



## Limiting similarity mediates plant community niche hypervolume across a desert-steppe ecotone of Inner Mongolia

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### ABSTRACT

Quantifying niche space occupation based on assessments of multiple resource utilization traits can improve an understanding of plant species coexistence within communities of varying resource availability. We used an ‘occupied functional niche space (OFS)’ method based on multiple leaf traits to examine how plant communities accommodate changes in water availability within a desert-steppe ecotone spanning a limited geographic region. Our study area (western Inner Mongolia) spanned a range of conditions from highly water-limited (desert, D) to less water-limited (desert steppe, S), with two areas capturing the ecotonal boundary between these two vegetation types – partial desert (pD) and partial desert steppe (pS). We tested whether environmental filtering, heterogeneity, or limiting similarity drove trait convergence versus divergence of OFS across a desert-steppe ecotone. We quantified changes in plant community weighted means of both functional (specific leaf area and leaf dry matter content) and stoichiometric (leaf nitrogen content and leaf carbon concentration) leaf traits. OFS in the ecotonal areas (pS and pD) had larger volumes than the most mesic (S) subregion. However, divergence in the centroid of OFS was apparent for the driest (D) subregion, relative to the other three sub-regions. Underlying changes to OFS were changes in plant functional types, with more functional groups found in D and the fewest in S. For community-weighted leaf traits, SLA was highest in the ecotone area (pD and pS), while lowest in D. Further, community weighted means based on leaf dry matter content in D was the highest of all sub-regions, while both community weighted means based on leaf nitrogen content and community weighted means based on leaf dry matter content decreased as precipitation decreased, consistent with expectations. Our results suggest that communities alter both the volume and the centroid of functional trait space to adjust to decreasing water resource availability. We posit that limiting similarity (i.e. competitive exclusion) in water-resource use traits among species, supported by changes in life histories, led to OFS divergence in the ecotonal areas (pS and pD) and D, while environmental filtering may have led to convergence of OFS within the most mesic region (S) as water-stress lessens. In total, our results contribute knowledge as to how plant communities alter trait space in resource acquisition across climatic gradients, and underscores the utility of multi-trait approaches in understanding patterns of species coexistence in response to climatic changes.

### 1. Introduction

Trait-based approaches are now widely used to quantify plant functional diversity (FD), and to elucidate rules governing the assembly of ecological communities (Díaz et al., 2007; Mouchet et al., 2010; Pérez-Harguindeguy et al., 2013; Villéger et al., 2008). Ecologists also often use null models based on samples from a metacommunity species pool to infer whether functional trait dispersion is convergent or divergent within the same habitat (Coyle et al., 2014; Díaz et al., 2016).

Functional trait *convergence* may arise in harsh habitats primarily as a result of environmental filtering (Lhotsky et al., 2016), as only highly specific traits (e.g. CAM photosynthetic pathway) may allow individual survival and population persistence under certain conditions (Cornwell and Ackerly, 2009). By contrast, the principle of limiting similarity (MacArthur and Levins, 1967; Schellenberger Costa et al., 2017; Travis and S.J., 2009) suggests that coexisting species develop different functional strategies to minimize fitness differences and avoid interspecific competition, leading to functional trait *divergence* within a

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given habitat. As a result, the functional diversity of communities is likely to be driven, in part, by tradeoffs related to functional trait convergence versus divergence.

Ecological mechanisms driving FD can operate both within and between habitats and thus across spatial scales (Julie et al., 2010; Siefert et al., 2015). For example, effects of environmental factors, such as precipitation, on ecosystem properties are often relatively stronger when viewed across sites and thus spatial scales (Huxman et al., 2004; Sala et al., 1988). By contrast, at the within-habitat scale, the effects of environmental heterogeneity and limiting similarity between species on ecosystem properties are often more pronounced (Kotler and Brown, 1988; Speziale and Ezcurra, 2011). Transition zones (e.g. ecotone shifts from grass to shrub or steppe to forest; (Okin et al., 2009; Sottile et al., 2015), are particularly ideal for assessing relationships between functional diversity and species traits across environmental gradients, as such areas typically see large changes in both species composition and climatic drivers. Along such gradients, both environmental filtering and limiting similarity are thought to facilitate the coexistence of species (May et al., 2013; Schellenberger Costa et al., 2017), yet the relative strengths of these mechanisms are uncertain. Divergence of life history strategies or plant functional group types (PFT) among species can allow the full occupation of resource space under stressful or highly variable conditions within ecotones. For example, in the northern Patagonia forest-steppe ecotone, the dominant exotic annual and biennial species have been documented to occupy open niche spaces of resource acquisition not occupied by native species (Speziale and Ezcurra, 2011). However, smaller scale environmental heterogeneity can also affect functional diversity and coexistence of different species (Speziale and Ezcurra, 2011).

