry and plant community diversity indices of eighteen communities in the upper reaches of Tarim River, northwestern China, were analyzed by multivariate analysis of variance in 2016. The correlation between ecological stoichiometry and plant community diversity was assessed by redundancy analysis (RDA). Results indicated that the Margalef index was significantly correlated with carbon (C) and P concentrations, the Simpson index and Shannon–Weaner index were significantly correlated with plant C concentration, and the Pielou index was significantly correlated with plant C and N concentrations. Moreover, C:N and C:P ratios had significant impacts on plant community diversity. Our results highlight the importance of ecological stoichiometry in driving plant community diversity in the upper reaches of Tarim River, northwestern China.

Full Text

Preamble

Relationship between Ecological Stoichiometry and Plant Community Diversity in the Upper Reaches of the Tarim River, Northwestern China

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Abstract: Changes in ecological stoichiometry reflect nitrogen (N), phosphorus (P), and combined N and P limitations in plant communities, which in turn affect plant diversity. However, the relationship between plant community diversity and ecological stoichiometry remains insufficiently researched in arid and semi-arid regions. We analyzed ecological stoichiometry and plant community diversity indices across eighteen communities in the upper reaches of the Tarim River, northwestern China, using multivariate analysis of variance in 2016. Redundancy analysis (RDA) was employed to assess correlations between ecological stoichiometry and plant community diversity. Results indicated that the Margalef index was significantly correlated with carbon (C) and P concentrations, the Simpson and Shannon–Wiener indices were significantly correlated with plant C concentration, and the Pielou index was significantly correlated with plant C and N concentrations. Moreover, C:N and C:P ratios had significant impacts on plant community diversity. Our findings highlight the importance of ecological stoichiometry in driving plant community diversity in the upper reaches of the Tarim River.

Keywords: Margalef index; Simpson index; Shannon–Wiener index; redundancy analysis; Tarim River

1 Introduction

Ecological stoichiometry serves as a crucial tool for exploring the dynamic balance of various nutrient elements (Sterner and Elser, 2002; Zechmeister-Boltenstern et al., 2015; Moorthi et al., 2016; Shang et al., 2018). Currently, ecological stoichiometry has been applied across multiple scales, from molecules and cells to individuals, communities, and entire ecosystems (Elser et al., 2007; Elser et al., 2010; Yan et al., 2016). It has also been used to estimate nutrient limitation in plants and reveal their nutrient utilization strategies (Sterner and Elser, 2002). Deficiencies in carbon (C), nitrogen (N), and phosphorus (P) can limit plant growth (Sperfeld et al., 2017; Zeng et al., 2017), thereby reducing plant community diversity (Conti and Díaz, 2013). Plant community diversity is essential for maintaining ecosystem stability and processes (Tilman et al., 1996; Naeem and Li, 1997; Yachi and Loreau, 1999; Snyder et al., 2006; Haddad et al., 2011; Pelini et al., 2014; Vilela et al., 2016; Zhang et al., 2017; Bustos-Segura et al., 2017; Saitta et al., 2018). Therefore, applying ecological stoichiometry methods to study plant communities and their relationships can help reveal the ecological strategies of plants in specific environments and is of great significance for understanding material cycling and energy balance within communities.

Since the 1980s, ecological stoichiometry has become an important approach in plant ecology research (Frost et al., 2002; Allen and Gillooly, 2009; Yan et al., 2016; Yu et al., 2017a; Castellanos et al., 2018; Li et al., 2019). Most research has focused on the effects of ecological stoichiometry on plant community diversity (Kerkhoff et al., 2005; Liu et al., 2018; Huang et al., 2018) and examined the ecological stoichiometry of plant communities with different functional groups, as well as changes in plant community diversity in grassland, forest, and wetland ecosystems (Sardans et al., 2011; Yan et al., 2015; Tao et al., 2016; Soufbaf et al., 2017). However, little research has been conducted on desert ecosystems (Conti and Díaz, 2013). Additionally, most ecological stoichiometry studies have been carried out at the individual level rather than the community level (Halvorson et al., 2017; Zeng et al., 2017).

