

ARTICLE

Macrosystems Ecology

Using local and regional trait hypervolumes to study the effects of environmental factors on community assembly

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Hainan University, Grant/Award Number: 20035; National Natural Science Foundation of China, Grant/Award Number: 41671208; State Key Laboratory of Frozen Soil Engineering of China, Grant/Award Number: SKLFSE-ZT-36; US National Science Foundation, Grant/Award Number: DEB-1354732

Handling Editor: Ginger Allington**Abstract**

Determining how local and environmental conditions affect community assembly processes is critical to understanding and preserving ecosystem functions. A combination of plant traits is required to capture the broad spectrum of strategies that species employ to respond to varying environmental conditions. The trait hypervolume (i.e., n -dimensional trait space) accurately describes such multi-trait characteristics. Here we use hypervolume mismatch metric, defined as the difference between the observed trait hypervolume and the trait hypervolume inferred from local and/or regional species pools, to investigate plant community assembly. Our method suggests plant traits should be categorized a priori to quantify trait hypervolumes associated with environmental variation (i.e., resource utilization strategies). Using the plant trait data from North American and South African grassland communities, this hypervolume mismatch metric can be applied to different categories of traits and scales, thus providing new insights into community assembly processes. For example, the trait hypervolumes calculated from physiological traits (e.g., mean stomatal length, stomatal pore index, and mean stomatal density) were highly correlated with regional environmental factors. By contrast, local species pool factors explained a greater proportion of variation in hypervolumes estimated from leaf stoichiometric traits (e.g., leaf nitrogen [N] content, leaf carbon [C] content, and leaf C/N ratio). Therefore, this hypervolume mismatch framework can accurately identify the separate impacts of regional versus local species pools on community assembly across environmental gradients.

KEYWORDS

community assembly, functional traits, grassland, hypervolume, species pool

INTRODUCTION

Plant species composition forms the backbone of community structure and ecosystem function. Understanding the

rules that govern plant community assembly and biodiversity has been a fundamental goal of ecological research for over a century (Hooper et al., 2005; Jarvis et al., 2019). The debate over which mechanism plays a

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dominant role in determining how species aggregate into communities has greatly enriched ecology as a science (López et al., 2021; Münkemüller et al., 2020; Tucker et al., 2018). For instance, “competitive exclusion” theory suggests coexisting species should be functionally distinct from one another (McGill et al., 2007), while “environmental filtering” theory suggests the opposite, that is, similar environmental constraints should lead to convergence of species traits toward an optimal strategy (Kraft et al., 2015). While these opposing mechanisms are not mutually exclusive, accurate quantification of the relative contribution of each process to local community assembly has been challenging, until recently. The rapid accumulation of species genetic and functional trait information, as well as the development of sophisticated statistical methods, have provided both the data and tools necessary for such analyses (Brunner et al., 2019; He et al., 2020; Violle et al., 2007). However, the generality of these rules is still under scrutiny (Blonder et al., 2015), with the residual variation in community assembly remaining quite large even after accounting for local processes such as habitat variation and species interactions (Wiszniewski et al., 2013).

In addition to local environmental variation and species interactions, regional processes, such as the regional species pool and geological history, could influence local species composition (Chen et al., 2012) and community assembly (Ordoñez & Svenning, 2018). We define a regional species pool as the total potential number and traits of species found across the focused regions (e.g., eastern North America). By contrast, the local species pool indicates the number and traits of species in sampled plot/community within a specific size at a local scale or in a certain region. The composition of regional pools is the product of evolutionary, environmental, and geological history. Moreover, regional pools serve as a source of species seeds for local communities. Differences in regional pools may explain why areas with similar climate, such as east Asia and eastern North America, differ drastically in local plant species diversity (Qian & Ricklefs, 2000). The fate of these species seeds within each locale is shaped by the local environment and species interactions (Sork et al., 2016; Tilman & Lehman, 2001), and it is particularly variable in regions with many different habitat types and/or significant barriers to dispersal.

Isolating the impacts of regional versus local processes on local community assembly, however, is difficult (Cornell & Harrison, 2014). Comparisons of species assemblages considered number and traits constructed from local and regional species pools may provide some clues, and this due to plant traits can act as proxies of species adaptive strategies to their environment (Forrestel et al., 2017; Kearney & Porter, 2009) and have been used to evaluate community functional diversity