In recent years, plant functional traits have been increasingly adopted as an effective proxy for scaling ecological dynamics from the individual to the ecosystems level (Reich, 2014). Leaf traits in particular offer a promising approach for quantifying differences in plant functional diversity and resource utilization strategies among coexisting species, given the fundamental role of leaves in plant energy dynamics (Violle et al., 2014). For instance, annual species often have high specific leaf area (SLA; leaf area divided by dry mass), which is generally related to high growth rates and rapid utilization of resources (Reich, 2014). By contrast, shrubs with lower SLA and higher leaf dry matter content (LDMC) often have low growth rates and resource acquisition, yet also relatively high resistance to physical damage or stressful conditions (Gratani and Bombelli, 2000; Reich et al., 1999). Such differences in leaf traits suggest that quantifying leaf niche space can advance understanding of community assembly dynamics across ecotone boundaries and environmental gradients (Butterfield and Suding, 2013; Díaz et al., 2016). However, multi-trait analyses have historically been limited by our ability to quantify shifts in multi-dimensional trait space.

To address this limitation, Blonder et al. (2014) developed a niche hypervolume approach to assess community occupied functional niche space (OFS) in n-dimensional trait space, which is particularly relevant when considering multiple traits. This approach allows the quantification of how plants occupy multidimensional trait space, and additionally how space occupancy changes along environmental gradients. This further allows the boundaries of n-dimensional trait space to be delineated (Blonder et al., 2014), enabling comparison of niche hypervolumes among different communities. In contrast, single trait approaches reflect the position of a species occupation with regards to one resource axis, and thus may not be sufficient to capture strategy changes or tradeoffs (Loranger et al., 2016a). This is because the functional diversity (FD) indicated by a single resource axis is limited by the trait itself, and may produce inconsistent results between other trait indicators (Sfair et al., 2016), resulting in a pressing need to study FD based on multiple traits (Blonder et al., 2014; Villéger et al., 2008).

Here, we focus on a desert-steppe ecotone in Inner Mongolia, which represents a dramatic species compositional shift within a limited

geographical region (Liu et al., 2016). Turnover in species composition among the adjoining ecosystems suggests a likely transition towards suitable traits that enable survival under increasingly stressful water-limited conditions in moving from steppe to desert. Such different plant functional types occupy different niches space, so changes to the ratio of PFT in the community may produce changes in community functional diversity. Indeed, the desert-steppe ecotone of Inner Mongolia sees dramatic shifts in species composition and life histories; from perennial grasses-dominated communities in the steppe to shrub-dominated communities in the desert. This begs the question as to whether functional diversity with the ecotone and across the climatic gradient is convergent or divergent, and by extension whether the mechanism driving functional diversity are due to environmental filtering or limiting similarity among species.

Our study had three major goals: 1) assess how different indices of functional diversity in plant communities change across an environmental gradient of aridity; 2) assess whether functional diversity was divergent or convergent within-habitats; and 3) elucidate what ecological mechanisms may drive observed patterns in functional diversity. Filtering caused by water-limitation may cause functional convergence with respect to specific drought tolerance, resistance, or avoidance traits (Lhotsky et al., 2016; Sircar and Parekh, 2015). At the same time, limiting similarity may lead to a divergence of resource use strategies under water-limited conditions, effectively reducing soil moisture competition within a community (Schellenberger Costa et al., 2017). Functional divergence may also be driven by high environmental heterogeneity that drives higher functional diversity (Price et al., 2017). We posited that changes in OFS are related to changes in community-weighted means of key leaf traits (CWM) among changing PFT across the xeric-mesic gradient of the desert-steppe ecotone in Inner Mongolia. Two key questions guided our research:

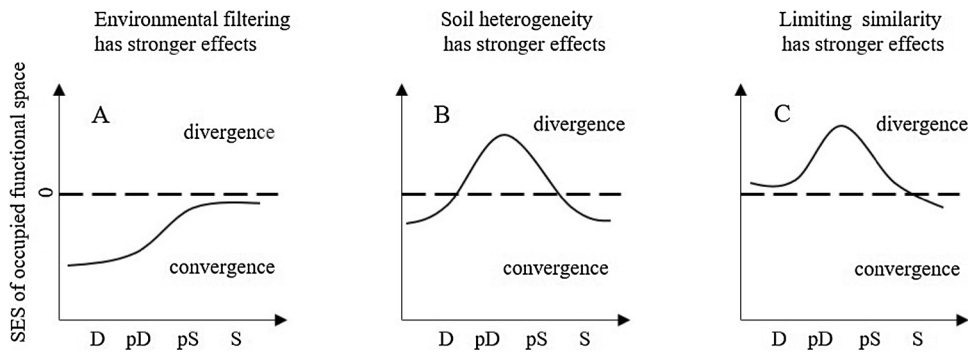
- 1) How does variation in plant functional types, community weighted trait means, and occupied functional niche space change across a desert-steppe transition, and what are the relationships between these factors?
- 2) Which factors – environmental filtering, environmental heterogeneity or limiting similarity – affect the convergence or divergence of OFS across the desert-steppe transition?