In northwestern China, frequent climate change and anthropogenic disturbances (Chen, 2013; Zhang et al., 2018) have made plant communities extremely vulnerable, with expected sharp reductions in community density in the future (Liu et al., 2005). Plant communities in the upper reaches of the Tarim River are located in an especially fragile ecological zone (Gong et al., 2016), yet remain poorly understood. Therefore, exploring the impact of ecological stoichiometry on plant community diversity provides a scientific basis for guiding vegetation restoration in this desert ecosystem. We hypothesize that (1) characteristics of ecological stoichiometry affect plant distribution, thereby influencing plant community diversity in the upper reaches of the Tarim River; and (2) distance from the Tarim River affects both ecological stoichiometry characteristics and plant community diversity indices, but does not alter the relationship between ecological stoichiometry and plant community diversity.

2.1 Study Area

The study area is located in the upper reaches of the Tarim River, northwestern China (40°25 -41°40 N, 80°10 -84°36 E; Fig. 1 [Figure 1: see original paper]). The annual mean temperature is 10.4°C, with mean annual precipitation and evapotranspiration of 50.4 mm and 1800.0 mm, respectively (Gong et al., 2016). The dominant plant species in this desert ecosystem include *Populus euphratica*, *Halostachys caspica*, *Tamarix chinensis*, *Phragmites communis*, *Lycium ruthenicum*, and *Glycyrrhiza uralensis*.

2.2 Methods

Data were collected at three sampling zones in the upper reaches of the Tarim River in August 2016 (Fig. 1). The three zones were selected on the southern side of the river and designated T1, T2, and T3. Within each sampling zone, six plant communities (sub-plots) were established for vegetation sampling, spaced at 1 km intervals to avoid pseudoreplication. Thus, a total of eighteen plant communities were sampled and coded accordingly (Table 1).

Different sub-plot sizes were used to sample trees, shrubs, and herbs. Trees were sampled in 20 m × 20 m plots, while shrubs and herbs were sampled in 10 m × 10 m and 1 m × 1 m plots, respectively. Approximately 50 g of leaf material from each plant species were collected and placed in envelopes with desiccant. After removing litter and stones, topsoil (0–15 cm) samples were collected and taken to the laboratory for soil characteristic analysis.

2.3 Leaf Analyses

Leaf samples were carefully cleaned and oven-dried at 60°C for 2 hours. Soil samples were air-dried after sieving through a 2-mm mesh, with visible roots and organic debris removed by hand. All samples were then ground to a fine powder for element analysis following standard soil agrochemical procedures (Bao, 2000). Total C content was determined using the potassium dichromate external heating method (Bao, 2000), total N content was determined using the Kjeldahl method (Bao, 2000), and total P content was determined using the molybdenum-antimony colorimetric method (Bao, 2000). All leaf analyses were repeated three times.

2.4 Alpha Diversity Indices

Alpha diversity indices were calculated using the following equations:

$$D = \sum P_i^2 \quad (1)$$

$$H' = -\sum P_i \ln P_i \quad (2)$$

$$Ma = \frac{S-1}{\ln N} \quad (3)$$

$$E = \frac{H'}{\ln S} \quad (4)$$

where D is the Simpson index, H' is the Shannon-Wiener index, Ma is the Margalef index, E is the Pielou index, P_i is the probability of occurrence of the ith species in a community, S is the total number of species in a community, and N is the total number of individuals in a community.

2.5 Ecological Stoichiometry

Leaf C, N, and P concentrations were used to calculate the importance values of each community for trees, shrubs, and herbs. Based on these importance values, stoichiometric parameters for all communities were weighted (Yan et al., 2008).

2.6 Statistical Analyses

One-way analysis of variance (ANOVA) with Duncan’ s post hoc multiple comparisons test (Hsu, 1996) was used to compare differences in C:N:P ratios among communities. All statistical tests were assessed at $P < 0.05$. Linear regressions were performed to describe relationships between C, N, P, C:N ratio, C:P ratio, and N:P ratio. These analyses were conducted using SPSS version 19.0 software

(Chicago, IL, USA). Redundancy analysis (RDA) was used to explore correlations between plant community diversity indices and C, N, and P concentrations and their ratios, conducted in CANOCO 4.5 software (Wright, 2014). A Monte Carlo test was performed to determine the relative importance of variables.

