

The variations in trait role, trait conservatism and habitat heterogeneity confound our understanding on community assembly

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Abstract

Proper conceptual framework of community assembly is critical for understanding biodiversity patterns. In this work, we raised the concepts, ‘predominant/ assistant trait’, to characterize distinct trait roles in the processes of community organizing. We further incorporated them into previous theoretical understanding. Upon this theoretical basis, we presented a case study with two rodent datasets in the Hengduan Mountains, China. Due to weak phylogenetic signal and extraordinary habitat heterogeneity, we detected most of the rodent communities appeared random at both phylogenetic and morphological facets, which have prevented us to identify the role of morphological attributes and major process structuring rodent communities. We inferred that the variations in trait role, trait conservatism and habitat heterogeneity are major noise confounding our understanding on community assembly. Based on theoretical modification and empirical demonstration, this work has offered a novel and comprehensive perspective to understand the patterns of phylogenetic and trait-based community structure.

Introduction

How and why biodiversity varies along environmental gradient is one of the fundamental issues in ecology and biogeography (Patino *et al.* 2017; Brown 2014; MacArthur & Wilson 2001). Proper answering this question is meaningful and essential, not only for understanding biodiversity *per se*, but also for promoting sustainable biodiversity conservation and relevant government-lead policy making. The observed pattern of biodiversity and underlying mechanism have been constantly debated for centuries (Hutchinson 1959; Darwin 1859). Earlier ecologists have paid more attention to the variation of taxonomic composition (i.e., species richness, evenness and variety) (Allen *et al.* 2002; Whittaker *et al.* 2001) and proposed many empirical explanatory hypotheses related to contemporary and/or historical environmental variance (i.e., habitat heterogeneity, energy, water-energy balance, area and geometric constrain) (McCain 2007; Evans *et al.* 2005; Boyce *et al.* 2003; Hawkins *et al.* 2003; Colwell & Lees 2000). Definitely, these traditional taxonomic approaches have provided a comprehensive understanding on community assembly. However, subsequent ecologists have realized that taxonomic measurements alone are insufficient to identify mechanistic processes without regard to interspecific ecological and evolutionary information (e.g., differentiations in ecological niche and evolution) (Guittaret *et al.* 2019; Blonder 2018; Martiny *et al.* 2015; Liu *et al.* 2013; Cavender-Bares *et al.* 2009; Swenson & Enquist 2009; Wiens & Graham 2005).

Recently raised phylogenetic and trait-based approaches provide a more reasonable perspective in mechanistic understanding of species assembly (Swenson 2013). Based on classical niche theory (Hutchinson 1959) and phylogenetic niche conservatism hypothesis (PNC) (Wiens & Graham 2005; Pagel 1999), Webb (2000) offered an approach to calculate community structure based on phylogeny. As a follow-up, Webb *et al.* (2002) later raised a framework of phylogenetic community structure with which species assembly process could be roughly estimated by measuring phylogenetic structure and evaluating trait conservatism. In the last decade, more and more studies have applied the information of phylogeny and functional trait into understanding community assembly process along environmental gradient (Chun & Lee 2018; Feng *et al.* 2014; Cianciaruso

et al. 2012) at various spatial and temporal scales (Maherali & Klironomos 2007; Cavender-Bares *et al.* 2006; Swenson *et al.* 2006). Meanwhile, the framework of community construction has been constantly modified (Kraft & Ackerly 2010; Kraft *et al.* 2007; Cavender-Bares *et al.* 2004). The effect of stochastic process, environmental complexity and the effect of negative density-dependence have been taken into account in later frameworks, which enabled it more practical in interpreting species assembly in real and complex ecosystems (Kraft & Ackerly 2010; Kraft *et al.* 2007). By examining trait similarity on phylogeny and correlation between phylogenetic and trait dispersion, Cavender-Bares *et al.* (2004) and Losos *et al.* (2003) have reported that long history of competitive interactions could produce trait convergence on phylogeny. This means that PNC can interpret trait evolution in some taxa, but does not so in any single case (Losos 2008). In other words, ecologists should carefully examine the magnitude of PNC rather than subjectively presuppose its existence in functional attributes (Losos 2008). This has enhanced the worldwide application of phylogenetic and trait-based approaches to study on the potential process driving community assembly.