By measuring key leaf traits of plant species and soil properties, we tested three hypotheses related to distinguishing the effects of environmental filtering, heterogeneity, and limiting similarity on plant functional diversity: 1) Across sites (and thus the climatic gradient), environmental filtering has the strongest effects, leading to community trait convergence (Fig. 1A); 2) Soil heterogeneity has a stronger effect in transition areas than either limiting similarity or environmental filtering, and thus communities at transition areas with high environmental heterogeneity will show trait divergence (Fig. 1B); 3) limiting similarity has a dominant effect in subshrub and shrub regions, leading to community divergence in the desert area (Fig. 1C).

## 2. Materials and methods

### 2.1. Study area

The study area is located in the northwest region of Inner Mongolia, China, situated in desert and steppe transition zone habitats (Liu et al., 2016). There is a precipitation gradient of decreasing rainfall from the southeast to the northwest (Liu et al., 2016), which is mirrored in an overall pattern of decreasing productivity (see Fig. 2B). The 200 ha study area covers steppe, desert grassland, desert, and other ecosystems (Yan et al., 2015). Among the sites, the dominant plant species are *Reaumuria soongorica* Maxim, *Salsola Passerina* Bge, *Oxytropis aciphylla* Ledeb, and *Stipa glareosa* P. Smirn. Soils are typical gray-brown desert soils. Due to long-term wind erosion, soil nutrient content is low (Liu et al., 2016); soil nitrogen ranges from 0.24 to 1.79 g / kg and soil



**Fig. 1.** Conceptual representation of occupied functional niche space (OFS) divergence versus convergence as affected by environmental filtering, heterogeneity and limiting similarity (D, desert; pD, partial desert; pS, partial desert steppe; S, steppe). The y axis denotes the standardized effect size (SES) of occupied functional niche space of the four sub regions along the desert-steppe ecotone.  $SES < 0$  indicates trait convergence, while  $SES > 0$  indicates trait divergence. A, here environmental filtering plays a larger role in driving functional space relative to soil heterogeneity and limiting similarity, so the OFS of plant communities in the four regions are convergent. B, in the transition zone (pD and pS), soil heterogeneity plays a stronger role and is stronger than environmental filtering, which causes the community to become divergent. C, here limiting similarity plays a more powerful role in D, pD, and pS regions, as compared to environment filtering and soil heterogeneity. Therefore, the OFS of plant communities in the D, pD and pS regions are convergent in panel C.

carbon content ranging from 2.37 to 13.53 g / kg. Mean annual precipitation for the region ranging from 106 to 239 mm, and mean annual temperature is 3.8 °C.