3.1 Characteristics of Ecological Stoichiometry in Different Communities

The highest C concentration occurred in the T13 community and the lowest in the T31 community. The highest N concentration occurred in the T23 community and the lowest in the T14 community. The highest P concentration occurred in the T34 community and the lowest in the T22 community. All highest stoichiometric ratios (C:N, C:P, and N:P) were found in the T1 zone and the lowest in the T3 zone (Table 2). Significant differences in C, N, and P concentrations and their ratios were observed both within and among zones. Additionally, N and P concentrations did not differ significantly among the T15, T25, and T35 communities (Table 2).

Figure 2 [Figure 2: see original paper] shows correlations among C, N, and P concentrations and their ratios. Strong correlations were found between C and N concentrations and between C and P concentrations. Significant negative correlations were observed between C:N ratio and N concentration and between C:N ratio and N:P ratio. Strong positive correlations were found between N:P ratio and N concentration and between C:P ratio and N:P ratio. Conversely, an opposite pattern was observed between C:P ratio and P concentration.

3.2 Characteristics of Plant Community Diversity Index in Different Communities

Significant differences in Simpson' s index were found between communities in T1 and T3 zones, though no significant differences were observed for other diversity indices between these zones (Fig. 3 [Figure 3: see original paper]). For the Shannon-Wiener index, significant differences were observed between communities in T1 and T2 zones and between T1 and T3 zones, but not between T2 and T3 zones (Fig. 3). For the Margalef and Pielou indices, no significant differences were found among communities in T1, T2, and T3 zones. Overall, all plant community diversity indices showed higher values in T1 zone communities compared to T2 and T3 zones.

3.3 Correlations between Ecological Stoichiometry and Plant Community Diversity Index

RDA was used to examine correlations between plant community diversity and ecological stoichiometry (Fig. 4 [Figure 4: see original paper]). The first axis explained 64% of the variation, while the second axis explained only 2%. Only axis

1 reflected the relationship between ecological stoichiometry and plant community diversity indices. RDA results indicated that C:N ratio and N concentration played important roles in explaining plant community diversity among all concentrations and ratios. The Simpson index showed strong positive correlation with P concentration and weak positive correlation with C and N concentrations. In contrast, C:N and N:P ratios showed strong negative correlations with the Simpson index, while C:P ratio showed weak negative correlation. A clear positive correlation was found between the Shannon-Wiener index and C, N, and P concentrations. Similar negative correlations were found among these ratios, with remaining indices showing comparable patterns.

The effects of concentrations and ratios on plant community diversity indices varied, making it difficult to determine which parameter had the greatest impact. Therefore, a Monte Carlo test was performed on C, N, and P concentrations and the three ratios to determine their relative importance. The results indicated that N concentration was the most important element (Table 3).

Figure 5 [Figure 5: see original paper] shows t-value results from RDA for individual stoichiometric factors influencing plant community diversity indices. The Simpson, Pielou, and Shannon-Wiener indices all fell within the solid circle, while the Margalef index partially fell into it (Fig. 5a). This implied that N concentration was strongly and positively correlated with the Pielou, Simpson, and Shannon-Wiener indices, and weakly positively correlated with the Margalef index. In other words, plant community diversity indices increased with increasing N concentration. The C:N ratio showed similar patterns to N concentration (Fig. 5c).

The Simpson and Shannon-Wiener indices fell completely within the solid circle, while the Pielou and Margalef indices partially fell into it (Fig. 5b). This suggested that P concentration was strongly and positively correlated with the Simpson, Pielou, and Shannon-Wiener indices, and weakly positively correlated with the Margalef index. The C:P ratio revealed similar patterns to the C:N ratio (Fig. 5d).

4.1 Characteristics of Ecological Stoichiometry

This study demonstrates substantial variation in C, N, and P concentrations among different plant communities. The highest C concentrations were found in the T13 community, which contains the largest number of *Phragmites* spp.—a unique xerophilous plant (Tuboi and Hussain, 2018). Because the T1 zone is closest to the water source among the three sampled zones, it supports extensive growth of *Phragmites* spp. Rapid growth of this species increases vascular bundles in leaves and enhances photosynthesis, leading to effective accumulation of organic matter (Behera et al., 2012). The highest N concentrations were observed in *Alhagi sparsifolia* Shap., which dominates the T23 community. *A. sparsifolia* is a naturally occurring, drought-tolerant plant that depends on groundwater (Xiang et al., 2018). While proximity to water sources may inhibit its growth (Zhang et al., 2018), insufficient water far from the source cannot meet its growth requirements. Thus, moderate water availability is most beneficial. Additionally, *A. sparsifolia* is a leguminous plant with high N fixation ability and utilization efficiency (Lei et al., 2014). Overall, ecological stoichiometry characteristics reflect community vegetation composition and nutrient absorption and utilization patterns.