Although ecologists have made a mass of efforts to open the ‘Pandora’s Box’ of community construction, the mechanism underlying community assembly are still poorly understood. Under prior frameworks of community structure, if relevant functional attribute is phylogenetically conserved on phylogeny, phylogenetic dispersion is expected to be concordant with the trait dispersion of concern (Kraft & Ackerly 2010; Kraft *et al.* 2007; Cavender-Bares *et al.* 2004; Webb *et al.* 2002). But discordant or opposing patterns between phylogenetic relatedness and phylogenetically conserved trait were also reported in flora (Yang *et al.* 2014; Swenson & Enquist 2009) and fauna (Du *et al.* 2017). Generally, most of empirical studies believed that these contradictory patterns were resulting from the low magnitude of phylogenetic signal (Du *et al.* 2017; Yang *et al.* 2014). An alternative explanation points to the potential erroneous inferences provided by phylogenetic signal metrics (Swenson & Enquist 2009).

Kraft and Ackerly (2010) have ever mentioned that some kinds of traits are more sensitive responding to ecological process than the others. However, it appears extremely challenge to quantify how much one functional attribute relates to a certain ecological function. This is because, on one hand, ecological process usually organizes community by acting on multiple phenotypes and their interactions (Miner *et al.* 2005; Norberg *et al.* 2001). Under a certain scenario, the functional roles of ecological attributes usually differs from each other and exhibits distinct dispersion. For instance, plant traits related to productivity should be functional clustering in local plant communities, whereas traits related to disturbance and regeneration are expected to be locally over-dispersed (Swenson & Enquist 2009; Grime 2006; Thompson *et al.* 1996). On the other hand, nonrandom patterns of functional structure along environmental gradient have implied the functional role of a certain phenotype likely varies across assemblages (Du *et al.* 2017). It means that the trait dominating species assembly within one habitat might act an assistant role in another habitat, *vice versa*. These evidences above mentioned have implied that disentangling distinct functional contribution of traits is essential for revealing the truth underlying community assembly.

A novel framework of phylogenetic and trait-based community structure

Well known, community assembly processes act on species through a series of phenotypes (or frequently called functional traits) (Chai *et al.* 2019; Laughlin & Messier 2015; Pawar 2015). According to distinct contributions of functional attributes in community assembly, we raised the concepts of “predominant trait” and “assistant trait” to refer major or supporting traits mediating assembly process. Combining prior theoretical efforts (Kraft & Ackerly 2010; Kraft *et al.* 2007; Cavender-Bares *et al.* 2004; Webb *et al.* 2002) and the thought of distinct contributions displayed by traits, we proposed a novel framework of phylogenetic and trait-based structure.

We built this modified framework on four key assumptions. Firstly, following with prior conceptual work, we assumed that phylogenetic relatedness was a comprehensive proxy of interspecific similarity at multiple ecological niches (Swenson 2013). Secondly, we assumed that functional traits were independent with each other in evolutionary and ecological processes. Because the relationship among phenotypes was extremely complicated and taxon-specified, which was beyond the research scope in this work. Thirdly, we assumed that environmental filtering effect, competitive exclusion and stochastic process are three major processes

driving community assembly. Other processes such as mutualism, host-pathogen interactions, plant-insect interactions and negative density-dependence mentioned in (Cavender-Bares *et al.* 2009) were not involved in this study, but deserved to be considered in future studies. Lastly, we assumed that phylogenetic signal metrics such as Pagel’s lambda (Pagel 1999) and Blomberg’s K (Blomberg *et al.* 2003) could accurately infer the phylogenetic conservatism in functional traits. These assumptions above have also clarified the baselines to apply this framework in interpreting the biodiversity pattern.

