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Synopsis

Using phylogenetic clade composition to understand biogeographical variation in functional traits

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Abstract. Assemblage-level studies of mean trait variation are common in macroecology. However, how phylogenetic relationships among species affect trait-based macroecological patterns is still unresolved. I used an approach based on variation partitioning analysis using environmental and phylogenetic lineage variation as predictors to investigate whether variation in mean trait values among Neotropical sigmodontine rodent communities is best explained by macroecological adaptation, biogeographical history, or joint effects of both – the latter resulting in phylogenetic niche conservatism (PNC) at the metacommunity scale. Metacommunity PNC best explained mean variation in body size and skull/mandible shape across assemblages, and the pattern of metacommunity PNC suggests that influence of environmental factors on mean trait variation relies heavily on spatial biogeographical clade sorting. This suggests that biogeographical lineage distribution should be taken into account in analyses seeking to correlate environmental variables with mean trait variation.

Keywords. Biogeographical history, community phylogenetics, functional biogeography, metacommunity ecology, metacommunity PNC, phylogenetic niche conservatism, geometric morphometrics, Sigmodontinae.

Introduction

Biogeography seeks to understand the underlying biotic and abiotic processes responsible for the spatial and temporal distributions of organisms (Brown and Lomolino 1998). Evolutionary biogeography uses phylogenetic data to integrate concepts from phylogenetic ecology and evolutionary biology (Morrone 2009) with ecological and historical biogeography (e.g., environmental filters, dispersion, vicariance); the goal is to elucidate biogeographic patterns and processes in a historical and evolutionary context. Biogeographical studies are traditionally focused on species diversity and distributions. However, in recent decades, the study of traits across spatial and temporal scales has proved useful for explaining and describing the diversity of forms on a biogeographical scale. Thus emerges the discipline of functional biogeography – "the analysis of the patterns, causes, and consequences of the geographical distribution of the diversity of form and function" (Violle et al. 2014 p. 13691).

Among the multiple approaches that can be used to understand the distribution of traits over space, one is the study of community-weighted means (CWM; Garnier et al. 2004). CWM is the average of trait values among members of a given community, weighted by their species abundances, which is thought of as an aggregated functional attribute which can integrate organizational scales of diversity (Violle et al. 2014). If calculated for a set of communities connected by dispersion of mutually interacting species (a 'metacommunity' *sensu* Leibold et al. 2004), CWM

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can express the functional dominance of a trait across communities, allowing determination of which environmental or historical gradients are related to the functional distribution of traits across space. This approach is also called 'ecometrics' by some authors (Lawing et al. 2016, Polly et al. 2017).

The distribution of average traits across metacommunities is the result of ecological and historical processes acting at both the level of species and in the aggregate of species forming the communities (Fig. 1). Thus, to explain the distribution of CWM, both environmental gradients and the evolutionary history of lineages that have colonized a given region must be considered (Pillar and Duarte 2010, Lawing et al. 2016). Nevertheless, the distribution of phylogenetic lineages is often neglected in studies associating CWM and the environment. One possible reason is that linking CWM and phylogeny is not straightforward, and we are still searching for a good framework in which to understand how phylogenetic relationships among species affect mean trait variation across metacommunities (Diniz-Filho et al. 2007, de Bello et al. 2015, Duarte et al. 2016, Lawing et al. 2016).