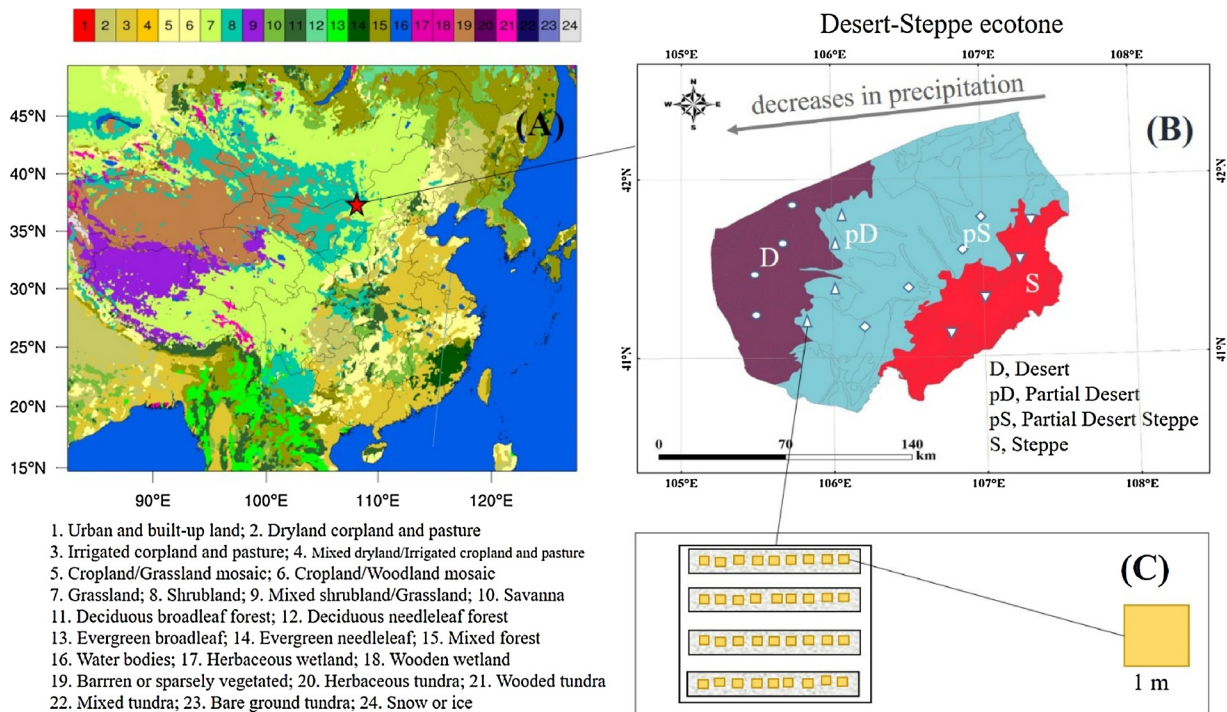
## 2.2. Vegetation sampling design

In order to study the shift in species composition and community niche space occupation across the desert-steppe ecotone, we divided the study area into four types of ecosystems from the southeast to the northwest according to vegetation, productivity, and soil type (Liu et al., 2016), which are referred to hereafter as steppe (S), partial desert steppe (pS), partial desert (pD) and desert (D). Within four sites in each ecosystem, we established 3–4 100 m transects, each with 8–10 1-m<sup>2</sup> quadrats located every 10 m along each transect (Fig. 2C). In total, we collected 115 quadrats in S, pS, and D habitats, and collected 80 quadrats in pD. Transects were located at least 500 m apart, with at least 5 km between each adjacent site. The total number of quadrats sampled was 425. Within each quadrat, we measured the height,

coverage, and number of all species. We divided all species in the study area into four PFT according to plant life history: annual, perennial herbs (hereafter perennial), subshrub, and shrub species. We defined subshrubs as a short woody plant, and further categorized every sampled species based on Flora of China. We used one way analysis of variance (ANOVA) to study the variation of PFT among the four research regions, and used pearson correlations to study the relationship between richness, PFT, and OFS.

## 2.3. Leaf traits sampling

We measured leaf traits following Pérez-Harguindeguy et al. (2013). Three leaves of every individual of each species within each quadrat were collected and leaf area of each individual was determined. In total, 23 species and 504 plants were selected for traits analysis. Dry mass to 0.01 g was then measured after 48 h of drying to 60 °C. We calculate SLA as the ratio of leaf area to dry mass, and calculate LDMC as the ratio of leaf dry mass to leaf fresh mass. The wet weight of collected



1. Urban and built-up land; 2. Dryland corpland and pasture
3. Irrigated corpland and pasture; 4. Mixed dryland/Irrigated corpland and pasture
5. Cropland/Grassland mosaic; 6. Cropland/Woodland mosaic
7. Grassland; 8. Shrubland; 9. Mixed shrubland/Grassland; 10. Savanna
11. Deciduous broadleaf forest; 12. Deciduous needleleaf forest
13. Evergreen broadleaf; 14. Evergreen needleleaf; 15. Mixed forest
16. Water bodies; 17. Herbaceous wetland; 18. Wooden wetland
19. Barren or sparsely vegetated; 20. Herbaceous tundra; 21. Wooded tundra
22. Mixed tundra; 23. Bare ground tundra; 24. Snow or ice

**Fig. 2.** Study area and sampling approach. A, location of study area in Inner Mongolia China. B, sampled areas in desert-steppe ecotone (D, desert; pD, partial desert; pS, partial desert steppe; S, steppe). The different colors denote different ecosystems according to their average productivity, with center blue representing the broad ecotone region (sampling occurred at the region edges with the other ecosystems). C, schematic representation of the sampling design used in the study. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

leaves was measured after 24 h of immersion in deionized water. In addition, ~ 1 g of leaf samples of each individuals within each transects were sub-sampled to determine the leaf nitrogen content (LNC) and leaf carbon concentration (LCC). We dried all leaf samples for 48 h at 65 °C before obtaining LNC and LCC, utilizing an Organic Elemental Analysis Instrument (Aiken et al., 2007). For our analysis, traits were split into leaf morphological (SLA and LDMC) and chemical composition (LNC and LCC) categories.