We simulated ecological processes and community structure using virtual species (A~H), phylogeny and traits (phylogenetic conserved traits: T1 and T3; phylogenetic convergent traits: T2 and T4) (Box 1). Two major parameters concerning trait conservatism (phylogenetically conserved or convergent) and trait contribution (predominant or assistant role) were involved in later prediction on phylogenetic and functional dispersion. Given the effects of environmental filtering and competitive exclusion produce opposite imprints on community structure, as a representative, we only simulated the assembly process driven by environmental filtering effect. Following with Kraft and Ackerly (2010), environmental filtering processes were discussed within simple (Fig. 1, scenario A and B) and complex (Fig. 2 scenario C, D and E) habitats, respectively. Besides, we simplified complex habitat with only two microhabitats, which contained independent predominant and assistant traits.

According to the phylogenetic and functional patterns demonstrated in Fig 1 and 2, the modified framework of phylogenetic and trait-based community structure was summarized in Table 1. Generally, in sample habitat, phylogenetic community dispersion was accordant with the functional dispersion of phylogenetically conserved predominant traits, and opposed to phylogenetically convergent predominant traits. While, dispersion comparison between phylogenetic relatedness and assistant traits in simple habitat became more complicated, which highly depended on the degree of phylogenetic conservatism and inter-trait relationship. In complex habitat, due to multi-directional effect across different microhabitats, phylogenetic and functional dispersion appear complicated and unpredictable.

The rodent communities in the Hengduan Mountains (HMs)

Rodents (Rodentia) are characterized as the mammal lineage with high reproductive capacity, rapid and strong environmental adaptive ability (Schenk *et al.* 2013; Kozak & Wiens 2010; Jansa *et al.* 2009). As the most diverse lineage in Mammalia, rodents have undergone an extraordinary adaptive radiation throughout the Cenozoic and have spread into almost all natural and artificial terrestrial ecosystems (Fabre *et al.* 2012). These ecological characteristics have entitled rodents a key role in local and global biomass cycling (Quintero & Wiens 2013; Schenk *et al.* 2013; Kozak & Wiens 2010; Jansa *et al.* 2009).

Under the extent of modified conceptual framework, we took rodents in the HMs, China, as our study model to present a case study and try to answer two questions. Firstly, we attempted to (1) reveal the process driving the elevational patterns of phylogenetic and morphological structure and their dependence on climatic variables. Secondly, we aimed to (2) identify the importance of trait conservatism, trait role and habitat heterogeneity in driving phylogenetic and trait-based community structure.

Material and Methods

Study location and datasets

The HMs (97°-106 °E, 21°-35°N) lies in the southwest of China, covering most part of Yunnan and Sichuan provinces as well as the east part of Tibet. Aiming to detect the role of trait conservatism, functional role of trait as well as habitat complexity in assembling rodent communities, we extracted two rodent datasets based on local sampling survey (local sampling dataset, LSD) and regional records along elevation (regional elevation-range dataset, RED). LSD was extracted from 15 field surveys along local elevational gradient in HMs, including 80 sampling sites containing 45 rodent species (20 genera, 5 families) (Du *et al.* 2017). Six sampling sites in LSD having been conducted within farmland were excluded in Du *et al.* (2017) to get rid of anthropic impacts on elevational pattern of rodent community structure. In this work, farmland sampling sites were included within LSD, as we also expected to compare patterns and underlying processes with

those in RED (which contains all typical vegetation types within HMs). Regional elevation-range dataset (RED) were extracted from historical studies, local surveys and museum records within HMs region (Wen *et al.* 2016a; Wen *et al.* 2016b). As some of historical collections were conducted according to administrative divisions (i.e., province and county), species surviving within non-typical montane habitats (i.e., arid and semi-arid desert) have been recorded within HMs. In order to get rid of this sampling bias in RED, we further conducted data cleaning and excluded species in non-typical habitats at the edges of HMs. The elevational scope in this work ranged from the base of HMs (< 1000 m) to 5000 m. The base zones below 1000 m were treated as one elevational band, as many historical records below 1000 m were hard been further divided. Areas above 1000 m were equally divided into 100-m elevation bands (i.e., 1000m~ 1100m; 1100m~ 1200m... 4900m~ 5000m). In total, RED contained 94 rodent species (46 genera, 7 families) distributing within 41 elevational bands in HMs. The taxonomy of rodent species followed Wilson and Reeder (2005), except that we recognize *Niviventer ling* as being distinct from *N. confucianus* (Du *et al.* 2017 and their reference).

