



# Patterns of phylogenetic beta diversity in China's grasslands in relation to geographical and environmental distance

Xiulian Chi, Zhiyao Tang\*, Jingyun Fang

*Department of Ecology, College of Urban and Environmental Sciences and Key Laboratory for Earth Surface Processes, Peking University, Beijing 100871, China*

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## Abstract

Patterns and determinants of beta ( $\beta$ -) diversity can be used to explore the underlying mechanisms regulating community assembly. Despite being the most commonly used measure of  $\beta$ -diversity, species turnover does not consider the evolutionary differences among species, treating all species equally. Incorporating information on phylogenetic non-independence or relatedness among species in the calculation of  $\beta$ -diversity may substantially advance our understanding of the ecological and evolutionary mechanisms structuring communities. Here, we investigate the relative influence of geographical distance and differences in environmental conditions (environmental distance) on the phylogenetic  $\beta$ -diversity between grassland communities expanding 4000 km across the Tibetan Plateau, the Inner Mongolia Plateau and the Xinjiang Autonomous Region in China. Both observed and standardized effect size of phylogenetic  $\beta$ -diversity were significantly correlated with geographical and environmental distance across all regions. However, the effect of geographical distance on the standardized effect size of phylogenetic  $\beta$ -diversity disappeared when environmental distance was controlled. We also found that within different regions, the effect of environmental distance on both observed and standardized effect size of phylogenetic  $\beta$ -diversity was more significant than geographical distance. Among environmental variables, climate played a more important role in shaping observed phylogenetic  $\beta$ -diversity across and within regions, and standardized effect size of phylogenetic  $\beta$ -diversity across regions. Soil properties played a more important role in shaping standardized effect size of phylogenetic  $\beta$ -diversity within regions. The phylogenetic  $\beta$ -diversity of species from dicot and monocot clades exhibited similar patterns along environmental and geographical distance. The results suggest that at the study scale, phylogeny of grassland communities in China is predominantly structured by environmental filtering, and the dominant environmental factors may be scale-dependent.

## Zusammenfassung

Muster und bestimmende Faktoren der  $\beta$ -Diversität können genutzt werden, um die zugrunde liegenden Mechanismen, die die Bildung von Gemeinschaften regulieren, zu erkunden. Obwohl häufig benutzt, berücksichtigt der Arten-turnover die evolutiven Unterschiede zwischen Arten nicht, da alle Arten gleich behandelt werden. Informationen zur phylogenetischen Verwandtschaft von Arten in die Berechnung der  $\beta$ -Diversität einzubeziehen, könnte unser Verständnis der ökologischen und evolutiven Mechanismen der Gemeinschaftsbildung voranbringen. Hier untersuchen wir den relativen Einfluss von Unähnlichkeit der Umweltbedingungen und geographischer Entfernung auf die phylogenetische  $\beta$ -Diversität zwischen Graslandgemeinschaften, die vom Plateau der Inneren Mongolei bis zum Hochland von Tibet und zum Uigurischen autonomen Gebiet Xinjiang 4000 km

\*Corresponding author. Tel.: +86 10 6275 4039.  
E-mail address: zytang@urban.pku.edu.cn (Z. Tang).

überspannen. Sowohl die beobachtete als auch die standardisierte Effektgröße der phylogenetischen  $\beta$ -Diversität waren mit der Unähnlichkeit der Umweltbedingungen und der geographischen Entfernung über alle Regionen signifikant korreliert. Indessen verschwand der Einfluss der geographischen Entfernung auf die standardisierte phylogenetische  $\beta$ -Diversität, wenn die Umweltunterschiede kontrolliert wurden. Wir fanden auch, dass innerhalb der Regionen der Einfluss der Umweltunterschiede auf sowohl beobachtete als auch standardisierte Effektgröße der phylogenetischen  $\beta$ -Diversität stärker signifikant war als der der geographischen Entfernung. Unter den Umweltvariablen spielte das Klima eine wichtigere Rolle für die phylogenetische  $\beta$ -Diversität zwischen und innerhalb der Regionen. Die Bodenfaktoren spielten eine wichtigere Rolle für die phylogenetische  $\beta$ -Diversität innerhalb der Regionen. Die phylogenetische  $\beta$ -Diversität der dikotylen und monokotylen Arten zeigten ähnliche Muster für Umweltunterschiede und geographische Entfernung. Die Ergebnisse legen nahe, dass im Rahmen der Untersuchung die Phylogenie der Graslandgemeinschaften vorwiegend durch Umweltfilter strukturiert ist und dass die wichtigen Umweltfaktoren skalenabhängig sein könnten.