and species assembly rules (de Bello et al., 2012; Moullot et al., 2013). However, a single trait cannot fully capture the complex ecological strategies that species exhibit for coping with environmental variability. The integration of multiple species traits into an n -dimensional trait “space,” as a concept analogous to the n -dimensional niche space proposed by Hutchinson (1957), may be a more appropriate means for understanding species ecological strategies (Blonder et al., 2014; Hutchinson, 1957). Moreover, the recent development of sophisticated statistical methods makes it possible to mathematically describe the n -dimensional trait space, here referred to a “hypervolume” (Blonder, 2018). The hypervolume’s boundary, size, and centroid of the multi-trait space can be studied individually to make inferences about species interactions and community assembly (Blonder et al., 2018; Mao et al., 2020). This method has been widely recognized as a useful tool for investigating many niche-related processes, including the delineation of niche spaces defined by climate and biological characteristics (Bilton et al., 2016; Echeverría-Londoño et al., 2018), species distribution modeling (Barros et al., 2016; Lamanna et al., 2014), and the assessment of the distribution of species diversity and its underlying mechanisms (Šímová et al., 2015). By comparing the multidimensional trait spaces of different constructed species assemblages, we may be able to disentangle the underlying regional and/or local mechanisms governing local community assembly.

Pre-classification of multiple traits into categories is helpful to understand the community assembly mechanisms. Without prior classification, integration of multi-traits may cause unwanted noise in the hypervolume algorithm (i.e., the potential correlation among traits and redundancy of data indicated by traits). Additionally, different traits relate to a different resource utilization strategy, for example, leaf traits versus root traits, stoichiometry, and physiological traits (Carvalho & Cardoso, 2020). Different categories of traits have different response strategies to environmental factors, various at different scales. For example, some traits such as root traits and stoichiometry traits may be related to the environmental variance at the local scale but not at the regional scale (Griffin-Nolan et al., 2018). In addition, the trait space calculated based on different types of traits can indicate information originating from different scales (Bittebiere et al., 2019; Forrestel et al., 2017). In brief, prior classification trait variables can differentiate traits that contribute more to the biological performance of the species.

Here, we integrate the concept of regional species pools with a multi-trait hypervolume algorithm to develop a testable model that can be used to quantify the relative contributions of regional versus local processes to

local community assembly. Specifically, we develop the traits hypervolume mismatch (THM) metric, which is defined as the distance between two community trait hypervolumes compared with that inferred from local and/or regional species pools. Using previously published plant trait data from North American (NA) and Southern African (SA) grassland communities, we demonstrate that the THM metric can provide new insights into the effects of regional and local processes on community species assembly. To avoid unwanted noise in the hypervolume model (Carvalho & Cardoso, 2020), we categorize trait data as either stoichiometric traits (e.g., leaf nitrogen) or physiological traits (e.g., stomatal pore index [SPI]). This was also done as certain traits are more likely to correlate with certain environmental characteristics (Griffin-Nolan et al., 2018). We test the following hypotheses: (1) the trait space among communities at a local scale should be similar in size and centroid; (2) if communities are similar, this similarity should be strongly affected by the regional environment, whereas local environment should drive dissimilarity; and (3) trait hypervolumes based on physiological versus stoichiometric traits should differ in their sensitivity to regional versus local environments.

MATERIALS AND METHODS

Site description

We applied the THM model to analyze differences between local and regional trait pools of 10 grassland communities in central North America and South Africa ($n = 20$ total sites; Appendix S1: Figure S1). Both NA and SA grassland communities were widely distributed along a precipitation gradient (200–1000 mm/year) and showed a significant productivity gradient. The growing season is different between these two regions, from May to mid-September in North America and mid-November to March in South Africa, but the growing season temperature is similar, ranging from 20.6 to 24°C. All sites with a history of light grazing management were un-grazed during the trait sampling period. In North America, the sampling sites spanned desert grasslands, shortgrass prairie, mixed grass prairie, and tallgrass prairie. In South Africa, the sampling site spanned the Little Karoo's desert grasslands in the Northern Cape, the Eastern Cape, the Free State, and the grasslands of Kwazulu-Natal (Axelrod, 1985; Echeverría-Londoño et al., 2018). As a result, herbaceous plants in each region exhibit different life history strategies (Forrestel et al., 2017). Despite these differences, both regions contain herbaceous communities dominated by C_4

grasses and share similar precipitation gradients (255–973 and 238–934 mm/year in North America and South Africa, respectively). These characteristics make NA and SA grasslands an ideal pair for studying the influence of local and regional processes on local community assembly.

Plant traits and sampling

Twenty sampling plots ($1 \times 1 \text{ m}^2$) were established at each site, resulting in a total of 400 plots for the final analysis across both regions combined. Within each plot, the height and coverage of the most common species were recorded. We define the most common species as the relative cover is $>10\%$ in any individual plot, or the mean relative cover is $>2\%$ at the site level. The total list of species found across all 10 sites of each region makes up the regional species pool S for the THM metric. All trait data are from Forrestel's study (Forrestel et al., 2017), and as described in this study, recently emerged, fully expanded leaves of each of the common species in each plot were collected to measure key leaf traits, including leaf nitrogen content (LNC), leaf carbon content (LCC), leaf C/N ratio (C/N ratio), mean stomatal length, mean stomatal density, and SPI. The functional traits were then divided into physiological (i.e., stomatal) traits and stoichiometric traits (LNC, LCC, and C/N ratio).