Phylogeny reconstruction

Phylogenies of rodents in phylogenetic analyses in this study were reconstructed using published DNA sequences downloaded from GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>) (last accessed in July, 2018). We inferred the phylogeny using four mitochondrial DNA genes (Cytb, CoI, 12s-rRNA and 16s-rRNA) and three nuclear DNA genes (IRBP, GHR, and RAG1) (Fig. S2 and S3). DNA sequences that used into phylogeny reconstruction could be found in Table S1. Phylogenetic relationships among rodent species were estimated through Bayesian inference (BI) using MrBayes (version 3.2.5) (Ronquist *et al.* 2012). Parameter settings and other detailed information in phylogenetic reconstructions can be found in Du *et al.* (2017).

Morphological attributes and phylogenetic signal

In this work, we quantified four major characters representing ‘size’ (head-body length, hind-foot length, ear length and tail length) and three characters representing ‘shape’ (tail/head-body ratio, hind-foot/head-body ratio and ear/head-body ratio) into morphological analyses. All morphological attributes were quantified by the mean values of eight (four males and four females) or four (two males and two females) adult individual specimens measuring (Du *et al.* 2017).

We examined the phylogenetic signal by estimating Pagel’s lambda (Pagel 1999) and Blomberg’s K (Blomberg *et al.* 2003). Pagel’s lambda is a parameter scaling the interspecific covariances under Brownian evolution and non-sensitive to taxon number (Pagel 1999), whereas Blomberg’s K is a scaled ratio trait variation than expected under Brownian motion (Wang & Clarke 2014; Blomberg *et al.* 2003). The values of lambda range from zero to one: if lambda = 0, trait evolution performs independent of the phylogeny; if lambda=1, trait evolve following a Brownian motion model (Wang & Clarke 2014; Pagel 1999). Blomberg’s K usually yields positive values (K> 0), and higher K values indicate stronger phylogenetic signal (Blomberg *et al.* 2003): if K = 1, trait evolves following Brownian motion model; if K > 1, interspecific trait similarity is higher than expected under Brownian motion model; if K < 1, interspecific trait divergence is higher than expected under a Brownian model (Wang & Clarke 2014; Blomberg *et al.* 2003).

Measuring phylogenetic and trait-based structure

In this work, the standardized mean phylogenetic distance (SES.MPD) and its functional analogy, the standardized pairwise trait distance (SES.PW) were applied to quantify phylogenetic and trait-based community structure (Swenson 2014). Using simulation procedure under a null model (independent swap) (Gotelli & Entsminger 2001), SES.MPD and SES.PW were calculated with the following equation:

$$SES = (\text{Mean}_{\text{obs}} - \text{Mean}_{\text{null}}) / \text{sd}_{\text{null}}$$

where, Mean_{obs} is the observed MPD or PW within community, $\text{Mean}_{\text{null}}$ is the mean value of MPDs or PWs of 999 randomly generated communities, sd_{null} is the standard deviations of MPDs or PWs of 999 randomized communities. As species data was binary in each community in two datasets, calculation for phylogenetic and trait-based structure were accomplished without abundance weighted (abundance weighted = false).

Environmental variables

There is unified opinion among ecologists that patterns of biodiversity across space (i.e., latitudinal or elevational gradient) is as a result of local adaptation to abiotic and biotic variables but not spatial gradient *per se*. With the aim to detect which variables have lead community assembly, we extracted six climatic variables (annual mean temperature, AMT; temperature seasonality, TS; annual precipitation, AP; precipitation seasonality, PS; net primary productivity, NPP and potential evapotranspiration, PET), which have been frequently reported relating to small mammals biodiversity (Wen *et al.* 2016b; Stevens & Gavilanez 2015; Wu *et al.* 2013).