The role of evolutionary history, ecology, and phylogenetic niche conservatism (PNC) is less clear at the functional metacommunity level than at species or community levels. Phylogeny is now indispensable for explaining the composition and diversity of communities (Webb 2002, Cavender-Bares et al. 2009), and for explanation of species-level adaptation (Harvey and Pagel 1991), however we still lack a consensus concerning the importance of phylogeny in explaining CWM (Pillar and Duarte 2010, de Bello et al. 2015, Lawing et al. 2016). One strategy that has been adopted to help resolve this issue involves removing phylogenetic non-independence before calculating the CWM (Diniz-Filho et al. 2007, Diniz-Filho et al. 2009, Olalla-Tárraga et al. 2010). These authors calculated the CWM of the specific component (the S component of a phylogenetic eigenvector regression), allowing exploration of the CWM independent of evolutionary history. However, this approach makes it difficult to investigate how much of the CWM is explained jointly by environmental variables and the phylogenetic distribution of lineages (the portion of variation corresponding to phylogenetic niche conservatism at the metacommunity level; see Pillar and Duarte 2010).
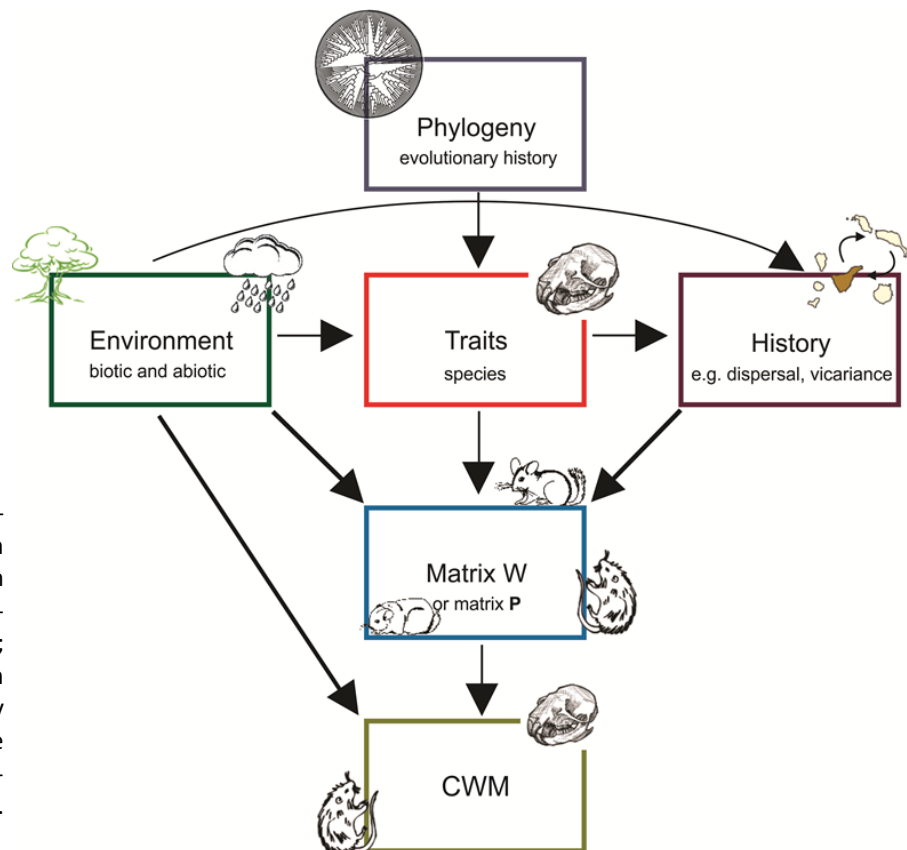

Figure 1. A theoretical path showing how species composition in communities (matrix W; with matrix P standing for phylogenetic community composition; Pillar and Duarte 2010) and mean trait values in each community (CWM) are affected by multiple historical and environmental factors. Modified from Maestri et al. (2017a).

Since the distribution of species belonging to distinct phylogenetic lineages across geographical space determines which species are present in a community, and by extension, the CWM, explicit consideration of the distribution of these lineages across an array of metacommunities may be important (Maestri et al. 2016a, 2017a). Failure to account for this distribution may lead to the detection of a spurious correlation between CWM and environmental factors, which could arise simply due to different spatial distributions of the ancestors that gave rise to entire clades (assuming clades with shared traits), distributed in allopatry across space (Lawing et al. 2016, Polly et al. 2017). To determine how much of the variation in mean traits can be explained by environmental effects, how much is explained by the historical distribution of the lineages alone, and how much is shared between them (metacommunity PNC), there is an interesting approach which involves the use of a metric that accounts for variation in community phylogenetic composition. The Principal Coordinates of Phylogenetic Structure (PCPS; Duarte 2011) captures this variation, allowing access to the spatial distributions of different phylogenetic lineages among communities, and enabling the segregation of historical and environmental drivers of CWM (Pillar and Duarte 2010).