The traits “hypervolume” mismatch metric

The “hypervolume” algorithm uses a high-dimensional kernel density method to estimate the shape and centroid of an n -dimensional niche space (Blonder et al., 2018). With this algorithm, we can also assess the space overlap and distance between the centroids of two hypervolumes. Based on this concept and a multi-trait dataset, we develop a THM metric to assess the distance between two trait hypervolumes (Figure 1, Table 1). Specifically, the observed trait space (H_{obs}) was calculated based on trait values of all species observed in each plot (assuming there are r species in the plot). The null trait space (H_{inf}) was derived from a random assembly of r species from the species pool of either the region or the local site that contained a particular plot. The steps followed in the THM model are as follows.

First, before implementing the hypervolume method with trait data, we categorize plant trait data into different groups based on their connections with major ecological processes (competition, environmental filtering, etc.)

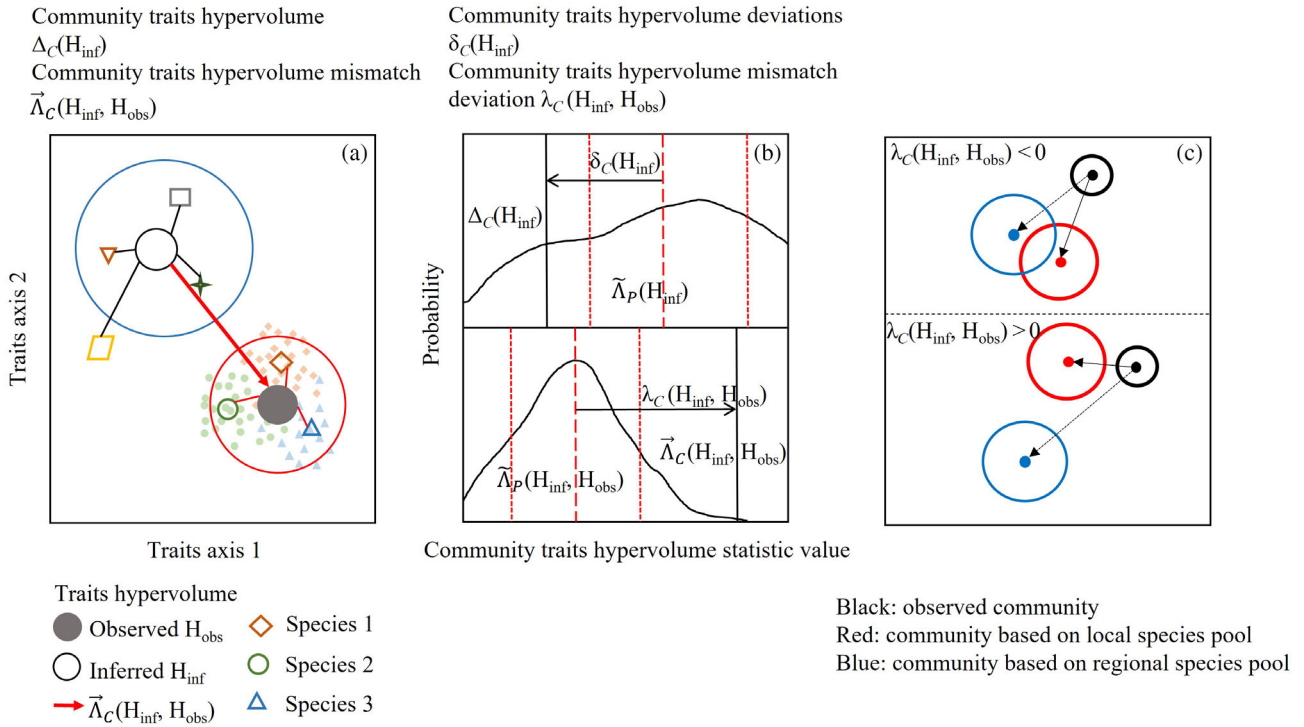


FIGURE 1 Depiction of the derivation of the traits hypervolume mismatch (THM) metric. This concept is obtained from Blonder's hypervolume framework (Blonder et al., 2015) and uses traits data instead of climate data. $\Delta_C(H_{inf})$ in panel (a) indicates the community traits hypervolume and $\delta_C(H_{inf})$ indicates the community traits hypervolume deviation. $\tilde{\Lambda}_P(H_{inf})$ indicates the value of the red long-dashed line at the upper panel in (b); $\tilde{\Lambda}_P(H_{obs})$ indicates the value of the red long-dashed line at the lower panel in (b); community traits hypervolume deviations, $\delta_C(H_{inf})$ (upper black arrow in [b]), and community THM deviation, $\lambda_C(H_{inf}, H_{obs})$ (lower black arrow in [b]), are computed by comparing the observed statistics (black vertical line) to the null distributions (black curves and vertical short-dashed red lines are 25% [left] and 75% [right] quartiles, and the vertical long-dashed red line is the median [i.e., 50% quartile]). At the upper panel in (c), $\lambda_C(H_{inf}, H_{obs}) < 0$ indicates community within site will produce similar hypervolume mismatch. At the lower panel in (c), $\lambda_C(H_{inf}, H_{obs}) > 0$ indicates community within site will produce different hypervolume mismatch.

and environmental factors on a variety of scales. For example, we can classify traits into morphological traits and physiological traits, or physiological traits and stoichiometric traits (Griffin-Nolan et al., 2018).

Second, we denote the trait niches as $D(S, \hat{T})$ for all available species (S), each with its individual trait value within each trait category (\hat{T}). In a given region R , we denote all available species as $\hat{S} \subseteq S$, where \hat{S} can be viewed as the regional species pool. For a local site S_I within R , all present species are included in the set $S(S_I)$, which can be viewed as the local species pool of the site. Note that this hierarchical division of species pools can be categorized further to the plot level within a single site (Figure 2, Table 1).