Lacking in detailed coordinate information for each sampling site and elevational bands, data extraction for each environmental variable was accomplished with local and regional digital elevation model (DEM). We constructed polygon layer for each local or regional elevation band by constraining vertical and horizontal scope. The mean values of environmental variable within sampling site or band polygons were extracted for each assemblage (details to see Du *et al.* 2017). AMT, TS, AP and PS were all downloaded from Worldclim (<http://www.worldclim.org/>) (last accessed in July, 2016) (Fick & Hijmans 2017) at 30 seconds resolution. NPP, and PET were obtained from MODIS products (MOD17A3 and MOD16A3) (Mu *et al.* 2011; Mu *et al.* 2007) accessed from LP DAAC (Land Processes Distributed Active Archive Center; <https://lpdaac.usgs.gov/>) (last accessed in July, 2016). We performed layer mosaic and projection transformation with ENVI (ver. 4.7) (VIS 2011) and ArcMap (ver. 10.0) (ESRI 2010).

Statistical analyses

Morphological attributes were all log-transformed and centralized before calculating trait-based community structure. Principal component analysis (PCA) was applied for size and shape related morphological attributes, and the first two components were used to calculate morphological dispersion. Standardized phylogenetic and trait-based dispersion (SES.MPD and SES.PW) were determined with two-tailed t-test: if community structure is significantly higher than those in null communities ($SES > 1.97$), community will be defined phylogenetically or functionally dispersed; if community structure is significantly lower than expected ($SES < -1.97$), community is characterized as phylogenetically or functionally clustered. If community structure is non-significant different from that in null communities ($-1.975 < SES < 1.975$), community is characterized as random (Kembel *et al.* 2010; Webb *et al.* 2008; Webb *et al.* 2002; Webb 2000). Underlying process (environmental filtering, interspecific exclusion and stochastic process) and the functional role of traits were estimated according to our revised empirical framework. The elevational patterns of phylogenetic and trait dispersion were determined using polynomial regressions. Best predictive model were selected according to Akaike information criterion (AIC). Besides, we also quantified the elevational pattern of species richness, which is reasonable in estimating environmental fitness and habitat heterogeneity (Brown 2001).

As ecological process and the functional role displayed by trait are habitat-specified, hence, the approach of linear regression model or correlation, to some extent, is more convenient but probably underestimate the dependence between phylogenetic and trait-based community structure. In contrast, pairwise comparison of this kind approach would be more accurate in predicting assembly process and the functional role of a certain trait. In order to obtain comparable results, we applied these two approaches (i.e., correlation analysis and pairwise comparison) in inferring the relationship between phylogenetic and morphological structure. In comparison analysis, if both phylogenetic and trait dispersion showed same status (clustered, random or dispersed), we called it phylogenetic-trait consistence or congruence; or else, we named it phylogenetic-trait inconsistency or incongruence. Pairwise comparison and correlation analysis have been repeatedly conducted between phylogenetic dispersion and morphological dispersion of size and shape related traits.

With the aim to estimate the environmental dependence for phylogenetic and trait dispersion, we conducted forward selection procedure to choose the best climatic predictor(s). Structure equation models (SEM) were applied to estimate the direct and indirect effects of climatic factors on phylogenetic and trait dispersion. Environmental variables were all log-transformed and centralized in best predictor selection and SEMs. All of these calculations were accomplished under R environment (ver. 3.5.1) (Team 2013). phylogenetic signal

detection was carried out with the package ‘phytools’ (Revell 2012); PCA analysis, correlation analysis and polynomial regressions were all accomplished with default packages in R (Team 2013); Following the approach in Swenson (2014), phylogenetic and trait-based structure was calculated with package ‘picante’ (Kembel 2009) and package ‘vegan’ (Oksanen *et al.* 2007; Dixon 2003); Forward selection in climatic factors was finished with ‘leaps’ (Miller 2002) and ‘vegan’ (Oksanen *et al.* 2007; Dixon 2003) packages; SEMs were performed with package ‘lavaan’ (Rosseel 2012).