Maestri (2017) and Maestri et al. (2016a, 2017a) aimed to investigate how the phylogenetic distributions of lineages interact with environmental variables to explain mean trait distribution across metacommunities. CWM was calculated using univariate body size (Maestri et al. 2016a) and, for the first time, using multivariate shape (Maestri et al. 2017a). I analyzed the data using a variance-partitioning analysis framework, whereby the effects of environmental variables and clade composition, both singly and jointly, can be teased apart (Fig. 2). Four different scenarios were predicted: (i) that environmental variables are the sole drivers of trait variation across metacommunities, i.e., that variation is purely due to macroecological adaptation; (ii) that phylogenetic lineage distributions are the sole driver of trait variation, i.e., that variation is purely due to biogeographical history; (iii) that environment and lineage distributions jointly explain variation in traits, i.e., phylogenetic niche conservatism exists at the metacommunity level; and (iv) that environmental variables and lineage distributions affect trait variation, but in an independent way. Some assumptions must be made in order for phylogenetic lineage distributions to have an effect on mean traits at this scale. First, a phylogenetic signal must exist for the trait of interest at the species level, such that different clades have trait resemblance among members. Second, the phylogenetic lineages must be geographically structured across space, otherwise a random distribution of species belonging to different clades in space are unlikely to influence mean trait variation.
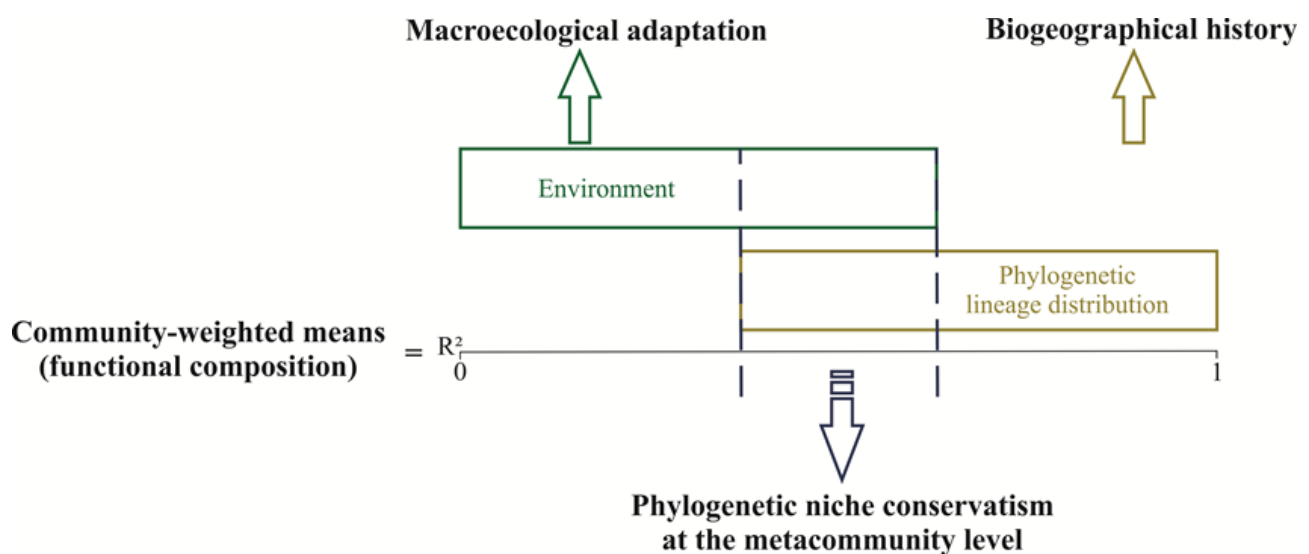
Figure 2. A conceptual model based on variance partitioning for teasing apart the joint and independent influences of environment and phylogenetic community composition on mean trait variation across metacommunities.

Study model: sigmodontine rodents

Sigmodontine rodents (Rodentia, Cricetidae, Sigmodontinae) are widespread in the Neotropical region, although few genera occur in Central America and southern North America (D'Elía and Pardiñas 2015). The largest burst of radiation for this group occurred in South America, where 86 genera and ~400 extant species exist (Patton et al. 2015). Sigmodontines rapidly diversified (~10 Ma, Schenk et al. 2013) to occupy virtually all Neotropical habitats, with high local richness and turnover throughout South America (Maestri and Patterson 2016). Moreover, the principal monophyletic clades within Sigmodontinae show complementary distributions in South America (Maestri and Patterson 2016), making sigmodontines an ideal group in which to investigate large scale patterns of trait variation at the level of assemblage.