#### 2.4. Soil heterogeneity

In order to test how soil heterogeneity effects plant functional groups and OFS, we collected soil samples from each quadrat. Five soil cores at 15 cm depth were collected in each quadrat and composited. The diameter of soil cores is 3 cm and depth is 15 cm. A total of 442 soil samples were taken. A 100 g subsample from each sample was used to determine soil particle size. According to Schaeztl and Luehmann (2013), the soil samples were divided into five categories; clay, silt, fine sand, coarse sand, and gravel, with soil particle size distinguished by laser diffraction (Schaeztl and Luehmann, 2013). Another 5 g subsample was used to determine the soil carbon content and soil nitrogen content utilizing the same method as leaf samples.

#### 2.5. Calculation of occupied functional space

To assess plant community change under different environmental conditions, we used a niche hypervolume method based on a multi-trait approach developed by Blonder et al. (2014). We calculated the trait hypervolume for each quadrat in each ecosystem using SLA, LDMC, LNC, and LCC. All the species selected to build the hypervolume were the ones sampled from the regional species pool and sampled across all quadrats. We then compared the overlap of the 4-dimensional hypervolumes among the different ecosystems utilizing the ‘hypervolume’ package in R.

Shifts in the 4-dimensional functional trait space among the different ecosystems were plotted along each trait axis to detect the centroid’s trajectories. We used a null model to test for significant differences in the centroid among ecosystems (Eq. (1)). The null model we selected is a null lottery model (Loranger et al., 2016b), which selects species from the regional species pool to generate null communities with the same number of species as the observed community, from which we calculated the standardized effect size (SES). We also generated the null communities with the same number of species as the observed community, then calculated SES as Eq. (2). When  $SES < 0$ , the observed hypervolume is dramatically lower than expected (indicative of trait convergence), while the opposite is true for  $SES > 0$  (indicated traits divergence). The equations are:

$$P = \frac{\sum (\text{null. values} < \text{obs. value}) + \frac{\sum (\text{null. values} = \text{obs. value})}{2}}{5000} \quad (1)$$

$$SES = (\text{observed metric} - \text{mean of the null distribution}) / \text{SD of null distribution} \quad (2)$$

Eq. (1) refers to the probability that the observed value is not less than the simulated value. The smaller the P value, the more likely the observation value is smaller than the simulated value; and conversely, the more likely the observation value is higher than the simulated value. In Eq. (2),  $SES > 0$  indicates that the OFS value is convergent, and  $SES < 0$  indicates that the OFS value is divergent (Fig. 1).

#### 2.6. Relationships among environmental heterogeneity, PFT, and OFS

The study area, located at the boundary between China and Mongolia, has only a few meteorological stations (Liu et al., 2016), and

thus limited climate data on a short-term resolution are available for the study sites. Because of this data limitation, we used the soil attributes sampled to analyze the effect of environmental heterogeneity on OFS across the qualitative precipitation gradient. The soil properties used for analysis included soil nitrogen content, soil carbon content, the ratio of soil gravel, coarse sand, fine sand, silt, and clay. We use sediment 4–12 to study the ratio of different soil particle (Schlüter and Vogel, 2016). Soil heterogeneity was quantified separately for each soil attribute utilizing the coefficient of variation ( $CV = \text{mean} / \text{SD}$ ) between quadrats in each transect. The overall effect of soil heterogeneity (based on all seven soil attributes) on total mean CWM (based on each trait across the entire study area) was determined using meta-analytic methods following Price et al., (2017). CWM was calculated as follows:

$$CWM = \sum_{i=1}^s p_i x_i \quad (3)$$

In this equation,  $p_i$  means percentage of  $i$  species based on abundance,  $x_i$  means the number of species in the given community. We used the `metacor.op` function within the `metacor` package in R (Laliberté, 2011). This approach allowed us to infer which soil properties had the largest impacts on CWMs. To assess the impact of PFT on OFS, we treated the number of PFTs within communities as four different categories (e.g. 1 vs. 4 PFT), i.e., factors, and used an analysis of variance (ANOVA) with a post hoc test. In addition, we analyzed differences between these four categories at three different levels of soil CV (see Fig. S2).

### 3. Results

#### 3.1. CWM variance across the desert-steppe transition zone

Overall, the results of the four CWM traits show an inconsistent or weak trend along the water-availability gradient (Fig. 3); this result does not support hypothesis one, which posits that environmental filtering has a dominant effect across the climatic gradient.  $CWM_{SLA}$  was highest in pD and pS, while lowest in D (Fig. 3A), whereas  $CWM_{LDMC}$  was highest in D and lowest in pD area (Fig. 3B).  $CWM_{LNC}$  and  $CWM_{LCC}$  tended to decrease with decreasing water availability, and thus both were higher for S and lower for D (Fig. 3C & D). In the transition zones, pD and pS had different  $CWM_{LNC}$  and  $CWM_{LCC}$ , indicating that there are differences in resource utilization strategies of these two types of ecosystems.