Third, we construct the trait space of site S_I with (randomly simulated) observed trait measurements for M times. Using simulated trait data, we calculate community trait statistics (see Table 1). After numerous simulations (e.g., $M > 500$), we expect to see that local/regional multi-trait species pools generate similar local/regional communities based on community trait

statistics. For each simulation step (i -th time), the detailed procedure and statistics computation are described below.

For each unique species (s_k) at site S_I , we randomly select one set of traits (t_k) of \hat{T} from multiple data records of the same species at the site, as well as the percent cover (c_k) of s_k within the community. Assuming there are N unique species in site S_I , we would have N total samples $\{s_k, t_k, c_k\}q$, $k = 1, \dots, N$. Based on the species cover $\{c_k\}$, we can calculate the averaged $\{t_k\}$ for each site S_I , denoted by t_{obs}^i . For each observed t_{obs}^i at site S_I , combined with local and regional species pools ($S[S_I]$ and \hat{S}) as well as trait niches $D(S, \hat{T})$, we can estimate four community trait statistics, that is, $\Delta_C(H_{inf})$, $\delta_C(H_{inf})$, $|\vec{\Lambda}_C(H_{inf}, H_{obs})|$, and $\lambda_C(H_{inf}, H_{obs})$ in Table 1. The algorithms used here for estimation are based on Blonder et al. (2015), although here we replace time with hypervolume information. Specifically, our algorithms use H_{inf} and H_{obs} in place of t_{inf} and t_{obs} used in Blonder et al. (2015). Thus, related formulations are described as follows:

TABLE 1 Summary of interpretation of community traits statistics.

Metric abbreviation	Metric	Interpretation	Smaller values mean	Larger values mean
$\Delta_C(H_{inf})$	Community traits hypervolume	Traits niche volume occupied by species in community H_{inf}	Species traits within community have a higher similarity, or there are some species within a smaller range of traits variance	Species traits within community have a higher dissimilarity, or there are some species with a broader range of traits variance
$\delta_C(H_{inf})$	Community traits hypervolume deviation	Traits niche volume occupied by species in community H_{inf} , relative to traits niche volume for species in a random sample from regional species pool	<0, environmental filtering; the local environment selects for species with certain traits	>0, environmental permissiveness
$ \vec{\Lambda}_C(H_{inf}, H_{obs}) $	Community traits hypervolume mismatch	Distance between the center of inferred traits volume H_{inf} and that of observed traits volume H_{obs}	Community close to the niche space center of biogeographic region	Community apart from niche space center of biogeographic region, or close to the edge of the region
$\lambda_C(H_{inf}, H_{obs})$	Community traits hypervolume mismatch deviation	Distance between inferred traits volume H_{inf} from observed traits volume at H_{obs} , relative to distance for species in a random sample from regional species pool	<0, community within site will produce similar hypervolume mismatch	>0, community within site will produce different hypervolume mismatch