Trait variation was explored by applying geometric morphometrics to analyze the skulls and mandibles of nearly 3,000 sigmodontine specimens (Maestri 2017). At the species level, geographical and historical process were found likely to be more important than ecological variables to explain the morphological evolution of skull and mandible size and shape (Maestri et al. 2017b). High functional versatility and limited morphological specialization of skulls and mandibles may account for this pattern (Maestri et al. 2016b, 2017b). Moreover, size and shape variation can be linked to different sets of predictors (Cardini and Elton 2009, Maestri et al. 2016c), suggesting that an analysis of both traits is necessary. Exploration of assemblage-level patterns of variation in size and shape was useful for detection of unknown patterns of trait variation, and to elucidate the role of historical biogeography and macroecological adaptation in the diversification of sigmodontine traits (Maestri et al. 2016a, 2017a).

Methods

Assemblage-level traits were calculated by first taking the mean size and shape for skulls and mandibles for each species, then calculating the mean size and shape for each 1°x1° grid cell across space, where the incidence (presence/absence) of sigmodontine species were calculated using range

maps from IUCN (2008) and Patton et al. (2015). The size of the grid cell chosen (1°x1° degree of lat/long) was found appropriate for mapping range maps on such large spatial scales (Hurlbert and Jetz 2007). Size and shape across assemblages were used as response variables in downstream analyses. To disentangle the influences of environment, phylogenetic composition, and their shared portion of explanation for variation in mean size and skull shape, I used redundancy analysis and variation partitioning, considering spatial autocorrelation. A subset of Principal Coordinates of Neighbourhood Matrices (PCNM) potentially related with trait variation were included as covariates to control residual spatial autocorrelation. Moreover, the biogeographical distribution of lineages itself (the PCPS) have broad spatial components resulting from the biogeographical history of taxa. This is a spatial legacy intrinsic to nature, and should be interpreted instead of corrected for (Hawkins 2012). Full details on the methods can be found in Maestri et al. (2016a, 2017a). The predictor variables were taken as follows.

Phylogenetic lineage distribution

The spatial distribution of phylogenetic lineages across metacommunities was measured using the phylogenetic fuzzy weighting method (Pillar and Duarte 2010) along with the Principal Coordinates of Phylogenetic Structure (PCPS; Duarte 2011). Accordingly, a matrix of community composition weighted by the phylogenetic relationships among species (matrix **P**) was calculated as follows: (1) construct a matrix of phylogenetic patristic distances among species, (2) transform it into a matrix of pairwise phylogenetic similarities among species, (3) perform a standardization by the marginal totals within the columns of the last matrix, and (4) multiply the resultant matrix (matrix Q) by the matrix of species abundances across communities (matrix W) (Pillar and Duarte 2010, Duarte et al. 2016). For sigmodontine rodents, matrix W consisted of a presence/absence matrix for species on a given site, with sites represented as cells in a 1°x1° grid of latitude/longitude across the Neotropical region (Maestri et al. 2016a, 2017a). In matrix **P**, each community is described by the fre-

quency of phylogenetic clades instead of species abundances (Duarte et al. 2016). After performing a principal coordinates analysis (PCoA) on matrix **P**, the PCPS (eigenvectors from the PCoA) were obtained (Duarte 2011). This method has been used successfully to understand metacommunity structure and phylobetadiversity (Brum et al. 2012, Gianuca et al. 2013, Loyola et al. 2013, Duarte et al. 2014, Carlucci et al. 2016), but seldom explored with the purpose of understanding mean trait variation (Pillar and Duarte 2010).

Each PCPS expresses a fraction of phylogenetic lineage distribution across metacommunities. PCPS with higher eigenvalues describe broad phylogenetic patterns related to the basal nodes of the phylogeny, while PCPS with lower eigenvalues describe gradients related to the terminal nodes of the phylogeny (Duarte 2011). The most important PCPS for explaining trait variation were selected based on a forward selection procedure, taking size or shape as the response variable and all PCPS as explanatory variables (details in Maestri et al. 2016a, 2017a), which were subsequently entered as predictor variables in the variance partitioning approach.

Environmental variables

A set of environmental variables by site were taken from the literature. The variables were selected based on previous studies indicating their importance for explaining size and skull shape variation in mammals (e.g., Monteiro et al. 2003, Cardini et al. 2007, Martínez et al. 2014), and based on lack of strong correlation with each other. Some of variables included were temperature, temperature seasonality, and mean elevation (from Bioclim; Hijmans et al. 2005), net primary productivity, NDVI, and land cover (from NASA[1]).