Results

Phylogenetic signal

In phylogenetic signal detection, magnitude and significance of phylogenetic signal detection for morphological attributes varied across two datasets. Both λ and K indexes for all morphological attributes were below one, some of which were approaching to zero (LSD: $\lambda_{\text{ear}} < 0.001$, $p > 0.999$; $\lambda_{\text{hindfoot-rat}} < 0.001$, $p > 0.999$. RED: $\lambda_{\text{ear-rat}} < 0.001$, $p > 0.999$) (Table S2). In general, phylogenetic signals in regional dataset (RED) were more significant than that in local dataset (LSD) (Table S2).

Pairwise comparison between phylogenetic and trait-based community structure

For 80 local sampling sites in LSD, nearly but more than a half assemblages presented clustered phylogenetic dispersion ($\text{SES.MPD} < 0$) (45, 56.25%); nearly but more than a half assemblages presented functional clustering ($\text{SES.PW} < 0$) (46, 57.50%) in size-related trait dispersion; less than a half assemblages exhibited clustering in shape-related trait dispersion (35, 43.75%). According to two-tailed t-test ($\alpha = 0.05$), most of rodent assemblages in LSD performed phylogenetic or/and functional random (Table S3).

Similar to LSD, nearly but less than a half assemblages in RED exhibited phylogenetic clustering (20, 48.78%); more than one third assemblages presented functional clustering in size-related attributes (14, 34.15%); nearly but more than a half assemblages were functional clustering in shape-related attributes (23, 56.10%). According to two-tailed t-test ($\alpha = 0.05$) in RED, only one rodent assemblage presented significant clustering on phylogeny ($\text{SES.MPD} < -1.975$) (1, 2.44%) with the rest all exhibiting phylogenetically random ($-1.975 < \text{SES.MPD} < 1.975$) (40, 97.56%); both size and shape related morphological structure exhibited functional random in all rodent assemblages ($-1.975 < \text{SES.PW} < 1.975$) (41, 100%) (Table S3).

As most assemblages in LSD and RED were random at phylogenetic and morphological dimensions, there was extremely high degree of phylogenetic-trait congruence in the pairwise comparison (Table S4).

Elevational patterns and environmental explanations

According to the results of polynomial regression, phylogenetic and morphological structure as well as species richness (SR) in LSD all exhibited significant ($p < 0.05$) linear or binomial pattern along elevational gradient (Fig. 3 and S1; Table S5). In RED, phylogenetic structure (SES.MPD) and morphological structure for size-related morphological attributes ($\text{SES.PW}_{\text{size}}$) exhibited non-linear relationship with elevation, shape-related morphological structure and SR exhibited significant linear and quadric relationship with elevation (Fig. 3 and S1; Table S5).

According to the results of forward selection, we found that the best predictors varied across datasets and facets of community structure (Table S6). In SEMs, there were positive correlations between phylogenetic and morphological structures in LSD (Fig. 4, a), which were extremely weak in RED (Fig. 4, b).

Discussion

The novel framework of phylogenetic and trait-based community structure: distinct trait roles

Since Webb *et al.* (2002) raised the framework of phylogenetic community structure, mechanistic understanding on community assembly has experienced remarkable progress in the last decade. However, phylogenetic approaches highly rely on phylogenetic relatedness being a comprehensive proxy of ecological similarity (Swenson 2013; Losos 2008), which implies the necessity of phylogenetic-trait intergration in revealing mechanism underlying community assembly.