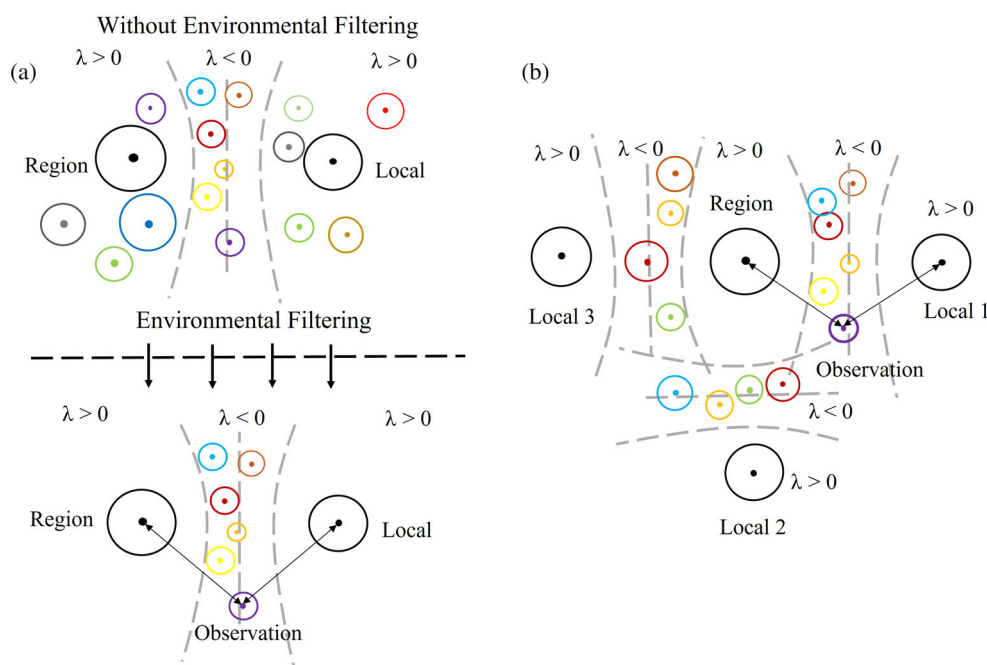


FIGURE 2 Expectations for the traits hypervolume mismatch (i.e., λ_C) metric under different scenarios of assembly of community traits. Only when $\lambda_C < 0$ can the community be assembled in the given environment, which reflects the balance of local pool effect and regional pool effect. Panel (a) is the schematic diagrams of community traits assembled together with one local pool (one site) and one regional pool. Panel (b) is with multi-local pools (each site indicates a local pool) and an integrated regional pool (combining the multi-local pools into one regional pool).

$$\delta_C(H_{\text{inf}}) = \Omega\left(\Delta_C(H_{\text{inf}}), \tilde{\Delta}_P(H_{\text{inf}})\right), \quad (1)$$

$$\lambda_C(H_{\text{inf}}, H_{\text{obs}}) = \Omega\left(\left|\tilde{\Lambda}_C(H_{\text{inf}}, H_{\text{obs}})\right|, \left|\tilde{\Lambda}_P(H_{\text{inf}}, H_{\text{obs}})\right|\right), \quad (2)$$

$$\Omega(X_{\text{obs}}, X_{\text{null}}) = \frac{X_{\text{obs}} - Q(X_{\text{null}}, 0.5)}{Q(X_{\text{null}}, 0.75) - Q(X_{\text{null}}, 0.25)}. \quad (3)$$

1. Community traits hypervolume $\Delta_C(H_{\text{inf}})$ is the mean median distance between the random samples from all species' niches (indicated by traits; Blonder et al., 2015) in the community and the samples' median.
2. Community traits hypervolume deviation as in Equation (1), where $\tilde{\Delta}_P(H_{\text{inf}})$ is the generated null regional distribution of community traits hypervolume calculated by randomly sampling the regional pool multiple times (e.g., 500 times).
3. Community THM $|\tilde{\Lambda}_C(H_{\text{inf}}, H_{\text{obs}})|$ is the distance between the observed sample and the hypervolume center of the inferred samples in the community.
4. Community THM deviation as in Equation (2), where $|\tilde{\Lambda}_P(H_{\text{inf}}, H_{\text{obs}})|$ is the generated null regional distribution of community THM calculated by randomly sampling the regional pool multiple times.
5. The abovementioned Ω function is the rescaling function that transforms the observed and null values of an arbitrary statistic X into a standardized effect size. As in Equation (3), $Q(x, y)$ in the equation is the y -th quantile of x .

Statistical analysis

We calculate the trait hypervolume among 10 sites along the longitude at two continents using the ‘‘Hypervolume’’

package (Blonder, 2018). Related meteorological data come from the Climate Data Store (Raoult et al., 2017). The correlation among mean annual precipitation, annual precipitation, growing season precipitation, and trait hypervolume is based on the Pearson's correlation. The change of $\delta_C(H_{\text{inf}})$ is based on the THM model, which is developed based on the ‘‘Hypervolume’’ package. All calculations are performed in R statistical software (R version 3.6.3; R Core Team, 2020).