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**Keywords:** Dispersal limitation; Distance decay; Environmental distance; Environmental filtering; Geographical distance; Phylogenetic  $\beta$ -diversity

## Introduction

Patterns and determinants of beta ( $\beta$ -) diversity can be used to test the underlying mechanisms regulating community assembly (Myers et al., 2013; Tang, Fang, Chi, Feng, & Liu, 2012a; Tang, Fang, Chi, Yang, & Ma, 2012b). How, and to what extent, environmental filtering and dispersal limitation influence community structure has been debated through the study of  $\beta$ -diversity (Chase & Myers, 2011; Myers et al., 2013; Tang et al., 2012a,b). Despite being the most commonly used measure of  $\beta$ -diversity, species turnover does not consider evolutionary differences among species, treating all species equally (Graham & Fine, 2008; Webb, Ackerly, McPeck, & Donoghue, 2002). Incorporating information on the phylogenetic non-independence or relatedness between species in biodiversity studies can shed light on ecological inferences made from the analysis of species turnover (Graham & Fine, 2008; Swenson, 2011; Zhang, Swenson, Chen, Liu, & Li, 2013). The past decade has witnessed a rapid development in phylogenetic metrics that quantify phylogenetic information within communities (e.g. phylogenetic  $\alpha$ -diversity; e.g. Cadotte, Jonathan, Regetz, Kembel, & Cleland, 2010; Faith, 1992; Webb, 2000; Yan, Yang, & Tang, 2013) and between communities (e.g. phylogenetic  $\beta$ -diversity; e.g. Lozupone & Knight, 2005; Swenson, 2011; Zhang et al., 2013). Phylogenetic  $\beta$ -diversity, which measures the change in phylogenetic relationships among species across space has been increasingly used to study the ecological and evolutionary mechanisms structuring communities (Cavender-Bares, Kozak, Fine, & Kembel, 2009; Graham & Fine, 2008; Webb et al., 2002).

Specifically, phylogenetic  $\beta$ -diversity of communities provides two valuable lines of evidence that can be analyzed to identify the degree to which the shared evolutionary histories of species explain ecological patterns observed today. First, from an evolutionary perspective, comparing taxonomic and phylogenetic  $\beta$ -diversity helps to reveal the evolutionary

history of the species pool (Eiserhardt, Svenning, Baker, Couvreur, & Balslev, 2013; Graham & Fine, 2008; Qian, Swenson, & Zhang, 2013). For example, a species pool composed of a high proportion of small-ranged species belonging to late-diverged clades (neoendemic species) may result in higher taxonomic  $\beta$ -diversity but low phylogenetic  $\beta$ -diversity. Whereas, a pool that includes a high proportion of small-ranged species belonging to early-diverged clades (paleoendemic species) may result in both high taxonomic and phylogenetic  $\beta$ -diversity (Eiserhardt et al., 2013; Graham & Fine, 2008; Qian et al., 2013). Second, from an ecological perspective, relating the phylogenetic  $\beta$ -diversity to environmental and geographical distance provides an evolutionary way to identify the effects of niche-based deterministic processes (e.g. environmental filtering) and spatial-based neutral processes (e.g. dispersal limitation) in regulating the community assembly at local scales (Graham & Fine, 2008; Hardy, Couteron, Munoz, Ramesh, & Pelissier, 2012; Zhang et al., 2013). The niche-based deterministic hypothesis predicts that, phylogenetic similarity of communities responds in different ways to geographical distance, but always declines with environmental distance. The dispersal limitation hypothesis predicts that, phylogenetic similarity of communities declines with geographical distance regardless of environmental distance (Eiserhardt et al., 2013; Graham & Fine, 2008). These competing hypotheses have been widely used by ecologists to test the application of niche and neutral theories in structuring species and phylogeny in different communities. For example, Zhang et al. (2013) found joint effects of geographical and environmental factors on the assembly of tropical tree communities in Panama, while Wang, Shen, Wu, Tu, and Soininen (2013) found a dominant role of deterministic processes on bacterial assemblages. It is widely reported that at large scales community assembly is regulated by climate (e.g. Hardy et al., 2012; Qian et al., 2013) and at fine scales communities are also influenced by local edaphic conditions (e.g. Hall, McKenna, Ashton, & Gregoire, 2004; John, Dalling, Harms, Yavitt, & Stallard,

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