#### 3.2. The effect of soil heterogeneity on CWM

Only CV of fine sand had an effect on the CWM values of each trait (Fig. S1), which is in contrast with hypothesis two, that soil heterogeneity has dominant effects on community trait convergence. In addition, heterogeneity of soil carbon had significant effects on  $CWM_{LCC}$ . However, the heterogeneity of other soil properties did not significantly affect CWM trait values. From Fig. S2, the differences of OFS at different number of PFT and at different levels of soil CV further suggests that the number PFTs and variation in fine sand content in the soil collectively acted to increase OFS. As a result, the higher the of number of PFT in a community, the higher OFS is (Table 1). This result is indicative of support for hypothesis three, that limiting similarity is a dominant driver of functional diversity, and that the mechanism underlying this may be variation in PFT, in concert with soil heterogeneity.

#### 3.3. Trait convergence versus divergence

We found evidence for functional trait divergence operating within the desert area ( $SES > 0$ ), which is in support of hypothesis 3 and further alludes to limiting similarity as mechanism operating in this area. We also found evidence of trait divergence in both the partial

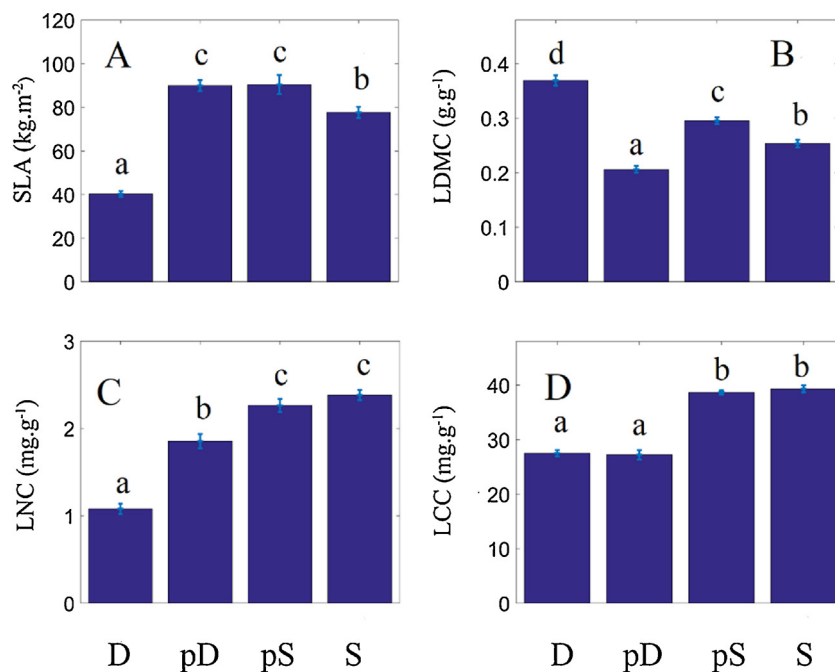


Fig. 3. Differences in community weighted means (CWM) of the four leaf traits among the different sub regions within the desert-steppe ecotone. Different letters indicate significant differences ( $P < 0.05$ ). Error bars denote standard error of mean.

Table 1

Correlation coefficient between PFT, species number and OFS.

	Species number	OFS
PFT	0.56**	0.29*
Species number	1	0.71**
OFS		1

\*\* Indicates p value < 0.01.

\* Indicates p value < 0.05. PFT is plant functional type, and OFS is occupied functional space.

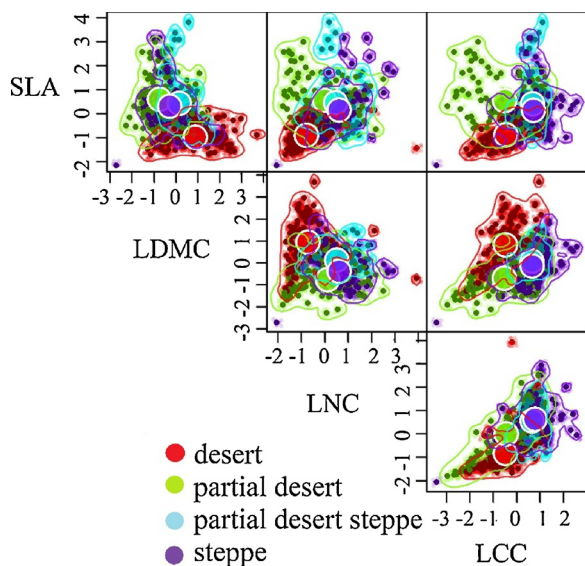


Fig. 4. The variance of occupied functional niche space (OFS) among the four different types of sub regions within the desert-steppe ecotone. Red is the desert (D) area; green is the partial desert (pD) area; blue is the partial desert steppe (pS) area; purple is the steppe (S) area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