RESULTS

Using the THM metric (Figure 1), we investigated the interregional and intra-regional differences in trait hypervolumes for the NA and SA grassland communities. The difference between H_{inf} and H_{obs} at two different scales (i.e., regional vs. local site) can measure the degree of relative influence from processes operating at the two scales (see Table 1 and Figure 1 for further details).

Overall, we found that the trait hypervolumes based on physiological traits were highly correlated with regional-scale environmental factors (Table 2). For $\Delta_C(H_{\text{inf}})$, which indicates the trait niche volume occupied by species in community H_{inf} , the trait hypervolume among the 10 sites of two continents has a noticeable trend with respect to longitude. For example, in South America, the trait hypervolume increased with longitude (Appendix S1: Figure S2). The trait hypervolume based on physiological traits was significantly affected by environmental factors in North America (Table 1). At the same time, it had a higher correlation coefficient with SA's climate (Appendix S1: Table S1). By contrast, the trait hypervolume based on stoichiometric traits was less correlated with climatic factors (Appendix S1: Tables S2 and S3).

Furthermore, for $\delta_C(H_{\text{inf}})$, we found that the deviation of the inferred traits niche volume (H_{inf}) from traits niche

TABLE 2 The relationship between hypervolume index and climate factors in North America based on mean stomatal length, mean stomatal density, and stomatal pore index.

Climate metric	VM		DV_VM		MMVM		DV_MMVM	
	CC	<i>p</i>	CC	<i>p</i>	CC	<i>p</i>	CC	<i>p</i>
MAP	0.518	0.000	0.412	0.000	0.131	0.000	0.056	0.016
Annual precipitation	0.542	0.000	0.423	0.000	0.093	0.000	0.083	0.000
Growing precipitation	0.589	0.000	0.459	0.000	0.093	0.000	0.117	0.000
MAT	−0.021	0.355	−0.578	0.000	−0.318	0.000	0.078	0.001

Note: MAP indicates the mean annual precipitation, MAT indicates the mean annual temperature, annual precipitation indicates 1 year of precipitation at the sampling year, growing precipitation indicates the values of months of the growing season (in North America, from May to September; in South Africa, from November to March), VM indicates the hypervolume, $\Delta_C(H_{\text{inf}})$, DV_VM indicates the hypervolume deviation, $\delta_C(H_{\text{inf}})$, MMVM indicates the hypervolume mismatch, $|\tilde{\Lambda}_C(H_{\text{inf}}, H_{\text{obs}})|$, and DV_MMVM indicates the hypervolume mismatch deviation, $\lambda_C(H_{\text{inf}}, H_{\text{obs}})$. CC refers to correlation coefficient, and *p* indicates *p* value.

volume (niche was indicated by species traits) for species in a random sample originated from regional species pool was generally less than zero, indicating that the observed community is close to the niche space center of the biogeographic region. This suggests that regional effects on community assembly are stronger than local effects (Figure 3; Appendix S1: Tables S4 and S5). The mismatch of physiological trait hypervolumes was affected mainly by mean annual temperature in North America (Table 2). Yet, in South Africa, the trait hypervolume mismatches based on physiological traits were affected by all climatic factors (Appendix S1: Table S5). Lastly, in both North

America and South Africa, $\lambda_C(H_{inf}, H_{obs})$ was less than zero (Figure 3), also indicating a similarity between communities at the local scale.

DISCUSSION

By integrating traits, region/local species pools, and the hypervolume algorithm, we developed the THM metric, which can be applied to different categories of traits and at different scales (local vs. regional) to understand environmental and evolutionary constraints on community