Results and Discussion

The most important result from these biogeographical studies is that phylogenetic niche conservatism at the metacommunity level is unequivocally the dominant pattern explaining mean trait variation (Fig. 3). The distribution of the main phylogenetic lineages across metacommunities and

the environment explain the same proportion of variation in mean traits (shared R^2= 0.68 for size – Maestri et al. 2016a; shared R^2= 0.47 for skull shape in ventral view, shared R^2= 0.50 for skull shape in lateral view, and shared R^2= 0.60 for mandible shape; Maestri et al. 2017a). Proportions of explanation for mean trait variation for individual predictors were low (Fig. 3). Therefore, macroecological adaptation interact with the biogeographical history of clades across South America to explain the distribution of mean traits. The principal conclusion taken from these results is that biogeographical sorting of clades has a massive effect on CWM, as was also found for Carnivora using a different approach (Polly et al.
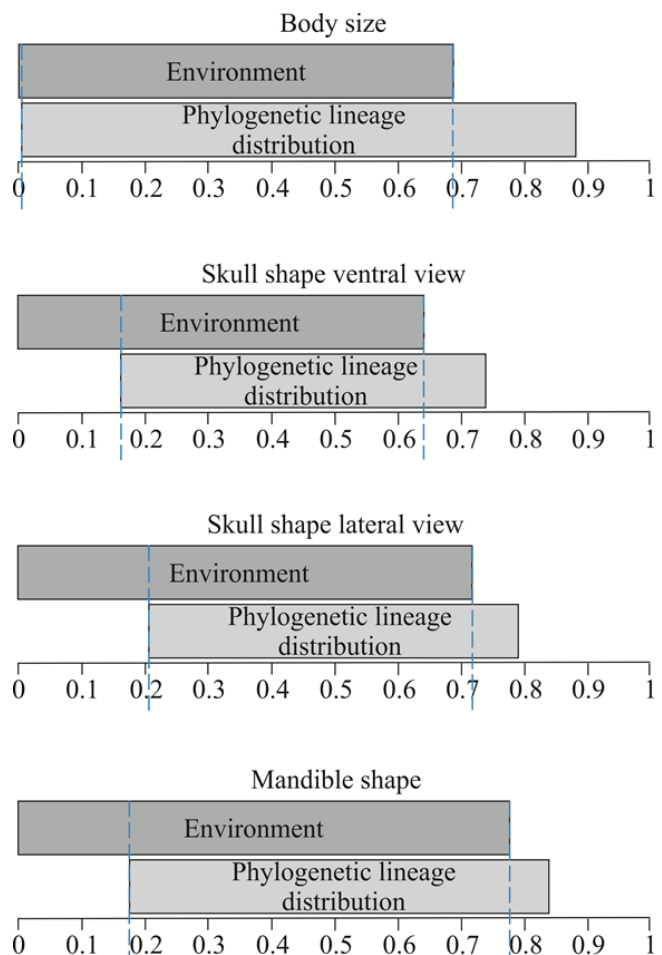
Figure 3. Bar plot depicting the variation partitioning approach, showing the exclusive (biogeographical history versus macroevolutionary adaptation) and shared (phylogenetic niche conservatism at the metacommunity level) proportions of explanation for variation in size (results from Maestri et al. 2016a) and skull shape in ventral and lateral view and mandible shape (results from Maestri et al. 2017a).