Nitrogen and P are generally considered the two most limiting elements for plant growth (Elser et al., 2000; Elser et al., 2007; Qu et al., 2017). We found significant differences in N:P ratios among plant communities. N:P ratios exceeding 16 in some communities indicated strong P limitation (Yan et al., 2015; Yu et al., 2017b), while ratios below 14 in other communities suggested N limitation (Plach et al., 2017). However, factors affecting plant N:P ratios are complex and comprehensive (Elser et al., 2007). Nutrient limitation in different communities is controlled by multiple factors, and interactions among plant elements complicate N:P ratios further (Yan et al., 2015; Plach et al., 2017). Therefore, the underlying mechanisms require further investigation.

4.2 Characteristics of Plant Community Diversity

This study showed that T1 zone communities had the highest Simpson index values, indicating strong anti-interference abilities. Long-term intermittent erosion by the Tarim River has made these communities more resistant to disturbance (Sures et al., 1999; Bu et al., 2017). However, other communities with poorer anti-interference abilities exhibit higher self-healing capacities after habitat destruction. These results indicate that dominant species play a leading role in maintaining community structure and ecological function (Zhang et al., 2017).

The Shannon–Wiener index values for T11 and T16 communities in the T1 zone were high, indicating more complex community structure and composition. In contrast, the T31 community in the T3 zone had low Shannon–Wiener values, reflecting simpler community structure. The T11 and T16 communities are located closer to the Tarim River and experience no drought stress. Relatively abundant water resources support survival of more plant species (Merritt et al., 2010). Conversely, the T31 community is far from the river, where only a few desert species capable of overcoming drought stress can survive.

Margalef and Pielou index values in T1 zone communities were higher than in other zones, reflecting high species richness and abundant species distribution. This may be attributed to T1 zone communities being closest to the water source, with sufficient water supporting more species survival and growth (Merritt et al., 2010).

4.3 Correlations between Ecological Stoichiometry and Plant Community Diversity Index

Our results support the hypothesis that ecological stoichiometry and plant community diversity are related, suggesting that ecological stoichiometry importantly drives plant community diversity. Previous studies have found that C is a major element for plants with relatively high and stable concentrations (Heyburn et al., 2017), but C is not a key limiting element for plant growth (Makino et al., 2003; Heyburn et al., 2007). Our finding of no significant correlation between plant community diversity and C concentration further confirms this view.

In our study, N and P concentrations were important for plant community diversity indices, showing significant correlations. Research has demonstrated that changes in N and P concentrations affect plant community diversity (Zhao et al., 2010). Both increases and decreases in N and P concentrations influence plant growth rates, thereby altering plant community diversity (Frenken et al., 2017). The importance sequence of ecological stoichiometry for plant community diversity shows that C:N and C:P ratios also had significant impacts, along with N concentration. The C:N and C:P ratios provide insight into plants' ability to absorb nutrients and assimilate C (Bell et al., 2018) and can reflect nutritional efficiency to some extent (Liu et al., 2010). Plant communities have different C sequestration efficiencies, while C accumulation efficiency and storage capacity are associated with N and P supplies that limit plant growth. Ultimately, ecological stoichiometry and plant community diversity appear closely linked (Castellanos et al., 2018).

5 Conclusions

This study confirms the importance of ecological stoichiometry in driving plant community diversity within desert ecosystems. First, stoichiometric concentrations, particularly C and N, were greater in communities closer to the riparian zone. Second, plant community diversity indices were also greater near the riparian zone, though this pattern reversed with increasing distance. Furthermore, RDA showed that N concentration was a key factor affecting plant community diversity in the Tarim River. In conclusion, under the extreme environmental conditions of nutrient and water scarcity, desert plants in the Tarim River have developed special ecological stoichiometry characteristics to maintain plant community diversity.

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Note: Figure translations are in progress. See original paper for figures.