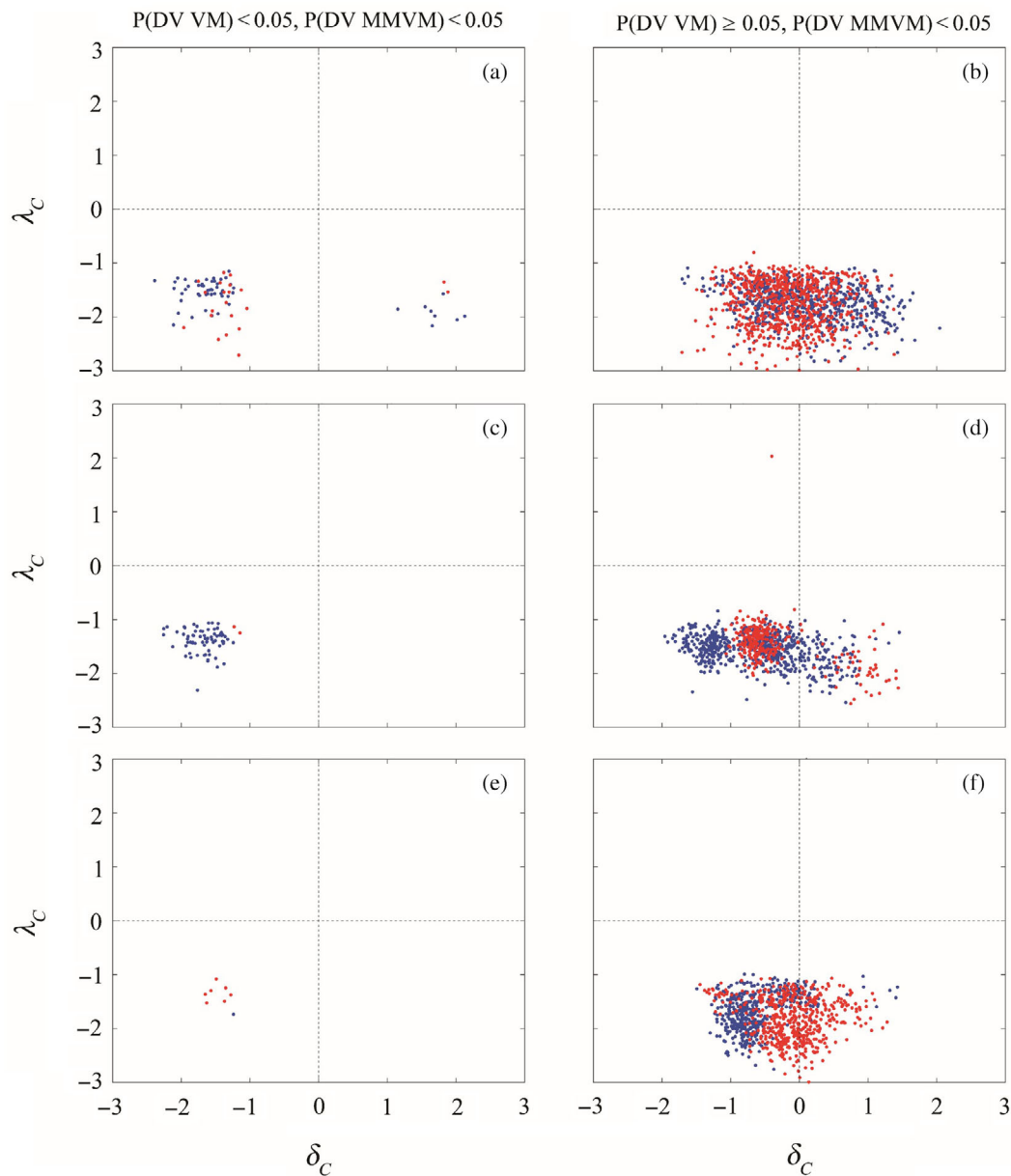


FIGURE 3 Hypervolume deviation (δ_C) versus hypervolume mismatch deviation (λ_C) for all traits, physiological traits, and stoichiometric traits. (a) and (b) indicate all traits, (c) and (d) indicate stoichiometric traits, and (e) and (f) indicate physiological traits. Blue is for South Africa, and red is for North America.

assembly. In the case study of NA and SA grassland communities, we found that λ_C , hypervolume mismatch deviation was less than zero for the estimated hypervolumes based on different types of traits. Although this is contrary to Hypothesis 1, this suggests that local plant communities have similar degrees of hypervolume mismatch. However, we can still emphasize some similarities among the plant communities that survived in similar habitats at the local scale. Furthermore, the non-zero λ_C suggests that community trait assembly processes are not completely random, with both local and regional processes influencing the assembly of community trait space. As a result, the regional effects have more substantial effects on community assembly than local effects, which support Hypothesis 2. It is worth noting that limiting our analysis to only common species in a community could contribute to the non-zero λ_C as trait range and variation often increase with the inclusion of rare species (Avolio et al., 2019; Ordonez & Svenning, 2018).

Our study also demonstrates that environmental influences on hypervolumes depend on trait categories. Regional environmental factors (i.e., precipitation drives stomatal trait variation) were highly correlated with trait hypervolumes based on physiological traits, but they were weakly correlated with those estimated from stoichiometric traits. The results support Hypothesis 3, that different categories of traits differ in their sensitivity to regional and local environments. This is likely because stoichiometric traits are highly influenced by local edaphic factors like nutrient availability and soil heterogeneity (He et al., 2015). Herbaceous plants tend to colonize microclimates within a landscape (Ricklefs & Latham, 1992), which vary extensively in edaphic qualities (i.e., soil thickness, soil properties, and water holding capacity) and may impact local niche differentiation in terms of leaf stoichiometry. This is an essential mechanism for maintaining local functional diversity (Bernard-Verdier et al., 2012). This observation is supported by previous work suggesting root traits and leaf stoichiometric traits are strongly affected by the variance of local-scale environmental factors, which aids in coexistence (Maire et al., 2009; Maire et al., 2012). Local variability in soil nutrients can also affect the niche dimension and alter species richness (Harpole & Tilman, 2007).