Distinct functional role and contribution of traits in assembling species has been mentioned in earlier empirical and theoretical studies (Kraft & Ackerly 2010; Swenson & Enquist 2009; Grime 2006; Thompson *et al.* 1996). Swenson & Enquist (2009) and Grime (2006) have detected that plant traits related to productivity often appeared clustered in local communities, while disturbance and regeneration related traits displayed locally over-dispersed. Kraft & Ackerly (2010) have ever predicted that functional traits related to resource use and environmental tolerance were more likely to answer habitat filtering, resource use strategy traits were more sensitive to interspecific competitive exclusion and niche differentiation, physical and chemical defense traits displayed a major role in responding to enemy-mediated negative density dependence. These information together have presented an apparent signal that part of traits are more important (predominant traits) in responding to a certain ecological process, and the others performed relatively less sensitive (assistant traits) response to assembling process. Absolutely, either predominant or assistant traits are indispensable niche components at both species and community levels. Actually, it appears extraordinarily challenge to decide which functional attributes display a more important role than the others, as they work as an alliance in most of cases (Zukswert & Prescott 2017; Grassein *et al.* 2014).

Based on prior understanding on community structure, we rethink over community assembly process by taking account of distinct functional role (predominant and assistant role) of phenotype. Through simulating assembly process in simple habitat, we found that phylogenetic dispersion was accordant with the functional dispersion of conserved predominant trait, and opposed to the structure of convergent predominant trait. This result of predominant traits could also occur in assistant trait, especially when assistant trait presented similar ecological and evolutionary characteristics (Table 1). But in most instances, the dispersion of assistant traits appeared unpredictable in simple habitat. By comparison, phylogenetic and trait dispersion in complex habitat appear extremely complicated, as community structure is resulting from similar or/and distinct assembly processes acting on conserved or/and convergent functional attributes. Therefore, it seems impossible to predict the functional role of a certain trait in structuring community within a complex habitat. These patterns have also provided two reasonable explanations for the incongruent dispersion between conserved trait and phylogenetic relatedness (Du *et al.* 2017; Yang *et al.* 2014; Swenson & Enquist 2009): the trait might act an assistant role organizing community in simple habitat; or the community is defined upon a heterogeneous habitat.

Pairwise comparison between phylogenetic and trait-based community structure: the variations in trait conservatism and habitat heterogeneity

Trait conservatism

Admittedly, basic understanding on trait conservatism through phylogenetic signal detection greatly affects our mechanistic interpretations on assembly process (Losos 2008). Even though prior studies have suggested that lambda is not sensitive to the size of species pool (Wang & Clarke 2014; Blomberg *et al.* 2003), however, we found both K and lambda metrics significantly varied across datasets. Besides, most of morphological traits were phylogenetically convergent, especially in LSD. Significant but weak signal ($K < 1$, $p < 0.05$) probably results from adaptive convergence to particular environment and indicates labile phylogenetic signal (Blomberg *et al.* 2003). These results in phylogenetic signal detection is not surprising especially in the most diverse mammalian lineage (Fabre *et al.* 2012). Environment driven convergent adaptation in functional traits can largely promote coexistence among distant species, efficiently reduce habitat resources caused competitive exclusion among relatives and ultimately facilitate interspecific differentiation in rodents (Cavender-Bares *et al.* 2009; Cavender-Bares *et al.* 2004). Absolutely, a single comparison between two species pools might be less comprehensive to infer general conclusion. However, to some sense, these results have provided us an opportunity to rethink about ‘what is phylogenetic signal *per se*’ and ‘how to understand the degree of PNC by detecting phylogenetic signal’. After all, phylogenetic signal obtained from a certain species pool could not represent the complete evolutionary history for every lineage (Swenson 2013).

Habitat heterogeneity

By examining phylogenetic signal and community structure, one of our primary aims is to interpret the

process driving rodent community construction. Under two-tailed t-test, most of phylogenetic and trait-based community structures in two rodent datasets exhibited random dispersion. Considering abiotic and biotic condition within artificially defined rodent community and the elevational pattern of community structure *per se*, we prefer to believe that multiple interactions between random and deterministic process in complex habitat have produced random rodent community structure.