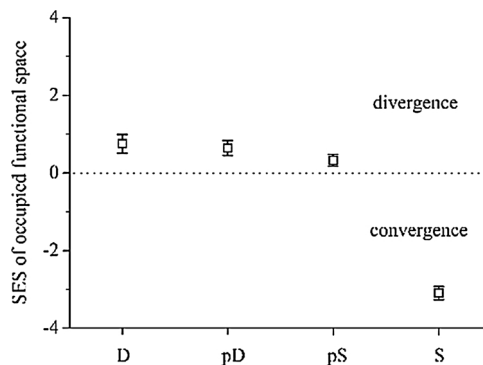


Fig. 5. The results of standardized effect size (SES) of occupied functional niche space of the four sub regions along the desert-steppe ecotone. A SES < 0 indicates trait convergence, while a SES > 0 indicates trait divergence. While there was strong evidence for trait convergence in steppe region (s), the three driest sites exhibited evidence for trait divergence in the three driest.

desert and partial steppe transitional zones (pD and pS; Fig. 5). By contrast, there was strong evidence for trait convergence in the steppe area (SES < 0), the most mesic area in the study region. In moving from steppe to desert, there was also significant variation in occupied functional space (OFS; Fig. 4), with the size of OFS in the pD area much larger than all other ecosystems. Using the centroid's distance as an indicator of the shift in OFS among the different study areas, the centroid of D had the furthest distance from the pD, pS, and S (Fig. 4, Table S1), indicating the largest shift in OFS occurred in the desert area.

#### 4. Discussion

In this study, we quantified functional niche space of a desert steppe ecotone, utilizing multiple leaf traits and a niche hypervolume approach (Blonder et al., 2014). In particular, we studied niche variation along gradient of water availability gradient from the perspectives of community weighted traits means (CWM) and occupied functional niche space (OFS). Within a constrained geographical region, the desert steppe ecotone of Inner Mongolia sees dramatic shifts in species

composition and life histories, in which plant communities shift from the perennial grasses-dominated community to shrub-dominated communities (Liu et al., 2016). Changes in species composition – and in particular functional groups – are likely to lead to changes in mean functional traits at the community scale, and thus niche space occupation. Here, we confirm the role that changes in life histories have on community weighted traits means, and its consequent effects on niche space occupation within this and potentially many other ecotone regions. In addition, we find evidence for functional trait divergence both transitional (partial desert, pD; partial steppe, pS) and highly stressful (desert, D) environments, with the most mesic area of our study (steppe, S) displaying evidence for functional trait convergence.

#### 4.1. Environmental filtering and trait convergence

Our results do not support hypothesis one; that environmental filtering has dominant effects on community traits convergence, because only in the steppe area – the most mesic area of the gradient - functional traits within the community demonstrated evidence for convergence. This may be due to environmental filtering being most prevalent in this specific area; where traits of species within the community may trend toward higher competitiveness (e.g. for light or nitrogen) as conditions become less stressful. In contrast, movement towards drier, more stressful conditions engendered a greater functional diversity in our study, suggesting stressful or less predictable environments promotes functional diversity. Such diversity may be related to resource capture traits for coexistence as soil moisture becomes increasing scarce, which would then produce increased functional trait dispersion (Friedman et al., 2015; McDonald et al., 2017).

#### 4.2. The role of environmental variability

We were not able to detect a strong effect of soil heterogeneity on functional trait dispersion at the community scale within the transition zone. Therefore, our results do not support hypothesis two, which posits that soil heterogeneity has a strong effect on community traits. Although heterogeneity in abiotic conditions can also affect functional dispersion, we found no strong correlations, with only fine sand heterogeneity impacting the CWM of all traits (Fig. S1). While surprising, this type of result has been observed before. For example, Price et al., 2017 reported that the CV of soil moisture and light did not strongly affect community functional diversity. We also found that OFS and plant functional group type (PFT) had a significant positive correlation under different levels of CV fine sand (Fig. S2). As a result, heterogeneity of soil particle size and soil carbon are likely not the cause of the shift among different life histories we observed in this desert-steppe ecotone. Therefore, we cannot conclude that soil heterogeneity, at least with respect to what we measured, is not a dominant driver functional diversity in our study region.