Most theories suggest that species can survive in a given environment by environmental filtering theory and similarity limitation theory (Belmaker & Jetz, 2012; Cornwell & Ackerly, 2009). Traits in ecology help to understand these theories, that is, after the species has been filtered by external environment (i.e., the species must have traits that can be filtered through the environment), and affected by competition among species within the community (i.e., the traits among species will have

divergent traits based on similarity limitation), then these species finally coexist in the community (Kraft et al., 2015; Schellenberger Costa et al., 2017). However, the current theories focus on an individual scale and do not consider what kind of community will assemble based on those survived species. What factors will affect these communities and are there similarities? Within the local area, species filtered by environmental and biotic factors have similar traits (de Bello et al., 2013; MacArthur & Levins, 1967); therefore, communities assembled by these species should also have similar characteristics, in fact this β diversity has proved these similarities from the perspective of species composition (Chase & Myers, 2011; Myers et al., 2013). Second, such theories suggest that species must first need to be filtered through the environment and then need to meet species competition. From a trait perspective, the species that can meet the requirements will be much larger than the observed. The results of this study suggest that species that survive together will try to assemble a similar community, and the similarity character is determined by the relationship of multi-traits of each species.

It is worth noting that this study does not consider the strong correlation between trait hypervolumes and phylogenetic diversity. Previous studies assumed that niche space and phylogenetic diversity are correlated and may be redundant as more evolutionary time allows for more trait changes to accumulate (Tucker et al., 2018). Phylogenetic diversity may explain some variance in trait hypervolumes along gradients of environmental factors such as soil nutrients (Coyle et al., 2014). However, previous work suggests that phylogenetic diversity is not affected by local-scale niche availability or niche differentiation (Anacker & Harrison, 2012) and is more likely affected by regional factors. Also, the THM metric can help extract orthogonal axes (Carvalho & Cardoso, 2020), which can eliminate possible correlations among different trait variables. Finally, due to the limitations in our dataset, we did not check environmental factors globally, which may pose an obstacle to the THM model's robustness at different scales.

The findings of this study can improve our understanding of biodiversity maintenance mechanisms in the context of global change. Local habitats are increasingly fragmented, and the simultaneous changes in local-regional climate can make modeling/predicting community process more complicated. There is a need to more accurately understand how the diversity of environmental factors influences community assembly, and the THM metric has a broad application to integrate these various factors. Furthermore, the metric can verify the speciation mechanism of different regions, to explore what factors determine community distribution and community assembly.

CONCLUSION

In summary, we demonstrated how the THM metric provides a different method to integrate plant traits and species pools to illuminate differential impacts of regional versus local processes on community species assembly. We recommend using multiple traits in future estimates of multidimensional trait space and hypervolume mismatch, especially the traits with mechanistic linking to environmental variables of interest. The THM metric presented here can improve predictions of community assembly processes under novel environmental conditions, and thus it is beneficial to species distribution modeling faced with climate change.

AUTHOR CONTRIBUTIONS

All authors contributed to the idea and design of the paper and its methodology, and to the writing and revision of the manuscript; Elisabeth J. Forrestel and Melinda D. Smith collected the data; Wei Mao and Zhibin Sun analyzed the data; Wei Mao, Anping Chen, Robert Griffin-Nolan, and Melinda D. Smith led the writing of the manuscript.

ACKNOWLEDGMENTS

Melinda D. Smith acknowledges support from the Drought-Net Research Coordination Network (US National Science Foundation DEB-1354732). This study was also supported by National Natural Science Foundation of China (41671208), the Start-up funding from Hainan University (kyqd 20035), and by the State Key Laboratory of Frozen Soil Engineering of China (SKLFSE-ZT-36). The authors also thank A. K. Knapp for insightful discussions.

CONFLICT OF INTEREST

The authors have no conflict of interest about this manuscript.

DATA AVAILABILITY STATEMENT

Data (Forrestel et al., 2017) are available from Dryad: <https://doi.org/10.5061/dryad.q1b6v>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Mao, Wei, Zhibin Sun, Elisabeth J. Forrestel, Robert Griffin-Nolan, Anping Chen, and Melinda D. Smith. 2022. “Using Local and Regional Trait Hypervolumes to Study the Effects of Environmental Factors on Community Assembly.” *Ecosphere* 13(10): e4253. <https://doi.org/10.1002/ecs2.4253>