Extraordinary habitat heterogeneity in HMs has been frequently reported in previous empirical studies (Wen *et al.* 2016b; Lei *et al.* 2015; Lei *et al.* 2014). Besides, there is an indisputable fact that the amount of microhabitats is highly related to local biodiversity (Mehrabi *et al.* 2014). Within same area, a regional band with 100 meters range along elevational gradient (RED) should contains more microhabitats than that in local sampling transect (LSD). This inference was supported by the pattern of species richness which is highly related to environmental heterogeneity (Brown 2001). We found that rodent species richness of assemblages in RED was much higher than that in LSD. This should be one reason that phylogenetic and functional community structure of almost all assemblages in RED exhibited random dispersion and elevational pattern (except for SES.PW_{shape} in RED) (further discussions to see in the following section).

Elevational patterns of phylogenetic and morphological structure at local and regional spatial scales

Resulting from interactions between stochastic and deterministic processes in heterogeneous habitat, phylogenetic and trait-based structure of most assemblages exhibited random dispersion in two datasets. However, significant linear patterns of SES.MPD, SES.PW_{size}, SES.PW_{shape} in LSD and SES.PW_{shape} in RED have implied that the relative importance of deterministic processes (i.e., environmental filtering and competitive exclusion) varied along the elevational gradient. We estimate that apparent elevational patterns of community structure in LSD are resulting from significant niche separation among lineages. Early study has mentioned that three families (Muridae, Cricetidae and Sciuridae) in Rodentia have acted key roles in assembling rodent communities in the HMs (Du *et al.* 2017). Therein, long-tailed murine species have occupied the complete gradient, whereas short-tailed species of Cricetidae mainly distribute at medium and higher elevations. In addition, hylaculous sciurine species mainly survive in broad-leave and coniferous forests ranging from mid-low to mid-high elevations, except for *Marmota himalayana* surviving in alpine desert steppe.

In contrast, non-significant linear elevational patterns of SES.MPD and SES.PW_{size} in RED are possible resulting from higher environmental heterogeneity and enlarged species component. In RED, the horizontal extent of each elevational band approach 9 degrees and 14 degrees at longitudinal and latitudinal directions. Resulting from extraordinarily neighboring topological and climatic heterogeneity in HMs, regional slice with a 100m-elevation range contains enormous subareas and microhabitats, which has harbored mass of rodent species without substantial overlap in distribution. This artificial treatment might slightly influence the pattern of species diversity, but greatly affect phylogenetic and functional diversity pattern, especially the loss or gain of rare species (Mi *et al.* 2012). To some extent, this offers an interpretation for the consistent patterns of species richness but distinct phylogenetic and morphological community structure patterns in two datasets.

According to best predictive model selection, we have detected that different facets of community structure performed distinct dependence to environmental variables, and the degree of environmental dependence was much lower at regional scale. Obviously, due to higher level of environmental heterogeneity, enlarged species component and less accurate treatment in extracting environmental variables, the interpreting power of climate predictive models deserve to sharply decline.

Conclusions

By combining prior theoretical efforts (Kraft & Ackerly 2010; Kraft *et al.* 2007; Cavender-Bares *et al.* 2004; Webb *et al.* 2002) and the thought of distinct contributions displayed by traits (predominant and assistant traits), we proposed a novel framework to understand community assembly. Relying on phylogenetic relatedness acts as an aggregate of interspecific niche dissimilarity, the phylogenetic dispersion in simple habitat deserve to be predictable by assessing the functional dispersion of predominant traits. However, phylogenetic and functional dispersion within complex habitat becomes extremely complicated, which highly

depends on the variations in trait role, trait conservatism and habitat heterogeneity.

With two datasets of rodents in the HMs, we presented a case study to reveal the dominant ecological process assembling community. Resulting from multiple interactions between stochastic and deterministic processes in heterogeneous habitat, most of rodent assemblages exhibited phylogenetic and functional randomness, which has prevented us to estimate the functional roles of morphological traits. Due to higher level of habitat heterogeneity and enlarged community components, phylogenetic and morphological structure of rodent community at regional scale exhibited random pattern along elevational gradient and performed weak dependence on environmental variables. Despite of a series of inevitable deficiencies, this work has improved our mechanistic understanding on community assembly.

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