#### 4.3. Limiting similarity and life histories as mediators of functional diversity

Our results indicate that functional divergence in transition areas and desert areas may result mainly from limiting similarity. Changes in PFT might change interspecific competition by producing variation in resource acquisition strategies, which would support limiting similarity as the chief mechanism operating within the communities of our study (de la Riva et al., 2017; Stubbs and Bastow Wilson, 2004). Changes in life histories of species within communities across our study gradient produced shifts in CWM and OFS of leaf functional traits (Fig. S3). For instance,  $CWM_{SLA}$  (community weighted trait means based on specific leaf area; SLA) was high and  $CWM_{LDMC}$  (community weighted trait means based on leaf dry matter content; LDMC) was low in the transition zone of our study region (i.e. pD area and pS area). Furthermore, decreases in precipitation led to decreases in both  $CWM_{LNC}$  (community weighted trait means based on leaf nitrogen content; LNC) and  $CWM_{LCC}$

(community weighted trait means based on leaf carbon content; LCC).

Such trait differences are likely due differences functional group representation. The pD, pS and S areas of our study having higher proportions of grasses, including both annual and perennials, which typically have higher growth rates than the primarily shrub species found in the D area. This is consistent with higher levels  $CWM_{SLA}$  and  $CWM_{LNC}$  in these three areas versus the driest region dominated by shrubs. LDMC is related to the content of structural carbohydrates, which typically indicates the resistance of plants to drought or herbivory-induced stress (Pérez-Harguindeguy et al., 2013). In support of this, LDMC was higher in the D area - which is dominated by subshrub and shrubs functional groups – in contrast to other ecosystem types (Fig. S4). In addition, intraspecific trait variation of species will also affect CWM (Julie et al., 2010; Mao et al., 2017; Violle et al., 2012). Thus, species with different functional similarity may result through changes in functional leaf traits within species or shifts in life histories between communities caused by species turnover.

Changes in PFT also informed changes in OFS (Table 1), where changes in OFS included changes to both the size and centroid. For example, the size of the OFS in the pD area was higher than all other ecosystems (Figs. 3, S5), while there was a notable shift in the location of the centroid of OFS in D area, relative to other areas. Shifts in the OFS centroid may reflect an ecological strategy to more fully capture and/or conserve increasingly scarce soil water resources with increased aridity. For instance, the desert area is more water limited relative to the other areas, leading the OFS to shift to different areas of resource utilization space. Changes in PFT representation can also reflect the change of the centroid. This may be driven by changes in life histories, as the plant community obtains a greater diversity of drought-resistant traits through occupying different niche space (Shriver, 2017), also leading to changes in the centroid of the community trait space.

As a consequence, we posit environmental filtering due to selection for higher resource acquisition to be the main factor that determines trait convergence within more mesic steppe communities. By contrast, in the transitional zone (pD, pS) and desert communities, we posit limiting similarity and shifting functional group representation to drive trait dispersion that supports hypothesis 3. Such trait dispersion was further reflected in shifts in both the size and centroid of occupied functional space. One limitation of our study is that the selection of traits is still limited to a few key leaf traits, and thus does not reflect belowground trait distributions, which are equally relevant for understanding occupied functional space in water-limited regions. As a consequence, future multi-trait approaches would benefit from assessment of root traits in concert with aboveground traits to more fully elucidate both below and aboveground resource utilization strategies across environmental gradients.

## 5. Conclusions

Our findings provide evidence for the notion that plant communities alter both the volume and centroid of niche hypervolumes in multiple resource acquisition traits across spatial scales to adjust to gradients of resource availability. The mechanism underpinning this here was likely through changes in PFT, and thus shifts in the means of different traits. Notably, OFS was highest in an ecotone subregion, reflecting a higher diversity of trait values, while the largest shift in the centroid of OFS occurred in the driest subregion, potentially reflecting the increasing influence of water scarcity on resource use strategies. Moreover, within the transition zones (partial desert and partial steppe area) and the driest area (desert), limiting similarity among species appears to cause OFS to diverge, as reflected by the shift of PFT along the precipitation gradient. In contrast, shifts towards increasingly rapid resource acquisition traits were reflected in trait convergence within the more mesic steppe region of our study. In total, our study clarifies the potential mechanisms underpinning links between functional traits, life histories, and niche space occupation for community assembly dynamics across

environmental gradients, and underscores the utility of multi-trait approaches.

#### Author contributions

- All authors conceived and designed the review and methodology; all contributed to writing and revising the manuscript.
- WM, XYZ, THZ, and YLL collected the data.
- WM, ZBS, and AF analyzed the data.
- WM and MS led the writing of the manuscript.

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#### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.envexpbot.2018.06.011>.

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