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1 http://neo.sci.gsfc.nasa.gov/
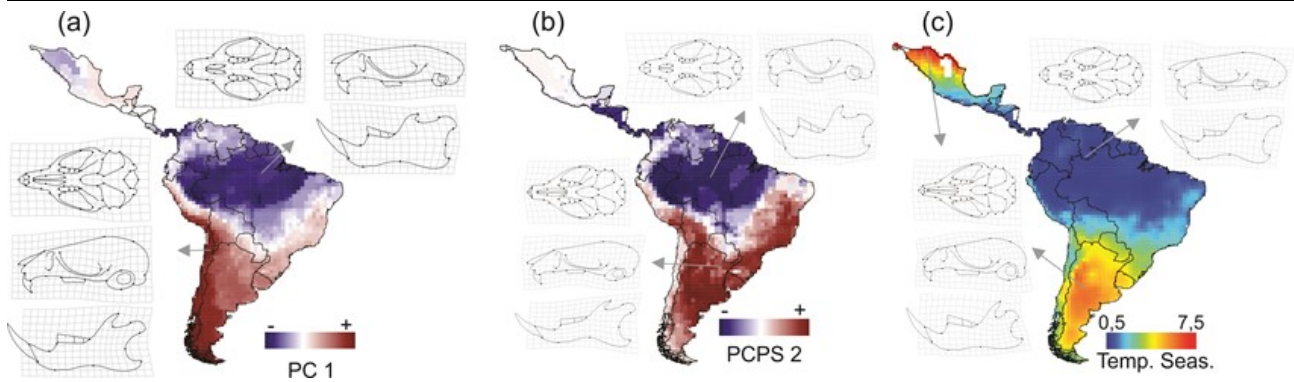
Figure 4. Geographical variation of **(a)** Principal Component 1 for shape, with the map corresponding to shape variation in the ventral view (other views showed similar patterns, see Maestri et al. 2017a), and associated shapes in all views; **(b)** geographical variation of the PCPS 2, corresponding to the differences between sites with high frequency of members of the tribe Oryzomini (in blue) and from other tribes (in red), with associated shape changes; and **(c)** geographical variation in temperature seasonality and associated shape changes. Figures modified from Maestri et al. (2017a).

2017). This concept should no longer be ignored in macroecological analyses investigating CWM and environmental variables.

The PCPS related to the basal nodes of the phylogeny explained most of the variation in mean size and shape (Maestri et al. 2016a, 2017a). The principal PCPS captured the different distributions of members of the tribe Oryzomyini from members of other tribes. The former is dominant throughout tropical regions of South America (Fig. 4b), and its distribution is clearly associated with trait variation (compare Figs. 4a and 4b). Other relevant PCPS captured differences between assemblages were members of Phyllotini and Abrotrichini tribes are dominant – which occur in the western Andes and southern portions of South America (Maestri et al. 2017a). Whether different lineages are distributed across space by historical contingencies or by means of a correlation between environmental variables and species functional traits has yet to be elucidated. Tracking the origins of traits and environments for sigmodontines in South America may help to illuminate the multiple factors affecting clade composition (Fig. 1).

The environmental variable most associated with size variation was annual mean temperature (Maestri et al. 2016a), which showed increase in size following increase in temperature. This pattern was also found in a broader dataset including South American mammals (Rodríguez et al. 2008). Temperature seasonality (Fig. 4c) and

land cover were the environmental variables most associated with shape variation (Maestri et al. 2017a). Sigmodontines from highly seasonal and open environments presented an enlarged tympanic bulla. This feature may be an adaptation for survival in xeric and open environments, as demonstrated for rodents (Mares 1999, Monteiro et al. 2003). A large tympanic bulla increases the ability to receive sound information, and can enhance prey capture performance and predator avoidance in open environments (Alhajeri et al. 2015). Species from the tribes Phyllotini and Abrotrichini colonize highly seasonal and open environments and also have a proportionally larger tympanic bulla, likely an adaptation. The maintenance of this morphological feature, together with the colonization of southern and western Andean regions by these tribes, exemplifies the metacommunity PNC pattern.

The PCPS method proved to be a powerful tool for investigating how differences in clade composition among assemblages influence mean trait variation, as envisioned by Pillar and Duarte (2010). While it has been extensively used to investigate variation in phylogenetic composition across communities and to discover the underlying causes (e.g., Carlucci et al. 2016), the complex relationships between clade composition, trait variation, and environmental variables still needs to be investigated to enhance understanding of how phylogeny affects CWM at the assemblage level. Evaluating clades with distinct levels of phy-

logenetic signal and geographical clade composition across space will be essential for clarifying the expected predictions under this framework.

Overall, I showed that the biogeographical distribution of phylogenetic lineages across space is an important predictor of variation in average traits (CWM) across communities. The interaction of clade distribution with environmental predictors sets the stage for a metacommunity PNC pattern, whereby the influence of environmental variables on trait variation are mediated by the distribution of phylogenetic clades across assemblages. The approach applied here has the potential to shed light on the multiple forces affecting CWM variation, and may help to avoid meaningless correlations between mean traits and the environment. The generality of this approach and the utility of phylogenetic lineage distribution for understanding trait variation should be further investigated.

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